Přírodovědecká
fakulta
Faculty
of Science

Jihočeská univerzita
v Českých Budějovicích
University of South Bohemia
in České Budějovice

Co víme o tom, jak ptáci rozpoznávají svoje predátory

Habilitační práce

2016

RNDr. Roman Fuchs, CSc.

Poděkování

Na prvém místě musím poděkovat všem svým studentům (ovšemže i studentkám) bakalářského, magisterského i doktorského studia, neboť naprostá většina ve spisu předložených ale i nepředložených článků využívá data shromážděná v kvalifikačních pracích všech hodnostních stupňů. Studentů, kteří prošli mýma rukama je ovšem velké množství, vyzdvihnu tedy jen ty, kteří se podíleli na článcích zařazených do tohoto spisu.

V případě studií na ťuhýcích musím na prvém místě zmínit Martina Strnada, s nímž jsme metodou pokusu a omylu dávali dohromady standardní metodiku, využívanou i jeho následovníky. Na dalším místě bych jmenoval Michala Němce, který se postupně vypracoval na zdatného organizátora terénních prací a školitele, formálního i neformálního mladších kolegů. Konečně bych vyzdvihl Michaelu Syrovou, která bez mé asistence vymyslela, jak testovat naši hypotézu o podivném chování ťuhýků vůči strace. Mě tak bláznivý ale vrcholně úspěšný experiment nenapadl. Vedle výše jmenovaných se na předložených ťuhýčích studiích podílela ještě Lenka Dokoupilová. V případě krmítkových studií byla klíčovou postavou nepochybně Kateřina Tvardíková. Mýma rukama prošlo mnoho studentů, žádný z nich se ale asi svojí výkonností nemůže s Kateřinou srovnávat, o čemž svědčí výsledky získané za pouhé tři roky terénního výzkumu. Z mladších studentů jsme zatím do podoby publikace dotáhli data Markéty Buršíkové. V klecových experimentech zaujala obdobné postavení jako Kateřina Tvardíková v experimentech krmítkových, Jana Beránková. Vedle vlastních pokusů navíc zpracovala i výsledky Jany Sýkorové.

Kolega Petr Veselý není sice autorem ani jedné z kvalifikačních prací, které posloužily jako podklad článků zařazených do tohoto spisu, na velké části se ale podílel, jak při terénním výzkumu, tak především ve všech fázích zpracování dat. Spolu s Janou Beránkovou se také významnou měrou účastnili práce na úvodní kapitole, která by se měla stát součástí větší publikace.

Vedle studentů a Petra Veselého jsem zavázán i třem posledním děkanům naší fakulty, tedy Zdeňku Brandlovi, Liboru Grubhofferovi a Františku Váchovi, kteří mě k předložení habilitační práce pobízeli, avšak netrestali za moje nekonání. Konečnou fázi přípravy spisu bych určitě nezvládl nebýt pomoci sekretářky naší katedry Jany Maxerové.

Nemaje rodiny, které bývá děkováno na tomto místě, nahradil bych ji všemi, kteří mi pomáhali odreagovat se od náročných pracovních povinností v Českých Budějovicích, Praze, středním Povltaví i jinde.

Obsah

I.
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 Fennicaica 89: 206-215.

II.
Němec M., Fuchs R. (2014): Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. Acta Ethologica 17: 149-154.

III.
Syrová M., Němec M., Veselý P., Landová E., Fuchs R. (2016): Facing a Clever Predator Demands Clever Responses - Red-Backed Shrikes (*Lanius collurio*) vs. Eurasian Magpies (*Pica pica*). PLoS ONE 11(7): e0159432

IV.
Tvardíková K., Fuchs R. (2012): Tits recognize the potential dangers of predators and harmless birds in feeder experiments. Journal of Ethology 30: 157-165.

V.
Tvardíková K., Fuchs R. (2011): Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behavioral Ecology and Sociobiology 65: 727-733.

VI.
Beránková J., Veselý P., Sýkorová J., Fuchs R. (2014): The role of key features in predator recognition by untrained birds. Animal Cognition 17: 963-971.

VII.
Beránková J., Veselý P., Fuchs R. (2015): The role of body size in predator recognition by untrained birds. Behavioural processes 120: 128-134.

VIII.
Veselý P., Buršíková M., Fuchs R. (2016): Birds at the Winter Feeder do not Recognize an Artificially Coloured Predator. Ethology 122: 1-8

IX.
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.

X.
Tvardíková K., Fuchs R. (2010): Tits use amodal completion in predator recognition: a field experiment. Animal Cognition 13: 609-615.

Co víme o tom, jak ptáci rozpoznávají svoje predátory

Fuchs R., Veselý P., Beránková J.

Každý živočich se během svého života musí vyrovnat se třemi úkoly: sehnat si potravu, nestát se potravou pro jiné živočichy a předat své geny následující generaci. Druhý z úkolů vyžaduje schopnost potenciální predátory rozpoznat od jiných objektů, především ovšem neškodných živočichů. Nikdo zřejmě nebude pochybovat o tom, že ptáci stejně jako ostatní živočichové v nějaké míře tuto schopnost mají, neboť může podstatnou měrou zvýšit šanci na přežití jich samých i jejich potomstva. Otázkou ovšem zůstává, které predátory rozpoznávají (a zda je rozlišují jen od neškodných živočichů nebo i navzájem), jaké jejich charakteristiky k tomu používají a v neposlední řadě, jak tuto schopnost získávají. V této stati se věnuji pouze prvními dvěma otázkám, neboť problematikou toho, jak ptáci znalost predátorů získávají, se žádná z následujících studií nezabývá.

1. Jak studovat rozpoznávání predátorů

Dříve než se budeme zabývat tím, co víme o schopnosti ptáků rozpoznávat své potenciální predátory, bude užitečné podívat se, jak lze tuto schopnost studovat. Chceme-li zkoumat, jak kořist rozpoznává své predátory, musíme splnit dva úkoly. Především je třeba zajistit jejich vzájemné setkání. Buď můžeme vyhledávat spontánní predační události v přírodě, což je relativně neefektivní a vyžaduje od pozorovatele vynaložení velkého úsilí, především co do objemu potřebného času. Druhou možností je přístup experimentální. Zorganizovat setkání kořisti s predátorem lze jak v přírodě, tak i v zajetí. Oba způsoby mají své silné i slabé stránky. V přírodě přináší problémy standardizace experimentů, neboť pokusná zvířata zde nikdy nejsou pod naší plnou kontrolou. V zajetí je problémem především reprezentativnost experimentů, neboť podmínky zde nikdy plně neodpovídají podmínkám v přírodě.

Máme-li zajištěno sekání kořisti s predátorem, je třeba ještě nalézt citlivé a spolehlivé indikátory toho, že kořist predátora rozpoznala. Především si ale musíme uvědomit, že to nejsme nikdy schopni dokázat přímo. My ve skutečnosti v pokusech s netrénovanými ptáky (na rozdíl od pokusů založených na diskriminačním učení) netestujeme rozpoznávání ale rozlišování mezi predátorem a jiným objektem. Citlivý indikátor by měl pak zachytit nejen, pokud kořist rozlišuje predátora od neškodného živočicha (či jen nějakého neutrálního předmětu) ale i různé skupiny či dokonce druhy predátorů navzájem. Spolehlivý indikátor by měl přinášet shodné výsledky při každém setkání predátora a kořisti. Zvláště druhý požadavek je nepochybně maximalistický. Reakci kořisti ovlivňuje jak její vlastní situace (např. kondice) tak vnější okolnosti (např. dostupnost úkrytů). S přihlédnutím k těmto komplikacím se jako vhodné indikátory jeví fyziologické parametry signalizující strach, neboť jsou s procesem rozpoznání predátora nepochybně spojeny bezprostředněji než behaviorální odpověď. Jejich využití ovšem komplikují metodická omezení. Přímo sledovatelné behaviorální indikátory, využívající rozmanité obranné reakce, proto nadále sehrávají a budou sehrávat hlavní roli.

Výzkum toho, jak ptáci rozpoznávají své predátory, nebyl sice nikdy příliš intenzivní, má ale dlouhou tradici sahající do samých počátků behaviorální ekologie a etologie. Stávající studie se proto liší nejen svými metodikami ale i korektností designu. V této kapitole je naším cílem podat přehled postupů, které se při studiu rozpoznávání predátorů používají, porovnat jejich přednosti a nedostatky, a pokusit se zhodnotit jejich vliv na dosažené výsledky.

1.1. Observační studie

Většina živočichů je ohrožována predací po většinu svého života a proto je antipredační chování nedílnou součástí jejich každodenních aktivit (Caro 2005). Antipredační chování však zahrnuje řadu dílčích na sebe navazujících prvků (Lima and Dill 1990). Především zvířata na okraji hejna či stáda nebo solitérní jedinci stráví značnou část dne tzv. vigilancí, neboli sledováním svého okolí, s cílem odhalit predátora dříve než on odhalí je (Elgar 1989). Pokud je úspěšný, mají velkou šanci se mu vyhnout, aniž by došlo k přímé konfrontaci (Sansom et al. 2009). Pak nemá pozorovatel šanci zaznamenat jakoukoliv interakci predátora a kořisti.

Pokud ke střetu kořisti a predátora dojde, je obvykle velmi krátký (např. Smith 1970) a je tedy pravděpodobné, že mu pozorovatel nebude přítomen. V případě ptáků je navíc univerzální reakcí útěk (Simmons 1955; Lima 1993; Hilton et al. 1999; Martín et al. 2006; van den Hout et al. 2010). Nejběžnější interakce ptáků s predátory tedy o jejich schopnosti predátory rozpoznávat přinášejí většinou jen málo informací.

Ptáci jsou ovšem velmi specifičtí jedním projevem antipredačního chování, který umožňuje pouhým pozorováním zhodnotit, nakolik predátory rozpoznávají - je jím obrana hnízda. Hnízdo s vejci a ještě více hnízdo s mláďaty představuje pro rodiče mimořádně cenný a současně zranitelný objekt. Mláďata na hnízdě se sama mohou bránit jen velmi omezeně (Redondo and Carranza 1989; Goławski and Meissner 2007; Hagelin and Jones 2007; Tillmann 2009; Londoño et al. 2015). Rodičovská investice do obrany hnízda proto výrazně zvyšuje jejich fitness (Knight and Temple 1986b; Redondo 1989; Tryjanowski and Goławski 2004; Müller et al. 2005; Remeš 2005; Goławski and Mitrus 2008). Platí to zvláště pro ptáky mírného a chladného klimatického pásma, kteří mají obvykle jen omezenou možnost náhradního hnízdění (cf. Skutch 1949) a jejichž přežití do další sezóny je často nejisté, ať již migrují nebo nikoliv.

I v případě obrany hnízda je ovšem její primární formou predátora na něj neupozornit. Toho lze dosáhnout především opatrností při stavbě, inkubaci vajec i krmení mláďat (Roos and Pärt 2004, Dale et al. 1996, Burhans 2000, Ghalambor and Martin 2000, Eggers et al. 2005, Amo et al. 2008, Peluc et al. 2008). Pokud je však hnízdo predátorem objeveno, jedinou možností, jak predaci zabránit, zůstává obvykle aktivní obrana, kterou označujeme termínem mobbing (Montgomerie and Weatherhead 1988). Aktivní obrana obvykle trvá déle než útěk a navíc zahrnuje větší počet aktivit lišících se rizikem, které bránící ptáci podstupují (Sordahl 1990). Volba, kterou z nich použít, bude mimo jiné záviset na nebezpečí, které přítomný predátor představuje pro bránící rodiče a/nebo jejich potomky

(Ash 1970, Curio 1975, Gottfried 1979, Curio et al. 1983, Curio and Regelman 1985, Elliot 1985, Curio and Onnebrink 1995, Hogstad 2005).

Predace je u většiny ptáků nejčastější příčinou hnízdního neúspěchu (Ricklefs 1969; Nilsson 1984; Martin and Roper 1988; Martin 1993a,b), podíl predovaných hnízd se může pohybovat od 1.4 % (Holway 1991) u dobře ukrytých hnízd lesňáčka Dendroica caerulescens až po 85 % u kardinála Cardinalis cardinalis (Filiater et al. 1994) nebo některých jihoamerických druhů pěvců (Skutch 1996). I tak ale pravděpodobnost zachycení pokusu o predaci jednotlivého hnízda zůstává poměrně nízká, neboť se jedná, o událost trvající obvykle nejvýše minuty (Weidinger 2010). V posledních desetiletích se objevila možnost kontinuálního sledování hnízd pomocí videokamer (rev. Cutler and Swann 1999, Cox et al. 2012), pro studium rozpoznávání predátorů bránícími ptáky však dosud využita nebyla. Jednou z příčin může být to, že u většiny druhů převážnou část hnízdních ztrát způsobuje několik málo specializovaných predátorů (e.g. Conner et al. 2010; Conkling et al. 2012; Friesen et al. 2013; Murray 2015).

Přesto sledování střetů hnízdících ptáků s predátory poznatky o jejich rozpoznávání přineslo, byť nemuselo být hlavním cílem příslušných studií. Velmi často se jednalo o druhy hnízdící na zemi v otevřeném terénu, jejichž hnízda mohou, alespoň teoreticky, snadno objevit všichni prolétávající ptáci. Tyto charakteristiky často splňují příslušníci řádu bahňáků, z nichž byli studováni kulíci (Brunton 1968, 1990; Byrkjedal 1987; Amat a Masero 2004), čejky (Green et al. 1990; Walter 1990), břehouši (Green et al. 1990), pisily a tenkozobci (Sordahl 2004), racci a rybáci (Kruuk 1964; McNicholl 1973; Brunton 1997, 1999; Cavanagh and Griffin 1993; Stenhouse et al. 2005; Palestis 2005), ale i zástupci jiných skupin např. kormoráni (Siegel-Causey and Hunt 1981) nebo kachny (Jacobsen and Ugelvik 1992).

Efektivitu těchto výzkumů u většiny studovaných druhů posilovalo i to, že hnízdí koloniálně či polokoloniálně. Podobné studie tedy mohly být provedeny také na koloniálně hnízdících pěvcích, např. vlaštovkách (Guillory and LeBlanc 1975; Winkler 1992); ale i jiných skupinách, např. pilanech (Murphy 2006). Hnízdní kolonie je pro predátory (i badatele) nepochybně nápadnější než jednotlivé hnízdo a navíc představuje lákavější kořist. Jinou předností je, že umožňuje sledovat chování většího množství jedinců, kteří se liší jak mírou bezprostředního ohrožení, tak i motivací k obraně, která závisí především na hodnotě jejich potomstva dané stářím a počtem mláďat či vajec (Barash 1976, Knight and Temple 1986a, Conover 1987, Burger et al. 1993, Clode et al. 2000; Montgomerie and Weatherhead 1988, Andersson et al. 1980). Měřítkem toho, nakolik byl určitý vetřelec vyhodnocen jako nebezpečí, lze pak použít např. počet ptáků, kteří se do antipredačního chování zapojili (Shields 1984, Brown and Hoogland 1986, Burger and Gochfeld 1992, Clode et al. 2000, Arnold 2000, Fuchs 1977, Bosque and Molina 2002).

Nicméně kromě těchto koloniálně hnízdících druhů byla sledována schopnost rozpoznávat přirozeně se vyskytující predátory i při obraně hnízd druhy, které hnízdí solitérně, jako jsou např. strnadi (Nice and Ter Pelkwyk 1941), straky (Buitron 1983) a palmovníci (Leger and Carroll 1981).

Za určitých okolností lze studovat přirozené antipredační chování také u nehnízdících ptáků. Trail (1987) například sledoval chování skalňáků vůči různým potencionálním predátorům na tokaništích, kde se samci vyskytují hromadně. Další situací, v níž jsou ptáci snadno pozorovatelní, je hledání potravy, neboť i při něm se někteří ptáci sdružují. V mírném pásmu severní polokoule jsou to například zimní hejna pěvců, především sýkor (Hill 1986; Gentle and Gosler 2001; Davies and Welbergen 2008; Soard and Ritchison 2009; Courter and Ritchison 2010; Tvardíková and Fuchs 2010, 2011,2012; Suzuki 2011), ale i pěnkavovitých (Whittingham et al. 2004; Quinn and Cresswell 2005) a krkavcovitých pěvců (Hauser and Caffrey 1994; Griesser 2008, 2009). Podobně lze využít i potravní hejna špačků (Conover and Perito 1981), holubů (Griffin et al. 2005) nebo bahňáků (Minderman et al. 2006; Mathot et al. 2009). Takováto hejna ale za normálních okolností bohužel neposkytují možnost soustavného sledování, neboť jsou velmi pohyblivá a to nejen v delších časových měřítcích ale i během dne (Tvardíková and Fuchs 2010, 2011,2012).

Tím není přehled studovaných druhů vyčerpán. Zajímavé výsledky týkající se schopnosti rozpoznávat predátory přinesla studie, v níž Nijman (2004) soustavně pozoroval různé druhy drongů lovících strategií „sit-and-wait“ a tedy dobře viditelné i v podrostu tropického lesa. Nicméně i tak studie vyžadovala osmiletý sběr dat. Při studiu sociálně žijících timálií využili Edelaar and Wright (2006) při svém výzkumu v izraelském Arava rift valley toho, že přes tuto lokalitu probíhá tah palearktických dravců. Během devítitýdenního výzkumu (1-6 hodin denně) se jim tak podařilo shromáždit necelých 250 kontaktů hejnek timálií s potenciálními predátory.

1.2. Experimenty

Je zřejmé, že observační přístup nabízí pro studium rozpoznávání predátorů jen velmi omezené možnosti. Většina stávajících poznatků proto pochází z různých typů experimentů. Ty především zvyšují efektivitu výzkumu, tím že inscenují setkání kořisti a predátora a to nikoliv náhodně přítomného, ale cíleně zvoleného. Zcela nezbytný je experimentální přístup, je-li výzkum zaměřen na proces rozpoznávání, což vyžaduje manipulaci potenciálních rozpoznávacích znaků (Edwards et al. 1950; Curio 1975; Scaife 1976; Smith and Graves 1978; Gill et al. 1997; Davies and Welbergen 2008; Trnka et al. 2012; Beránková et al. 2014), kterou umožňují jen atrapy predátorů.

Nicméně i v experimentech platí, že preferovanou formou antipredačního chování je vyhnout se setkání s predátorem (Krätzig 1940; Scaife 1976; Palleroni et al. 2005). To je ovšem, alespoň v přírodních experimentech, obecně snadné a pro ptáky vyznačující se mimořádně velkou mobilitou to platí dvojnásob. Od náhodné expozice predátora v terénu lze tedy jen stěží očekávat jednoznačné výsledky. Přes výše uvedenou nevýhodu několik studií s tímto designem, které prezentovaly dravce (Rainey et al. 2004), ťuhýky (Chu 2001) nebo i savčí predátory (Naguib et al. 1999; Rainey et al. 2004; Randler 2006) vzniklo. Někdy se tyto studie dokonce zaměřovaly na konkrétní, obvykle sociální ptačí druh (Naguib et al. 1999; Rainey et al. 2004; Adams et al. 2006; Randler 2006; Magrath et al. 2007). Ve většině však nebyli testovaným ptákům předkládáni přímo predátoři ale nahrávky konspecifických či heterospecifických varovných hlasů, popřípadě akustických projevů predátora. Lze ovšem předpokládat, že reakce na akustické signály bude aktivnější, neboť adekvátní odpověď vyžaduje potvrdit či upřesnit povahu a míru hrozícího nebezpečí.

Jedna výjimka nicméně existuje. Aktivně obvykle ptáci ve dne reagují, bez ohledu na jiné okolnosti, na přítomnost sov (Naguib et al. 1999; Yorzinski and Vehrenkamp 2009). Ty pro ně představují významné nepřátele, ve dne jsou však dočasně handicapovány. Aktivní obrana má zřejmě za cíl vystrnadit je z teritoria či domovského okrsku a předejít tak nočnímu ohrožení. Pro studium rozpoznávání predátorů byla tato metoda použita opakovaně, a to jak ve studiích porovnávajících reakce na sovy a jiné predátory (Naguib et al. 1999; Yorzinski and Vehrenkamp 2009), tak ve studiích porovnávajících různé druhy sov (Miller 1952; Altmann 1956; Reudink et al. 2007). Dokonce byla tato metoda využita pro zhodnocení nebezpečí reprezentovaného modifikovaným predátorem. Deppe et al. (2003) používali dřevěné atrapy kulíška (Glaucidium gnoma), které se lišily přítomností očních skvrn v zátylku, a autoři sledovali, z jaké strany se přibližují mobbující ptáci.

Nicméně, nepochybně výhodnější je, pokud se podaří uspořádat terénních experimenty tak, abychom přiměli testovaná zvířata nevolit preferovanou formu antipredačního chování, tedy vyhnutí se predátorovi. Toho lze dosáhnout tím, že navodíme situaci, v níž vzniká trade-off mezi vyhnutím se predátorovi a jiným zájmem (Caro 2005).

1.2.1. Hnízdní experimenty

Jak jsme již zmínili v kapitole 1.1., je pro ptáky asi nejvýznamnější takovouto situací obrana hnízda. I při obraně hnízda má ale přednost snaha zabránit v jeho objevení. Například ťuhýk obecný výrazně omezuje intenzitu aktivní obrany již tehdy, nachází-li se vycpanina sojky ve vzdálenosti 10 m od hnízda (Tichá unpublished observation). Predátor v polních experimentech bývá proto obvykle umístěn v bezprostřední blízkosti hnízda a v případě atrap jeho pohled směřuje k hnízdu, tak aby navodil dojem akutního ohrožení. Experimenty jsou obvykle prováděny ve fázi krmení mláďat, kdy rodiče reagují nejaktivněji. To je způsobeno především tím, že hodnota potomstva v průběhu hnízdění z řady důvodů vzrůstá (Knight and Temple 1986c; Montgomerie a Weatherhead 1988; Amat et al. 1996; Halupka 1999; Campobello and Sealy 2010). Nemalý význam ale může mít i obtížná utajitelnost hnízda ve fázi krmení (Rytkönen et al. 1995; Goławski and Mitrus 2008).

I přes veškeré úsilí o standardizaci bývá reakce testovaných ptáků variabilní. Vedle rozdílné hodnoty potomstva dané počtem a stářím mláďat (Andersson et al. 1980; Montgomerie and Weatherhead 1988; Halupka and Halupka 1997; Halupka 1999; Pavel and Bureš 2001; Tryjanowski and Goławski 2004), ale i poměrem pohlaví mláďat (Radford and Blakey 2000) nebo šancí na jejich úspěšné vyvedení a přežití (Hakkarainen and Korpimäki 1994), může být příčinou i rozmanitost rodičů. Především byl prokázán vliv jejich odlišného stáří respektive zkušenosti (Montgomerie and Weatherhead 1988), pohlaví (Wiklund 1990; Tryjanowski and Goławski 2004; Hogstadt 2005), aktuální kondice (Hamer and Furness 1993; Hogstadt 1993, 2005; Griggio et al. 2003), hormonálního vyladění (Cawthorn et al. 1998), ale i personality (Hollander et al. 2008). Intenzitu obrany však může ovlivňovat i prostředí v okolí hnízda (Kleindorfer et al. 2005) a jeho ukrytí respektive přístupnost (Montgomerie and Weatherhead 1988; Holway 1991; Weidinger 2002; Kleindorfer et al. 2003; Remeš 2005; Goławski and Mitrus 2008).

Poměrně často se vyskytují i páry, které na jednoznačně nebezpečného predátora nereagují buď vůbec, nebo jen velmi slabě (Strnad et al. 2012). Vedle výše uvedených faktorů nelze jako příčinu, především v případě využití atrap predátorů, vyloučit ani nevěrohodnost experimentu (Knight and Temple 1986a; Weatherhead 1989; Rytkönen et al. 1990; Grim 2005; Němec et al. 2015). Získání hodnověrných výsledků proto vyžaduje poměrně velký objem dat. V stávajících pracích se pohybuje od 13 (Csermely et al. 2006) do 120 (Arroyo et al. 2001) testovaných párů.

Přes určité nevýhody jsou experimenty simulující ohrožení hnízda široce využívány a to nejen pro výzkum rozpoznávání predátorů. Asi nejintenzivnější byla takto studována schopnost rodičů řešit trade-off mezi investicemi do obrany a hodnotou potomstva pro rodiče (Greig-Smith 1980; East 1981; Burger et al. 1989; Rytkönen et al. 1990, 1995; Hamer and Furness 1993; Curio and Onnebrink 1995; Ghalambor and Martin 2000; Rytkönen 2002; Fischer and Wiebe 2006). Výzkum schopnosti rozpoznávat predátory je ale nedílnou součástí, byť často nikoliv hlavní řešenou otázkou, další poměrně velké skupiny prací, zaměřených na trade-off mezi investicemi do obrany a nebezpečím, které predátor představuje pro rodiče a mláďata (Tab. v elektronické příloze). Poslední a nejmenší skupinu prací využívajících hnízdní experimenty představují ty, které studují proces rozpoznávání predátorů (a hnízdních parazitů), konkrétně znaky, kterými se při něm ptáci řídí (Tab.).

Většina prací zaměřených na rozpoznávání predátorů a založených na hnízdních experimentech využívá pěvce (Tab.), zřejmě především kvůli vyšším hnízdním hustotám usnadňujícím získání dostatečného materiálu. Z téhož důvodu jsou mezi pěvci nejpopulárnější druhy koloniálně hnízdící (Barash 1976; Smith and Graves 1978; Shields 1984; Brown and Hoogland 1986; Knight and Temple 1986a,c, 1988; Winkler 1992, 1994) a druhy ochotně využívající hnízdní budky. Nejčastěji se jedná o sýkory (Curio et al. 1983; Curio and Regelman 1985; Ficken et al. 1994; Curio and Onnebrink 1995), ale i lejsky (Curio 1975; Shalter 1978; Dale et al. 1996; Bureš and Pavel 2003) nebo brhlíky (Ghalambor and Martin 2000). Vedle nich se uplatňují drozdi (Shedd 1982; McLean et al. 1986; Hogstad 2005; Rodriguez-Prieto et al. 2009), pěnicovití (Edwards et al. 1950; Halupka 1999; Bureš and Pavel 2003; Kleindorfer et al. 1996, 2005) a různé druhy zrnožravých pěvců (Patterson et al. 1980).

Výhodou při vyhodnocování experimentů je, pokud testovaný druh používá agresivní formy obrany (Edwards et al. 1950). V střední Evropě je takovým druhem ťuhýk obecný (*Lanius collurio*, Ash 1970; Strnad et al. 2012; Němec and Fuchs 2014; Němec et al. 2015), který ve vhodných biotopech dosahuje poměrně vysokých hnízdních hustot (Roos and Pärt 2004; Goławski and Meissner 2007), jehož hnízda jsou snadno nalezitelná (Müller et al. 2005) a kterému jeho fyzické dispozice umožňují použít nejagresivnější formy obrany (Tryjanowski and Goławski 2004, Strnad et al. 2012). Podobně lze na severoamerickém kontinentu využít např. tyrany (Blancher and Robertson 1982).

Nepěvci se v hnízdních experimentech zaměřených na rozpoznávání predátorů využívají méně často (Tab.). Jedná se především o koloniálně hnízdící druhy (Elliot 1985; Conover 1987; Burger and Gochfeld 1992; Clode et al. 2000; Stenhouse et al. 2005), jejichž přednosti byly zmíněny v souvislosti s observačním přístupem, ale existují i práce na dravcích (Arroyo et al 2000; Csermely et al. 2006) nebo sovách (Hakkarainen and Korpimäki 1994).

1.2.2. Krmítkové experimenty

Jinou situací, kdy můžeme ptáky přimět k tomu, aby se predátorovi nevyhýbali, je nabídnout jim atraktivní zdroj potravy. V chladném a mírném klimatickém pásmu jsou takovým zdrojem zimní krmítka. Krmítko může představovat významný zdroj potravy, především v období omezení jejích přirozených zdrojů (Lack 1954, Robb et al. 2008a, b). Návštěva krmítka pak může významně přispět k přežití jedince a zvýšit tak jeho fines (Jansson et al. 1981). Zimní krmítka nicméně představují zajímavý zdroj potravy i pro predátory, kteří zde mají jistotu objevení kořisti (Dunn and Tessaglia 1994). Ptáci tedy na krmítcích čelí permanentnímu nebezpečí predace a musí při jeho návštěvě řešit trade-off mezi rizikem predace a využitím potravního zdroje (např. Abrahams and Dill 1989, Carrascal and Alonso 2006; Carrascal and Polo 1999).

Pokud umístíme v blízkosti krmítka predátora, navodíme situaci, kdy se přilétající ptáci musí rozhodnout, zda na využití nabízené potravy rezignují, či zda se rozhodnou riziko podstoupit. Míru rizika můžeme upravovat změnou vzdálenosti predátora od krmítka, stávající studie zaměřené na rozpoznávání predátorů ho však umísťovaly v těsné blízkosti (Hill 1986; Davies and Welbergen 2008; Tvardíková and Fuchs 2010, 2011, 2012) nebo max. do 1 metru (Soard and Ritchison 2009, Courter and Ritchison 2010). Výjimkou jsou studie Griessera (2008, 2009), který umísťoval vycpaniny predátorů 5 m od krmítka, na které létaly sojky zlověstné (Perisoreus infaustus).

Na prvý pohled by se tedy mohlo zdát, že krmítkové experimenty nabízejí ideální přístup k výzkumu rozpoznávání predátorů. Bohužel však přinášejí i nepominutelné nevýhody. Pokud se v případě hnízdních experimentů potýkáme s jejich standardizací, o experimentech krmítkových to platí dvojnásob.

Hlavním problémem je naprostá anonymita ptáků navštěvujících krmítko. Většina druhů využívajících krmítka vytváří hejna, která v nejbližším okolí krmítka nepobývají trvale ale pouze jednorázově (Tvardíková a Fuchs 2011), nepochybně proto, aby snížila nebezpečí predace (Elgar 1989, Lima 1995, Beauchamp 2001). Frekvence i pravidelnost návštěv se u jednotlivých ptačích skupin liší. Poměrně často a pravidelně navštěvují krmítka hejnka sýkor (Jansson et al. 1981; Shedd 1983; Hinsley et al. 1995; Koivula et al. 1995; Kullberg 1998; Pravosudov and Grubb 1998; Krams 2000, 2001; Gentle and Gosler 2001; Krams et al. 2006), intervaly mezi návštěvami hejn zrnojedů (Fringillidae, Emberizidae) jsou delší a nepravidelné, pravděpodobně proto, že mohou jednorázově přijmout větší množství potravy (Lilliendahl 1997; Quinn and Cresswell 2005; Roth et al. 2008).

Krmítka navštěvují i druhy, které se v jeho okolí zdržují trvale, neboť mají více méně stálá zimní teritoria či okrsky. V střední Evropě jsou to například červenky (*Erithacus* *rubecula*), kosové (*Turdus merula*), brhlíci (*Sitta europaea*), strakapoudi (Tvardíková and Fuchs 2012), ve Švédsku (Jansson et al. 1981) sýkory lužní (*Poecile montanus*) a parukářky (*Lophophanes cristatus*). Objevují se ale na krmítku obvykle jednotlivě a změny jejich početnosti proto nepřinášejí dostatek informací o tom, jak hodnotí nebezpečí predace.

Nerovnoměrné využití krmítek v čase lze kompenzovat dvěma způsoby. Buďto je prezentace predátora velmi krátká (5 minut ve studiích Davies and Welbergen 2008; Soard and Ritchison 2009; Courter and Ritchson 2010) a postihne tedy homogenní vzorek populace ptáků právě aktuálně přítomných v okolí krmítka. Naopak lze pak predátora prezentovat tak dlouho, aby velká část celkové populace ptáků krmítko stihla navštívit (30 minut v případě studií Griesser 2008, 2009; Tvardíková a Fuchs 2010, 2011, 2012).

Problematika anonymity ptáků navštěvujících krmítko je v některých případech beze zbytku vyřešena. Jedná se např. o studie na sojce zlověstné (Griesser 2008, 2009). Zde měli badatelé k dispozici pochytanou a barevně označenou skupinu ptáků, jejichž vzájemné sociální vztahy byly dobře známy (Ekman et al. 2001, Griesser 2003, Griesser et al. 2008, 2009). Tyto práce, společně se studií Hauser and Caffrey (1994) na vráně *Corvus brachyrhynchos* jsou také jediné, které při výzkumu rozpoznávání predátorů na krmítku nepoužívaly jako studijní objekty sýkory (Tab.).

V jejich případě není problém s anonymitou beze zbytku řešitelný. Složení sýkorčích hejn se totiž mění v čase, někteří jedinci je opouštějí, jiní naopak přicházejí (Tvardíková and Fuchs 2011). Rychlost obměny je u různých druhů různá. Většina evropských sýkor, s výjimkou sýkory parukářky a lužní, které jsou v průběhu zimy vysoce sedentární (Jansson et al. 1981), vytváří anonymní hejna s nízkou stabilitou (Gaddis 1980). Severoamerické druhy sice obvykle také vytvářejí hejna, avšak se stabilním složením a hierarchickou strukturou. Platí to pro druhy *Poecile atricapilla* (Shedd 1983; Apel 1985; Smith 1997; Gunn et al. 2000), Poecile carolinensis (Freeberg and Lucas 2002; Soard and Ritchison 2009*), Poecile sclateri* (Ficken et al. 1994) i *Baelophus bicolor* (Hill 1986; Pravosudov and Grubb 1998; Courter and Ritchison 2010).

Stabilita hejn s sebou přináší problém pseudoreplikací. Pokud by byla hejna absolutně stabilní v průběhu celé zimy, neměli bychom na jednom krmítku respektive na jedné lokalitě experimenty opakovat. To je ovšem obtížně splnitelné a to nejen z technických důvodů (viz níže). Přinejmenším v případě druhů vytvářejících anonymní hejna však k obměně složení dochází. Vzhledem k tomu, že provedení série experimentů obvykle zabere několik dní (Tvardíková and Fuchs 2011), nejsou tedy stabilita hejn a z ní plynoucí pseudoreplikace fatálním problémem, měly by však být při hodnocení výsledků zohledněny. Rychlost obměny lze stanovit opakovaným odchytem a individuálním kroužkováním. Quinn et al. (2012) tuto metodu obohatili o značení odchycených sýkor pasivními čipy (PIT), které byly odečítány zapisovači, umístěnými u jednotlivých krmítek.

Stejně jako v případě experimentů hnízdních ovlivňuje krmítkové experimenty také prostředí. Naprosto zásadní význam má především dostupnost úkrytů. Pokud mají ptáci navštěvující krmítko možnost rychlého útěku do úkrytu, jejich ochota riskovat se i násobně zvyšuje. V jedné ze studií Tvardíkové a Fuchse (2012) bylo ochotno riskovat přílet na krmítko, v jehož blízkosti se nacházel krahujec 31 % sýkor, zatímco v druhé (Tvardíková and Fuchs 2011) maximálně 5 % sýkor. V prvém případě bylo pokusné krmítko ze tří stran obklopeno ve vzdálenosti do 2 m keři, v druhém bylo umístěno na louce ve vzdálenosti 7 m od křovinaté meze. Zásadní vliv dostupnosti úkrytu na ochotu ptáků navštěvujících krmítko riskovat způsobuje, že mezi jednotlivými lokalitami (krmítky) nelze srovnávat chování vůči témuž druhu (modifikaci) predátora ale jen rozdíly v chování vůči různým druhům (modifikacím).

Frekvenci i pravidelnost návštěv krmítek zřejmě ovlivňuje také nabídka jiných potravních zdrojů v okolí. Nasvědčovala by tomu vyšší variabilita reakcí sýkor na téhož predátora zjištěná v městech, kde je široce rozšířeno zimní přikrmování ptáků (Fuller et al. 2008; Davies et al. 2012), ve srovnání s venkovskou krajinou (Fuchs personal observation). Vcelku nepřekvapivě ovlivňuje významně ochotu riskovat také počasí. V situaci s velmi nízkými teplotami a vysokou sněhovou pokrývkou se motivace ptáků navštívit krmítko i přes přítomnost predátora zvyšuje a jejich ochota riskovat vzrůstá (Tvardíková and Fuchs 2011). Tyto parametry je proto nutné vždy zahrnout do analýzy získaných dat.

Z předchozích odstavců je zřejmé, že absolutní počty příletů na krmítko ovlivňuje řada měnících se faktorů a nemohou proto sloužit jako spolehlivé měřítko ochoty ptáků riskovat. Je tedy nutno je vztáhnout k nějaké kontrole. Nejjednodušeji ji získáme tak, že střídáme uspořádání, při nichž je krmítko volně přístupné, s uspořádáními, při nichž je u krmítka instalován predátor. Měřítkem ochoty ptáků riskovat, je pak pokles počtu příletů na krmítko po expozici predátora. Ani tento způsob korekce dat však nemůže eliminovat krátkodobé fluktuace v pohybu jednotlivých hejn, která mohou například jinak pravidelně navštěvované stanoviště vynechat.

Optimální řešením by bylo, kdyby kontrola probíhala současně s expozicí predátora. To umožňuje „dvoukrmítkový“ design (Tvardíková and Fuchs 2010, 2011). Přítomným ptákům jsou nabídnuta dvě krmítka nacházející se na dohled od sebe. Na jednom z nich je umístěn testovaný predátor, na druhém kontrolní druh. Kontrolním druhem může být extrémně nebezpečný predátor (ve střední Evropě krahujec obecný), nebo neškodný pták obdobné velikosti jako predátor (ve střední Evropě například holub domácí).

Pokud během pokusu k testovanému predátorovi přilétne více ptáků než ke krahujci, znamená to, že testovaný predátor vzbuzuje menší strach než krahujec. Sýkory v něm sice mohly rozpoznat nebezpečného ptáka nikoliv však krahujce. Toto srovnání je důležité, pokud modifikujeme potenciální rozpoznávací znaky krahujce (ať již sdílené s jinými dravci nebo druhově specifické). Pokud během pokusu k testovanému predátorovi přilétne méně ptáků než k holubovi, znamená to, že testovaná atrapa vzbuzuje větší strach než holub. Sýkory v ní tedy rozpoznávají nebezpečného ptáka. Pokud ale atrapa nevzbuzuje větší strach než holub, žádný z jí nesených znaků nepostačuje k tomu, aby byla rozpoznána jako predátor.

Krmítkové experimenty byly dosud pro výzkum antipredačního chování využívány poměrně zřídka. Nejčastěji posloužily pro studium fyziologické odpovědi na ohrožení predací (např. Gentle and Gosler 2001). Pro studium rozpoznávání predátorů byly krmítkové experimenty využity spíše ojediněle (Tab.). Na vině jsou zřejmě metodické problémy s nimi spojené. Ty jsou však alespoň částečně řešitelné a navíc je vyvažuje jednoznačnost odpovědi testovaných ptáků. Proto se domníváme, že krmítkové experimenty nabízejí pro další výzkumy zajímavé možnosti. Jejich použití by navíc nemuselo být omezeno na zimní období a mírné respektive chladné pásmo severní polokoule. Doplňkové zdroje potravy lze předkládat i hnízdícím ptákům (Hauser and Caffrey 1994) a ptákům v teplých klimatických pásmech (Griffin et al. 2005).

1.2.3. Voliérové a klecové experimenty

Antipredační chování ptáků je možné zkoumat také v zajetí. Tento přístup, na rozdíl od polních experimentů, umožňuje standardizaci experimentálních podmínek. S tím spojenou nevýhodou ovšem je, že se tyto podmínky zásadně liší od podmínek v přírodě. Pokud jsou testováni ptáci v přírodě odchycení, je pro ně zřejmě hlavním zdrojem stresu zajetí a to i tehdy, jsou-li na nové prostředí habituovány (Van Dongen et al. 2001). Sýkory v klecových a voliérových experimentech tráví nejvíce času explorací, nepochybně vedeny snahou uniknout. Přítomnému predátorovi sice pozornost věnují, avšak menší než v experimentech přírodních (srovnej Beránková et al. 2015 and Veselý et al. 2016).

Studie zkoumající antipredační chování s využitím experimentů probíhajících v zajetí mají dlouhou tradici. Výlučně voliérové experimenty používaly pionýrské práce zaměřené na hledání znaků, kterými se při rozpoznávání predátorů ptáci řídí (Lorenz 1939; Krätzig 1940; Nice and Ter Pelkwyk 1941; Melzack et al. 1959; Hinde 1960). Velkého rozvoje se tento přístup dočkal od šedesátých let (Schaller and Emlen 1962; Melvin and Cloar 1969; Scaife 1976; Klump and Curio 1983; Evans et al. 1993a, b; Flasskamp 1994; Kullberg 1998), opět především při studiu rozpoznávání letových siluet dravců (Green et al. 1968; Mueller and Parker 1980; Moore and Mueller 1982; Canty and Gould 1995). S rozpoznáváním predátorů souvisí také studie zaměřené na funkci varovných hlasů (Bautista and Lane 2000; Dessborn et al. 2012) nebo na rozpoznávání pachů (Fluck et al. 1996; Hagelin et al. 2003).

Klecové experimenty v posledních letech zažívají výraznou renesanci a jsou po experimentech prováděných u hnízd nejčastější metodou při studiu rozpoznávání predátorů (Lind et al. 2005; Palleroni et al. 2005; Templeton et al. 2005; Azevedo and Young 2006a,b; van den Hout et al. 2006, 2010; Zaccaroni et al. 2007; Carter et al. 2008; Cresswell et al. 2009; Mathot et al. 2009; Binazzi et al. 2011; Sieving et al. 2010; Schleidt et al. 2011; Dessborn et al. 2012; Schetini de Azevedo et al. 2012; Beránková et al. 2014, 2015).

Uspořádání experimentů se pochopitelně u jednotlivých studií liší. Zpočátku byly pouze sledovány reakce ptáků na náhodně se vyskytnuvší volně žijící predátory (Gyger et al. 1987), brzy ale nastoupily experimenty využívající různé formy simulované prezentace predátorů.

Především starší studie pracovaly s domestikovanými (kur domácí, kachna, husa, krocan) nebo v zajetí odchovanými (bělokuři, křepelové, orebice, strnadi) druhy (Tab.). To ovšem omezuje jejich výpovědní hodnotu, neboť významnou část znalostí o predátorech ptáci zřejmě získávají učením (Curio 1975, Maloney and McLean 1995, McLean et al. 1999, Kullberg and Lind 2002). Domestikované druhy mají navíc tendenci omezovat svoje antipredační chování a spoléhat částečně na ochranu člověka (Schaller and Emlen 1962).

Domestikace může konečně pozměnit jejich kognitivní schopnosti a repertoár chování (např. Kagawa et al. 2014). Speciálním případem, kdy jsou v zajetí odchovaným ptákům prezentováni predátoři, je snaha stimulovat antipredační chování u ohrožených druhů před jeho vypuštěním do přírody (Hölzer et al. 1996; McLean et al. 1999; Wong 1999; Göth 2001; Azevedo and Young 2006a,b; Schetini de Azevedo et al. 2012).

Z ptáků odchycených ve volné přírodě byly v zajetí jednoznačně nejčastěji testovány sýkory (Klump and Curio 1983; Hogstad 1995; Alatalo and Helle 1990; Kullberg 1998; Pravosudov and Grubb 1998; van der Veen 1999; Bautista and Lane 2000; Kullberg and Lind 2002; Baker and Becker 2002, Lind et al. 2005; Templeton et al. 2005; Sieving et al. 2010; Beránková et al. 2014, 2015). Kromě nich byli občas použiti také drozdi and špačci (Flasskamp 1994; Carter et al. 2008), pěnice (Fransson and Weber 1997), zrnojedi (Hinde 1960; Cresswell et al. 2009) nebo bahňáci (Hagelin et al. 2003; Mathot et al. 2009; van den Hout et al. 2006, 2010).

U řady druhů je stres způsobený zajetím zřejmě tak vysoký, že nejsou schopny projevovat normální antipredační chování (Dickens and Bentley 2014). Sýkory se v tomto ohledu jeví jako jednoznačně nejvhodnější skupina. I v případě druhů přizpůsobivých je však třeba počítat s určitým časem na adaptaci. Ptáci si musí nejen zvyknout na zajetí jako takové ale i seznámit se s pokusnou voliérou či klecí. Sýkory koňadry testované Beránkovou et al. (2014) byly před pokusem drženy v zajetí 1-3 dny. Do pokusné klece pak byly umístěny 10 minut před vlastním pokusem. Toto uspořádání se ukázalo jako vyhovující, neboť ptáci projevovali bohatý repertoár antipredačního i komfortního chování, které se zřejmě vcelku dobře shodovalo s chováním přirozeným.

1.2.4. Prezentace predátorů

Experimentální přístup ke studiu rozpoznávání predátorů s sebou přináší otázku, v jaké podobě a jakým způsobem je testovaným ptákům prezentovat. Živí predátoři jsou používáni spíše méně často (Tab.). Vedle obtíží se získáním jsou zřejmě příčinou nesnáze spojené s vlastní prezentací. Ta musí být věrohodná, současně ale taková, aby zabránila přímému kontaktu predátora s testovanými ptáky. To lze zajistit umístěním do klece (Curio et al. 1983; Curio and Regelmann 1985; Flasskamp 1994; Sieving et al. 2010), je ale otázkou, nakolik ptáci vnímají, že predátor v kleci představuje reálné ohrožení. Vhodnější je přivázání predátora k bidýlku (Curio et al. 1983). Chování predátora by navíc mělo být ve všech opakováních obdobné. Tyto požadavky lze, především v případě predátorů ptačích, jen obtížně splnit.

Přesto existují studie, kterým se to podařilo. Palleroni et al. (2005) použil ve svých experimentech tři zástupce rodu *Accipiter*. Cvičení jedinci přelétávali nad voliérou se slepicemi, které projevovaly různé antipredační chování odrážející míru vnímaného nebezpečí. Templeton et al. (2005) dokonce prezentovali sýkorám černohlavým 13 druhů sov a dravců, kteří seděli na bidýlku u jejich domovské voliéry. Vedle ptáků se v několika studiích objevují i živí psi (Göth 2001; Azevedo and Young 2006a,b), kočky (Naguib et al. 1999; Göth 2001; Sieving et al. 2010; Templeton et al. 2005), norci (Hakkarainen and Korpimäki 1994;

Dessborn et al. 2012), fretky (Winkler 1992, 1994; Templeton et al. 2005) nebo krysy (Schaller and Emlen 1962), ale třeba i živí hadi (Suzuki 2011).

V naprosté většině experimentů prováděných nejen v rámci studia rozpoznávání predátorů, ale i dalších aspektů antipredačního chování byly použity místo predátorů živých jejich atrapy. V případě predátorů ptačích se většinou jednalo o vycpaniny v pozici vzpřímeně sedících jedinců, u nichž nepůsobí nepřirozeně absence pohybu. Výjimkou jsou studie používající letící vycpaniny s roztaženými křídly, většinou tažené na drátu (např. Gentle and Gosler 2001; van den Hout et al. 2006, 2010; Mathot et al. 2009). S vycpaninami pracovaly i nečetné studie zaměřené na predátory savčí (Tab.).

Vycpaniny plně vyhovují pro výzkum schopnosti ptáků rozpoznávat predátory. Výzkum samotných rozpoznávacích procesů, však vyžaduje manipulaci znaků, které předkládaní predátoři pro rozpoznávání nabízejí. Její možnosti jsou ale, především u ptačích vycpanin, poměrně omezené. Přesto byly vycpaniny k tomuto účelu využívány (Edwards et al. 1950; Curio 1975; Scaife 1976; Smith and Graves 1978; Gill et al. 1997; Davies and Welbergen 2008; Tvardíková and Fuchs 2010; Trnka et al. 2012). Optimálním řešením se zdá být jejich nahrazení modely (Tab.). Ty navíc řeší špatnou dostupnost kvalitních vycpanin. To byl zřejmě také důvod, proč modely použily i studie, které s jednotlivými znaky nemanipulovaly (Tab.).

Použití modelů a v menší míře i vycpanin ovšem přináší problém s jejich věrohodností. Výše uvedené studie jej většinou neřešily a spokojily se s tím, že testování ptáci na předkládané atrapy obvykle reagovali. Několik prací porovnávalo, nakolik úspěšně nahrazují vycpaniny živé predátory (Curio 1975; Shalter 1978; East 1981; Blancher and Roberson 1982; Shedd 1982; Knight and Temple 1986a; Meilvang et al. 1997), nicméně testování efektivity modelů bylo provedeno pouze jednou (Němec et al. 2015). Srovnání vycpanin a modelů zhotovených z textilu a plastu ukázalo, že snížená věrohodnost reakci testovaných ptáků ovlivnit může. Pozornost je třeba věnovat především povrchovému materiálu. Nejméně problémů zřejmě způsobuje díky snadno napodobitelnému povrchu těla použití plastických modelů v případě hadů (Patterson et al. 1980; Kleindorfer et al. 1996, 2005; Göth 2001).

V laboratorních podmínkách se jako další možnost samozřejmě nabízí prezentace statických obrazů, nebo i videí, obvykle na monitoru (Krätzig 1940; Nice and Ter Pelkwyk 1941; Evans et al. 1993a, b). Ta ovšem přináší další potenciální zdroj obtíží – 2D zobrazení. Otázku, nakolik ptáci vnímají 2D stimuly jako reálné, řeší již desítky let behaviorální psychologie, avšak bez jednoznačných závěrů (review Weisman & Spetch 2010).

Jak již bylo zmíněno, je společným nedostatkem běžných vycpanin i modelů absence pohybu. Nápadné je to především v případě savčích, ale i plazích predátorů (Bažant 2009; Dessborn et al. 2012). Některé studie jím proto předkládané predátory vybavily (Frankenberg 1981; Gentle and Gosler 2001; Cockrem and Silverin 2002; van den Hout et al. 2006, 2010; Mathot et al. 2009; Dessborn et al. 2012). Efekt takovéto úpravy ale nebyl testován.

1.3. Detekce rozpoznání predátorů

Pokud zkoušíme ze znalosti predátorů (a ostatních živočichů) studenty, nemusíme se problematikou, jaké indikátory signalizují, že je student poznal, zabývat. Máme pro jednotlivé druhy i vyšší taxony vytvořena více či méně obecně přijímaná jména, které po studentech samozřejmě vyžadujeme. Nicméně to neznamená, že student, který, například poštolku, neumí pojmenovat, ji opravdu nezná. Mohla vyhnízdit na balkóně jeho kolejního pokoje, kde ji pravidelně vídal, neobtěžoval se ale dohledat její konvenční jméno.

V situaci zkoušejícího se ocitáme i tehdy, když se snažíme zjistit, zda testovaní ptáci znají predátory, které jim předkládáme. S jednou částečnou výjimkou, která bude popsána později, nemáme ovšem k dispozici jména, na která bychom se jich mohli tázat. Musíme se tedy pokusit získat odpověď z jejich reakcí v průběhu setkání s predátorem. Tato reakce může být buď behaviorální, nebo fyziologická. Předpokládáme při tom, že pokud testovaný pták predátora rozpozná, bude na něj reagovat a že podoba této reakce bude záviset na velikosti a povaze nebezpečí, které pro něj predátor představuje (MacLean and Rhodes 1991, Caro 2005).

Tyto předpoklady nejsou ovšem samozřejmé, což je nutno mít trvale na paměti. Pokud testovaný pták vyhodnotí aktuální nebezpečí jako zanedbatelné, nebude reagovat vůbec. A v případě, že vyhodnotí nebezpečí hrozící od různých predátorů jako shodné, nebude se reakce na ně lišit. Ani v jednom z obou případů to ale neznamená, že predátory nerozpoznal. Z toho mimo jiné plyne, že čím bude nebezpečí hrozící od předkládaných predátorů podobnější, tím menší šanci máme prokázat, že je testování ptáci rozlišují. Je tedy zřejmé, že pro výzkum rozpoznávání predátorů platí neúprosněji než pro jiná témata řešená behaviorálními vědami, že pokud se nepodaří falsifikovat nulové hypotézy, nelze z toho vyvozovat žádné závěry.

1.3.1. Behaviorální doklady

Naprostá většina studií zabývajících se rozpoznáváním predátorů využívá behaviorální odpověď testovaných ptáků na reálné či simulované nebezpečí (Tab.). Nepochybně je tomu tak z metodických důvodů, neboť naše možnosti zaznamenat fyziologickou odpověď jsou, především v terénních experimentech velmi omezené (např. množství tuku u koňader na krmítku - Gentle and Gosler 2001).

Jak již bylo uvedeno na několika místech, je preferovaným antipredačním chováním vyhnout se střetu s predátorem (Caro 2005). Ve většině typů experimentů se snažíme ptáky dostat do situace, kdy tuto volbu nepoužijí, buď proto, že dají přednost obraně hnízda či získání potravy, nebo proto, že jim v tom fyzicky zabráníme. V posledním případě nemá testovaný pták možnost volby a musí se s blízkostí predátora „smířit“. To ovšem může vést k tomu, že jeho chování nebude adekvátní hrozícímu nebezpečí, neboť není na takovou situaci připraven (Van Dongen et al. 2001).

Snaha vyhnout se predátorovi bývá velmi často sledovaným ukazatelem v laboratorních experimentech. Reakcí, která má zamezit objevení predátorem je tzv. freezing. Dobře ji lze sledovat především u větších ptáků, jako jsou hrabaví a vrubozobí (Krätzig 1940;

Melvin and Cloar 1969; Klump and Curio 1983; Göth 2001; Kullberg and Lind 2002; Zaccaroni et al. 2007; Binazzi et al. 2011; Dessborn et al. 2012; Schetini de Azevedo et al. 2012). V řadě studií jsou hodnoceny také pokusy o útěk, které se ovšem obtížně kvantifikují (Lorenz 1939; Melzack et al. 1959; Schaller and Emlen 1962; Green et al. 1968; Canty and Gould 1995; Göth 2001; Palleroni et al. 2005; Zaccaroni et al. 2007; Cresswell et al. 2009; Binazzi et al. 2011; Dessborn et al. 2012; Schetini de Azevedo et al. 2012). Jednoznačnost útěkových reakcí zvýšíme, pokud testovaným ptákům nabídneme úkryt (Lorenz 1939; Krätzig 1940; Melzack et al. 1959; Green et al. 1968; Canty and Gould 1995; Palleroni et al. 2005).

Dobře kvantifikovatelným parametrem může být vzdálenost od predátora, v níž se testovaný pták zdržuje po dobu experimentu (Scaife 1976; Beránková et al. 2014). Ta je často sledována v experimentech založených na obraně hnízd (Barash 1975; Hauser and Wrangham 1990; Burhans 2000; Kleindorfer et al. 1996; Csermely et al. 2006; Rodriguez-Prieto et al. 2009) a ojediněle i v krmítkových experimentech (Hauser and Caffrey 1994; Soard and Ritchison 2009). V obou případech se jedná o jeden z významných parametrů ochoty riskovat.

V hnízdních i krmítkových experimentech jsou testovaní ptáci vystaveni situaci, kdy musí volit mezi vyhnutím se predátorovi a jiným, žádoucím chováním. V případě krmítkových experimentů řeší trade-off mezi rizikem predace a ziskem z nabízené potravy. Jak již bylo zmíněno výše, míru rizika i zisku ovlivňuje celá řada faktorů (Abrahams and Dill 1989), které ptáci při rozhodování zohledňují, respektive měli by zohledňovat, nicméně výsledek je na úrovni jedince jednoznačný, krmítko buď navštíví, nebo nenavštíví. Pokud se tedy ve srovnání s kontrolou počet návštěv krmítka s predátorem sníží, znamená to, že jej ptáci rozpoznali, a pokud se počet návštěv krmítka s různými predátory liší, znamená to, že je ptáci rozlišovali. Jedna otázka nicméně zůstává. Směřuje k ptákům, kteří krmítko navštívili.

Návštěva krmítka může mít dvě příčiny: rozhodli se podstoupit riziko, nebo predátora, na rozdíl od ostatních, nepoznali, což je, zajímáme-li se o jejich kognitivní schopnosti, dosti zásadní rozdíl. Jak ukázali Tvardíková a Fuchs (2011), i na tuto otázku může vhodně uspořádaný experiment odpovědět. V případě, že měli sýkory na výběr mezi krmítkem s poštolkou a krmítkem s holubem, byl počet ptáků přilétajících k poštolce minimální, zvýšil se však násobně, pokud byl na druhém krmítku místo holuba umístěn krahujec. Tento přírůstek lze jednoznačně připsat ptákům, kteří poštolku znali a přiletěli do její blízkosti, jen tehdy představovala-li menší riziko.

Na prvý pohled je jednoduchá i volba ptáků v hnízdních experimentech. Ti řeší trade-off mezi rizikem predace a ziskem ze záchrany potomstva (Cordero and Senar 1990; Sordahl 1990). Ve skutečnosti ale při obraně hnízd existuje riziko dvojí - pro potomstvo a pro rodiče (Montgomerie and Weatherhead 1988; Rytkönen et al. 1990; Forbes et al. 1994; Campobello and Sealy 2010). Prvé z nich ochotu investovat do obrany zvyšuje, druhé naopak snižuje. Vedle toho zřejmě bránící ptáci zohledňují i svojí šanci na úspěch (Lemmetyinen 1971; Knight and Temple 1986c; Burger and Gochfeld 1992; Winkler 1992; Olendorf and Robinson 2000). Neúspěšná obrana může totiž naopak pravděpodobnost predace zvýšit (Gill et al. 1997b). Správná predikce toho, jak intenzivně budou ptáci hnízdo bránit proti konkrétnímu predátorovi je proto obtížná (Knight and Temple 1986a; Weatherhead 1989). Pro výzkum rozpoznávání predátorů to však nemusí být závažnou překážkou, důležité je především, aby byli prezentovaní predátoři hodnoceni bránícími ptáky odlišně. Jistý problém ale nastává, pokud se bránící ptáci rozhodnou na aktivní obranu zcela rezignovat (Neudorf and Sealy 1992; Burhans 2000, Strnad et al. 2012). Takovýto výsledek lze jen velmi obtížně odlišit od toho, že nepovažují daného predátora za nebezpečí, respektive že ho nerozpoznávají (Syrová et al. 2016).

1.3.1.1. Mobbing

Zatímco v krmítkových experimentech je odpověď ptáků na simulované riziko predace velmi jednoduchá, antipredační chování používané při obraně hnízd se vyznačuje vysokou mírou komplexnosti. V literatuře se pro ně vžil termín mobbing (Hartley 1950). Zahrnuje veškeré prvky chování, jejichž funkcí je odradit predátora od napadení hnízda, ale také varovat jedince vlastního i cizích druhů nacházející se v okolí místa střetu, především ovšem mláďata na hnízdě (Curio et al. 1978; Templeton and Greene 2007; Magrath et al. 2010). Mobbing má mnoho podob od pouhé přítomnosti rodičů v blízkosti predátora (Curio and Onnebrink 1995; Deppe et al. 2003; Hogstad 2005; Welbergen and Davies 2008, 2011), přes vydávání varovných hlasů (Knight and Temple 1988; Stone and Trost 1991; Bazin and Sealy 1993; Ficken et al. 1994; Nealen and Breitwisch 1997; Burhans 2001) až po fyzické napadání (Shields 1984; Winkler 1994; Strnad et al. 2012, Němec and Fuchs 2014) nebo odvádění pozornosti od hnízda (Gochfeld 1984; Byrkjedal 1987; Sordahl 2009).

Mobbing bývá rozdělován na pasivní a aktivní (Curio 1976; Harvey and Greenwood 1978; Conover 1987; Caro 2005). Pasivní mobbing zahrnuje pobyt rodičů v blízkosti predátora a vokalizaci, tedy aktivity, při nichž je podstupované riziko poměrně malé. Pobyt v blízkosti predátora doprovázejí specifické postoje těla, jako jsou čepýření, pohyby ocasem nebo křídly a podřepování (Ash 1970; Kumar 2003; Griffin et al. 2005). K pasivnímu mobbingu lze řadit i formování hejnek a létání v kruzích okolo predátora (Shields 1984; Conover 1987). Aktivní mobbing zahrnuje fyzické obtěžování a napadání predátora (Shields 1984; Winkler 1994; Strnad et al. 2012, Němec and Fuchs 2014), při kterém bránící rodiče podstupují velké riziko zranění či smrti (Brunton 1986; Curio and Regelmann 1986; Poiani and Yorke 1989; Sordahl 1990). Pokud jsou ale přiměřeně fyzicky disponovaní, může být aktivní mobbing velmi efektivní.

Většina prvků chování s mobbingem spojená je poměrně nápadná a tedy relativně snadno měřitelná. V případě mobbingu aktivního lze kvantifikovat počet útoků, které rodiče provedou. Existuje přitom několik stupňů aktivního mobbingu, které je možno hodnotit samostatně, od přiblížení se do definované vzdálenosti, přes přelety nad predátorem až po nálety se snížením výšky anebo přímo s fyzickým napadením predátora (Ash 1970; Curio 1975; Kruuk 1976; Shields 1984; McLean et al. 1986). V případě mobbingu pasivního bývá měřena doba, kterou rodiče stráví v určité vzdálenosti od predátora, počet provedených varování a typických postojů nebo přeletů v okolí predátora (Curio and Onnebrink 1995; Deppe et al. 2003; Hogstad 2005; Welbergen and Davies 2008, 2011). Pasivní mobbing je komplexnější chování než mobbing aktivní a proto bývají při jeho hodnocení využívány indexy (Schaller and Emlen 1962; Kleindorfer et al. 2005; Avilés and Parejo 2006; Honza et al. 2006; Liang and Møller 2015) nebo mnohorozměrné statistické metody, jako je analýza hlavních komponent (Beránková et al. 2014) s cílem redukovat počet analyzovaných proměnných.

V případě obou typů mobbingu může být účelné odlišovat jeho intenzitu, kterou lze měřit celkovým počtem útoků či celkovou dobou zájmu, od riskantnosti, o které vypovídá míra agresivity útoků či průměrná vzdálenost od predátora. Například ťuhýci v experimentech Strnada et al. (2012) útočili na většinu předložených predátorů s obdobnou intenzitou, agresivita útoků ale klesala s rostoucí nebezpečností predátorů pro rodiče.

V klecových experimentech se sýkorami bylo možné pozorovat pouze určité prvky pasívního mobbingu – čepýření, varovnou vokalizaci, podřepování a třepání křídly (Kullberg and Lind 2002, Beránková et al. 2014). Vedle nich se ale běžně vyskytovaly i prvky exploračního a potravního chování. Pro hodnocení bylo proto nutno využít analýzu hlavních komponent, která ukázala tři základní postoje zaujímané vůči predátorovi - strach, exploraci a nezájem.

S pasivním mobbingem se lze setkat i při krmítkových experimentech. K jeho využití pro hodnocení chování testovaných ptáků vůči předkládaným predátorům však dosud nedošlo. Je to zřejmě způsobeno především tím, že aktivity probíhající v poměrně širokém okolí krmítka nelze jednoduše zaznamenávat. Navíc je mobbing v okolí krmítek méně častý respektive méně intenzivní, než bychom očekávali, zřejmě proto že vyhnutí se nebezpečnému potravnímu zdroji je pro ptáky méně nevýhodné než rezignace na obranu potomstva.

1.3.1.2. Varování

Jak již bylo uvedeno, jednou z funkcí mobbingu je varování vlastního i cizích druhů nacházející se v okolí místa střetu (Curio 1976). Slouží k tomu především specifická skupina zvukových signálů, nazývaných varovné hlasy (Naguib et al. 2009). Je zřejmé, že se jejich účinnost zvýší, pokud budou obsahovat informaci o povaze hrozícího nebezpečí. Není tedy úplně pravda, že nám ptáci nemohou poskytnout přímou informaci o tom, jak rozlišují predátory, s nimiž se setkávají. Otázkou je pouze přesnost této informace.

Opakovaně bylo doloženo, že ptáci ve varovných signálech odlišují velké skupiny predátorů, lišící se svými loveckými schopnostmi, konkrétně ptáky a hady (Sieving et al. 2010; Suzuki 2011, 2012), pozemní a vzdušné predátory (Knight and Temple 1988; Kleindorfer et al. 1996, Walters 1990). Informace o jednotlivých skupinách predátorů může být předávána zcela odlišnými signály (Knight and Temple 1988; Griesser 2008, 2009; Sieving et al. 2010), častěji ale změnami kvantitativních parametrů obecně užívaného základního signálu. Ty mohou zahrnovat rozdílné počty varovných hlasů vydaných za jednotku času (Evans et al. 1993a; Burhans 2001; Rainey et al. 2004) rozdílné počty jednotlivých slabik v rámci jednoho varovného hlasu (Walters 1990; Naguib et al. 2009; Binazzi et al. 2011) nebo i rozdílné délky a frekvence jednotlivých slabik (Stone and Trost 1991; Ficken et al. 1994).

Mimořádně podrobné informace zřejmě předávají ve svých varovných hlasech druhy vytvářející neanonymní society. První doklady pocházejí od polopouštních timálií *Turdoides squamiceps* (Naguib 1999), nejpodrobněji však tato problematika byla studována na severoamerických sýkorách *Poecile atricapillus*. Ty vydávají dva hlavní typy varovných hlasů: tiché "seet" užívané, když dravec poblíž letí, a hlasité širokospektré "chick-a-dee" upozorňující na sedícího predátora. První hlas způsobuje, že se ostatní sýkory ukryjí do porostu, na druhý hlas reagují společným mobbingem (Ficken et al. 1978; Smith 1991; Templeton and Greene 2007). Specialitou sýkor *Poecile atricapillus* je variabilita druhého typu varovného hlasu. Čím aktuálnější a intenzivnější nebezpečí predátor představuje, tím víc slabik "chick" se v něm objevuje. Prodloužená závěrečná slabika "dee" vyvolává intenzivnější skupinový mobbing (Baker and Becker 2002), počet „dee" slabik informuje o velikosti predátora (Templeton et al. 2005). Rychlejší opakování celého volání "chick-a-dee" upozorňuje na jeho kratší vzdálenost (Baker and Becker 2002). Souvislost mimořádné komplexity varovných hlasů sýkory *Poecile atricapillus* s její socialitou podporuje mnohem chudší rejstřík varovných hlasů těch druhů sýkor, které vytvářejí pouze nestabilní anonymní hejna (Lind et al. 2005; Courter and Ritchison 2010).

Stávající znalosti nepochybně dokládají, že varovné hlasy poskytují více či méně podrobné přímé informace o tom, zda ptáci rozlišují predátory, se kterými se setkávají. Zároveň však ukazují na jedno úskalí komplikující interpretaci této informace. Varovné hlasy přinášejí informaci nejen o samotném predátorovi ale i okolnostech jeho výskytu, například vzdálenosti (Templeton et al. 2005). Ani varovné hlasy tedy nepředstavují ideální doklad rozpoznání predátora, který by bylo možno upřednostňovat před ostatními.

1.3.2. Fyziologické doklady

Střetnutí s predátorem nepochybně představuje pro potenciální kořist stresující událost a stress ovlivňuje celou řadu fyziologických parametrů (např. Orchinik 1998). Zdálo by se tedy, že jsou fyziologické ukazatele předurčeny ke studiu reakcí ptáků na střetnutí s predátorem. Navíc lze předpokládat, že budou méně ovlivněny dalšími okolnostmi, neboť jsou přímou odpovědí organismu na stresující podnět (Scheuerlein et al. 2001).

Přesto byly při výzkumu rozpoznávání predátorů využity poměrně vzácně (Tab.). Příčiny jsou zřejmé a spočívají v obtížně řešitelných metodických problémech. Častěji se uplatnily jen nepřímé ukazatele stresové zátěže, jako je tělesná hmotnost (Adriansen et al. 1998; van der Veen 1999; Bautista and Lane 2000; van den Hout et al. 2006, 2010) nebo tvorba prsní svaloviny (van den Hout et al. 2006, 2010) a tukových zásob (Pravosudov and Grubb 1998; Gentle and Gosler 2001; Scheuerlein et al. 2001).

Z přímo měřitelných projevů stresové zátěže organismu se jako nejsnáze použitelné jeví měření tepové frekvence (review Butler et al. 2004), které bylo na ptácích použito již překvapivě dávno (Owen 1969). Aby je však bylo možné provádět v terénních a voliérových experimentech, které v současnosti při výzkumu rozpoznávání predátorů převládají, musely by snímače tepové frekvence splňovat náročné požadavky, především malé rozměry (pracuje se nejčastěji s pěvci), což je zatím hlavní komplikace. Nejstarší studie využívaly snímač zvuku nalepený na prsou ptáka, který zesiloval hlasitost srdečního tepu (Mueller and Parker 1980, Moore and Mueller 1982), později se využívaly snímače elektrické aktivity srdce (EKG) implantované do břišní dutiny ptáka, a to jak v laboratorních (McPhail and Jones 1998), tak terénních podmínkách (Ely et al. 1999; Ackerman et al 2004), ovšem nikoliv na pěvcích. Nicméně chirurgický zákrok představuje riziko ovlivnění přirozeného chování ptáka.

Nově lze použít EKG připevněné na zádech ptáka (Enstipp et al. 1999; Storch et al. 1999). Nicméně toto zařízení je stále vhodné jen pro větší druhy ptáků (kormoráni). Nedávno byla vyvinuta elegantní neinvazivní metoda aplikovatelná i na drobné pěvce, kdy je snímač tepu umístěn do falešných vajec (Arnold et al. 2011). Tato metoda se ale samozřejmě pro studium rozpoznávání predátorů také využít nedá. Velikostně by vyhovovaly snímače tepu určené pro pokusy s drobnými savci (např. Gilson and Kraitchman 2007) které ovšem předpokládají pohyb v omezeném prostoru či dokonce jen po monitorovací podložce (Harkin et al. 2002). Budoucnost pravděpodobně tkví v použití EKG upevněných na povrch těla ptáka (Johnson-Delaney 2003) nicméně jejich převedení do miniaturních a terénně použitelných forem zatím není dořešeno.

Lákavou možnost nabízí měření hladiny stresových hormonů (Cook 2012; Johnstone et al. 2012). V posledních 20 letech se poměrně rychle rozvíjí stanovení jejich metabolitů z trusu (Lane 2006). Nehledě na pravděpodobně odstranitelné problémy s přesností metody jako jsou fluktuace v průběhu dne (Carere et al. 2003) a sezóny (Astheimer et al. 1994), ale i závislost na pohlaví, potravě a individualitě (Goymann 2012), zůstává otázkou, zda je vhodná pro zachycení krátkodobých stresových událostí, mezi které patří i střetnutí s predátorem. Vztah mezi intenzitou stresu a hladinou metabolitů totiž nemusí být jednoduchý (např. Chávez-Zicchinelli et al. 2014 and Albano et al. 2015). Stanovení dlouhodobé respektive opakované stresové zátěže nicméně možné je a přináší i výsledky s určitým vztahem k tématice antipredačního chování (Ylönen et al. 2006). Nově se navíc objevuje možnost stanovení metabolitů stresových hormonů z peří (Jenni-Eiermann et al. 2015).

Druhou možností je přímé stanovení (Breuner et al. 2013). Zde je kromě přirozené variabilty mezi jedinci (Cockrem 2013) hlavním zdrojem problémů velmi rychlá odezva na stresující podnět (Deviche et al. 2012). Hormony je nutno stanovit co nejrychleji a vyhnout se přitom tomu, aby jejich hladinu ovlivnil samotný odběr (Van Hout et al. 2010). To lze v terénních experimentech jen stěží splnit a ani v laboratoři to není jednoduché (Canoine et al. 2002). Proto byly hladiny stresových hormonů použity v terénních studiích především v situaci, kdy ptáci byli vystaveni predátorovi dlouhodobě. Scheuerlein et al. (2001) prokázali, že bramborníčci černohlaví hnízdící v teritoriu predátora mají vyšší hladiny kortikosteroidů v plasmě. Obdobně Clinchi et al. (2011) ukázali, že strnadi *Melospiza melodia* mají vyšší koncentrace glukokortikoidů, pokud byl v jejich teriroriu zaznamenán vyšší predační tlak. Některé práce (Dufty and Crandall 2005; Tilgar et al. 2010) také ukázaly, že ptačí mláďata mají zvýšené hladiny stresových hormonů poté, co jsou jim po určitou dobu přehrávány varovné hlasy. Vliv predátora na okamžitou hladinu kortikosteroidů v krvi testovali Canoine et al. (2002). Ručně odchovaní bramborníčci černohlaví byli konfrontováni se třemi stresovými zátěžemi. Výsledky ukázaly, že okamžitá (do 30 minut po pokusu) hladina kortikosteroidů v plasmě byla nejvyšší, když byli ptáci vystaveni přítomnosti živého puštíka obecného, menší když byli umístěni do klece, a ještě menší, když byli ponecháni v tmavém pytlíku.

Přes veškeré výše uvedené překážky je ale nepochybné, že využití fyziologických ukazatelů pro výzkum antipredačního chování ptáků v nejširším smyslu slova stále představuje lákavou cestu. Především by umožnilo vypořádat se se situací, kdy testovaný pták rezignuje na zřetelnou behaviorální odpověď na predační ohrožení.

2. Doklady schopnosti rozpoznávat predátory

Studujeme-li schopnost ptáků rozpoznávat predátory, musíme si především ujasnit, jak přesné rozpoznání nás zajímá. Je to stejné, jako bychom u dětí zjišťovali jejich schopnost rozpoznávat automobily. Mohou rozpoznávat automobily jako takové, automobily osobní a nákladní, osobní Volkswageny a Mercedesy, ale i Volkswageny Passat a Volkswageny Golf.

Obdobné úrovně přesnosti rozpoznávání bychom se měli pokusit vymezit i tehdy, zabýváme-li se ptáky a predátory. Jak ale bylo uvedeno v první kapitole, nemůžeme se ovšem ptát na to, zda ptáci, například „Volkswageny“ a „Mercedesy“, rozpoznávají, ale jen zda je rozlišují. Pro vymezení úrovní přesnosti rozlišování se však nabízejí dvě různá kritéria.

Na první pohled by bylo logické řídit se podobností vzhledu živočichů, jejichž rozlišování studujeme. Narazíme ovšem na problém, jak podobnost vzhledu kvantifikovat, neboť současná zoologie se touto problematikou, až na výjimky, jakou je například studium aposematismu (měření reflektance pro kvantifikaci podobnosti zbarvení - např. Cibulková et al. 2014) nebo hnízdního parazitismu (měření podobnosti vajec kukačky a hostitelů – např. Honza et al. 2014), téměř nezabývá. Navíc podobnost vzhledu nemusí být kritériem toho, zda rozlišovat či ne, pro potenciální kořist. Jak již bylo uvedeno v první kapitole, nelze předpokládat, že se testovaní ptáci budou chovat odlišně k predátorům, kteří se neliší loveckými schopnostmi ani potravními preferencemi.

Právě rozdíly v míře nebezpečnosti predátorů dané jejich loveckými schopnostmi a potravními preferencemi se tedy nabízejí jako kritérium alternativní, neboť by měly potenciální kořist k rozlišování mezi predátory motivovat. Navíc jsme schopni nebezpečnost jednotlivých druhů predátorů poměrně přesně stanovit, protože údaje o jejich způsobech lovu i potravě jsou, byť v různé kvalitě, k dispozici. Nevyhneme se ovšem opačnému problému než v případě podobnosti. Rozdíly v nebezpečnosti predátorů nemusí korelovat s nároky spojenými s jejich rozlišením. Lze nalézt velmi podobné druhy, jejichž nebezpečnost se bude významně lišit. Například z malých dravců představuje pro drobné pěvce větší nebezpečí vertebratofágní poštolka obecná než dosti podobná převážně insektivorní poštolka jižní (cf. Cramp 1979).

Je tedy zřejmé, že při hodnocení stávajících znalostí o schopnosti ptáků rozpoznávat respektive rozlišovat predátory, budeme muset zohlednit obě kritéria, tedy ptát se nakolik je rozlišování účelné i nakolik je obtížné. Omezíme se přitom na čtyři úrovně: 1) rozlišování predátorů a neškodných živočichů, 2) rozlišování pozemních a vzdušných predátorů, 3) rozlišování vzdušných predátorů dospělců a hnízd, 4) rozlišování jednotlivých druhů ptačích predátorů lišících se loveckými schopnostmi a potravními preferencemi.

2.1. Predátoři vs. neškodní ptáci a další „živočichové“

Schopnost rozlišit predátora od neškodného živočicha je nezbytným předpokladem efektivního antipredačního chování, které může podstatným způsobem zvýšit fitness napadeného jedince (Caro 2005). Není proto překvapivé, že tato schopnost byla prokázána nejen u ptáků (McLean and Rhodes 1991) či savců (McLean et al. 1996), ale i bezobratlých (např. Cannicci et al. 2001, Aizaki and Yusa 2010). Není proto překvapivé, že z celkového počtu 37 studií, které schopnost ptáků rozlišit predátory od neškodných živočichů (ale i jiných objektů) testovaly (Tab.), ji 34 v té či oné podobě prokázalo. Nejčastěji pracovaly s vizuálními stimuly, ať již s vycpaninami, živými zvířaty nebo modely (Tab.). Zájem o stimuly akustické byl mnohem menší (Bautista and Lane 2000, Bump 1986, Hakkarainen et al. 2002, Betts et al. 2005, Eggers et al. 2005, Peluc et al. 2008, Randler 2006) a olfaktorické stimuly byly z pochopitelných důvodů testovány jen výjimečně (Fluck et al. 1996, Hagelin et al. 2003, Godard et al. 2007, Amo et al. 2008, Amo et al. 2015, Gérard et al. 2015), nicméně i ony někdy s pozitivním výsledkem.

Mohlo by se tedy zdát, že je otázka schopnosti ptáků rozlišovat predátory od neškodných živočichů vcelku jednoznačně zodpovězena a nemá smysl se jí dále podrobněji zabývat. Byla by to ale pravda jen v případě, že by rozlišení predátora od neškodného živočicha bylo vždy stejně obtížné. Tak tomu ale určitě není. Obtížnost úlohy ovlivňuje nepochybně především míra odlišnosti vzhledu predátora a kontroly. Je zjevně jednodušší odlišit od holuba krahujce obecného než sojku obecnou. To ale není vše, druhou stranu problému představuje motivace k rozlišování. Ta má dvě složky, nebezpečnost predátora, danou jeho loveckými schopnostmi a potravními preferencemi, a pravděpodobnost střetu s ním, danou především jeho početností ale i biotopovými nároky. Je nepochybné, že sýkora koňadra je motivována více k rozlišování specializovaného predátora drobných ptáků, krahujce obecného než specializovaného predátora drobných savců, poštolky obecné. Obdobně je středoevropská sýkora koňadra motivována více k rozlišování běžně se vyskytující poštolky obecné než velmi vzácné poštolky rudonohé.

Pokusy prováděné s ptáky odchovanými v zajetí bez možnosti naučit se predátory rozpoznávat ukazují, že ptáci mají zřejmě určité znalosti o existenci a podobě potenciálních predátorů vrozené (Nice and Ter Pelkwyk 1941, Scaife 1976, Evans et al. 1993a, Evans et al. 1993b, Göth 2001, Zaccaroni et al. 2007, Binazzi et al. 2011, Dessborn et al. 2012, Lorenz 1939, Melzack et al. 1959, Green et al. 1968, Melvin and Cloar 1969, Mueller and Parker 1980, Moore and Mueller 1982, Canty and Gould 1995, Fluck et al. 1996). Tento závěr potvrzují i některé práce zaměřené na antipredační reakce ptáků z izolovaných ostrovů, kteří se s predátory také nikdy nesetkali (McLean et al. 1999, Maloney and McLean 1995, Peluc et al. 2008). Tyto znalosti však zřejmě nejsou příliš detailní a zpřesňují se v průběhu života individuálním (např. Griffin et al. 2001, Azevedo and Young 2006a) ale především sociálním (např. Griffin 2004, 2008, Cornell et al. 2012) učením. Dalším faktorem, který ovlivňuje schopnost ptáků rozlišovat predátory od neškodných živočichů, je tedy nepochybně individuální zkušenost.

Nejčastěji testovanými ptačími predátory byli pochopitelně dravci a sovy (Tab.). Z prvé skupiny se uplatňovali především jestřáb a poštolka obecná; z druhé pak kulíšci (*Glaucidium* spp.), výr *Bubo virginianus* and výreček *Megascops asio*. Mezi zvířaty, která sloužila jako neškodná kontrola, byla diverzita použitých druhů mnohem větší. Nejčastější volbou byli různí měkkozobí - holubi (*Columba livia f. domestica*, *C. oenas*, *C. palumbus*) i hrdličky (*Streptopelia turtur*, *S. decaocto*, *S. orientalis*), kromě nich pak byli často používáni také nejrůznější druhy drozdů (*Turdus philomelos*, *T. merula*, *T. pallidus*, *T. viscivorus*, *T. pilari*s – Tab.). Dravce i sovy charakterizuje poměrně uniformní vzhled a přítomnost nápadných, více či méně jedinečných znaků (zahnutý zobák, pařáty, nadoční kostěný val, závoj). Není tedy překvapivé, že téměř ve všech studiích testování ptáci predátory a kontrolu rozlišovali.

Druhou nejčastěji testovanou skupinou byli zástupci čeledi krkavcovitých (*Corvus cornix*, *C. corone*, *C. corax*, *C. frugilegus*, *C. brachyrhynchos*, *C. macrorhynchos*, *C. caurinus*, *Pica pica*, *Cyanocitta cristata* – Tab.), což jsou celosvětově jedni z nejvýznamnějších ptačích predátorů hnízd. Na rozdíl od dravců a sov jsou krkavcovití vzhledově poměrně variabilní a navíc jim, snad až na mohutný zobák, chybějí jedinečné charakteristické znaky. Na druhou stranu, mají jednotlivé druhy obvykle nápadné a dobře rozlišitelné zbarvení. Přestože rozpoznávání krkavcovitých představuje na prvý pohled obtížnější úkol, testovaní ptáci je dokázali odlišit nejen od kontroly, ale i jednotlivé krkavcovité mezi sebou v závislosti na jejich nebezpečnosti.

Zajímavou skupinou z hlediska rozpoznávání jsou také hnízdní parazité. Nejedná se sice o predátory, jejich dopad na fitness hostitelů je nicméně přinejmenším srovnatelný (Rothstein 1990). Hnízdní parazité nedisponují žádnými obecnými znaky, které by je odlišovaly od neškodných ptáků, jejich rozpoznávání by tedy mělo být obtížné. Navíc při něm lze jen omezeně využít individuální učení, neboť střet s parazitem a jeho následky na sebe bezprostředně nenavazují. Aktivní obrana proti hnízdnímu parazitovi může být nadto často neúčinná až kontraproduktivní, oproti tomu rozpoznání a odstranění cizího vejce je časově i energeticky nenáročné a při správném rozlišení od vlastních vajec i velmi efektivní metodou, jak se hnízdnímu parazitismu bránit (Rothstein 1990). Přesto existuje nemalé množství prací, které se problematikou rozpoznání hnízdního parazita (a ne jen jeho vajec) zabývají. Nejčastějšími druhy hnízdních parazitů, jejichž rozpoznání bylo testováno, je jednak evropská kukačka obecná a z amerických druhů pak vlhovec *Molothrus ater*.

Stávající znalosti o rozpoznávání pozemních predátorů jsou mnohem skromnější než u predátorů vzdušných (Tab.). Vcelku nepřekvapivě byli nejčastěji testováni zástupci více či méně specializovaných skupin, tedy šelem a hadů (Tab.). Ty se zásadně liší jak variabilitou svého vzhledu, tak přítomností znaků umožňujících odlišení od neškodných živočichů. Zatímco vzhled hadů je mimořádně uniformní a navíc, pomineme-li beznohé ještěry, zcela odlišný od ostatních pozemních obratlovců, šelmy jsou skupinou poměrně heterogenní a navíc jim chybí nápadné unikátní znaky, které by je jako celek odlišovali od neškodných savců.

Většina studií zaměřených na rozpoznávání šelem a hadů bohužel ve svém designu opomíjí kontrolu a o schopnosti rozpoznat predátora se zpravidla usuzuje na základě přítomnosti nebo nepřítomnosti aktivního či pasivního mobbingu (Tab.). Pokud je kontrola v pokusu použita je jí zpravidla buď neškodný ptačí druh (Dessborn et al. 2012, Patterson et al. 1980, Elliot 1985, Halupka 1999, Stenhouse et al. 2005, Leger and Carroll 1981, Nealen and Breitwisch 1997, Peluc et al. 2008, Griffin et al. 2005, Randler 2006) či neživý objekt (Azevedo and Young 2006a,b, Schaller and Emlen 1962, Göth 2001, Schetini de Azevedo et al. 2012, Knight and Temple 1988, McLean et al. 1999, Maloney and McLean 1995, Griffin et al. 2005). Pouze výjimečně sloužili jako kontrola někteří savci, a to konkrétně králík (Clode et al. 2000, Schetini de Azevedo et al. 2012, Nice and Ter Pelkwyk 1941, Murphy 2006), skot (Murphy 2006) a mravenečník (Schetini de Azevedo et al. 2012). Takovýto přístup však neumožňuje zjistit, zda testovaní ptáci skutečně rozpoznají šelmu, případně hada, či zda reagují negativně na cokoliv, co šelmu nebo hada pouze vzdáleně připomíná.

Zatímco ptačí dospělce loví ze savců téměř výlučně šelmy, hnízda, zvláště ta, která jsou umístěna na zemi, ohrožují i zástupci dalších skupin, především hlodavců, ale i hmyzožravců. Schopnost jejich rozpoznání však byla testována jen výjimečně. Konkrétně se jedná o dvě nám známé studie. Schaller and Emlen (1962) zjistili, že v zajetí odchovaná kuřata nerozpoznají nebezpečí v bílé laboratorní kryse, a Hobson et al. (1988) ukázali, že lesňáček *Setophaga petechia* útočí na vycpanou veverku *Sciurus carolinensis* umístěnou u hnízda.

V případě savců je pak také možné testovat nejen rozpoznávání predátora jako vizuálního stimulu, ale i případnou reakci ptáků na jeho pach. Takovéto studie byly prováděny buď v laboratorních podmínkách (Fluck et al. 1996, Hagelin et al. 2003, Amo et al. 2015, Gérard et al. 2015) nebo na hnízdě (Godard et al. 2007, Amo et al. 2008). Výsledky těchto prací jsou však dosti nejednoznačné. Alkouni *Aethia cristatella* se vyhýbali zápachu skunka (Hagelin et al. 2003), hýlové *Carpodacus mexicanus* pachu vačice *Didelphis marsupialis* (Amo et al. 2015) a sýkory modřinky reagovaly na pach fretky v blízkosti hnízda (Amo et al. 2008). Avšak pouze část kuřat reagovala na pach kočky (Fluck et al. 1996), buřňáci *Puffinus pacificus* se nevyhýbali pachu krysy (Gérard et al. 2015) a drozdi *Sialia sialis* se navzdory předpokladům nevyhýbali hnízdním budkám s pachem křečka *Peromyscus maniculatu*s (Godard et al. 2007).

Jak již bylo zmíněno, schopnosti rozpoznávat predátory se u ptáků přinejmenším zdokonalují učením (Griffin 2004). Přesto existuje jen minimum studií, ve kterých by shodní predátoři byli předloženi naivním a zkušeným jedincům téhož druhu. V naprosté většině jde o práce zkoumající schopnost různé drůbeže (kuři, kachny, krocani) rozpoznávat predátora v dravčí siluetě (review Schleidt et al. 2011). Tyto studie však vždy srovnávali ptáky odchované v uzavřených místnostech s ptáky z venkovních voliér, jejichž zkušenosti s predátory byly přinejlepším velmi omezené. Jedinou nám známou prací, kde byly srovnávány reakce ptáků odchovaných v zajetí s ptáky odchycenými ve volné přírodě, je studie Kullberg and Lind

(2002). V ní byla zkoumána schopnost sýkor rozlišovat mezi vycpaným krahujcem a koroptví. Zatímco naivní jedinci ve věku 30 dní reagovaly na obě vycpaniny stejně, v přírodě odchycené (asi 4 měsíce staré) sýkory již mezi nimi rozlišovaly.

Do určité míry nám o významu učení při rozlišování mezi predátorem a nepredátorem mohou napovědět pokusy prováděné na ptácích, kteří žijí dlouhodobě bez kontaktu s predátory, nejčastěji na izolovaných ostrovech. Bylo například zjištěno, že lejsčík *Petroica australis* žijící na malém ostrůvku nedokáže rozlišit mezi lasicí a papírovou krabicí stejné velikosti. Oproti tomu lejsčíci z hlavních novozélandských ostrovů, kde se lasice běžně vyskytují, reagovali na předkládané stimuly odlišně (Maloney and McLean 1995).

Naivní ptáci, ovšem bez srovnání s ptáky zkušenými, byli použiti i v řadě dalších studií. Konkrétně se jednalo o kura domácího (Scaife 1976, Schaller and Emlen 1962), nandu *Rhea americana* (Azevedo and Young 2006a,b; Schetini de Azevedo et al. 2012), tabona *Alectura lathami* (Göth 2001), kachnu divokou (Dessborn et al. 2012) a křepela *Colinus virginianus* (Melvin and Cloar 1969). Výsledky těchto studií jsou však nejednoznačné. Kuřata se bála poštolky (Scaife 1976), ale ne výrečka z rodu *Megascopus* (Schaller and Emlen 1962). Nandu nerozlišoval mezi kontrolou a různými druhy savčích predátorů (Azevedo and Young 2006a,b; Schetini de Azevedo et al. 2012). Oproti tomu kachny a křepelové predátory rozpoznávali (Dessborn et al. 2012, Melvin and Cloar 1969). Z testovaných druhů byli v rozpoznávání predátorů nejlepší taboni. Ti nejenže rozlišovali mezi predátorem a neškodným objektem, ale na jednotlivé druhy predátorů reagovali specificky podle druhu nebezpečí, které představovaly (Göth 2001). Důvod jejich úspěšnosti bez jakékoliv předchozí zkušenosti je nepochybně třeba hledat v osobitém způsobu rozmnožování tabonů. Ti jsou extrémně precociální, ihned po vylíhnutí se musí spoléhat pouze na své vrozené schopnosti a na rozdíl od jiných druhů ptáků nemohou počítat s ochranou od rodičů či možností učit se od nich.

Kromě volby testovaného druhu a jeho zkušeností může výsledek experimentu významným způsobem ovlivnit i použitá kontrola. Jako nejjistější se jeví použití hojného neškodného zvířete (ptáka) velikostí srovnatelného s testovanými predátory. V takovém případě se snižuje riziko, že prezentovaná kontrola bude u testovaného zvířete vyvolávat strach ať už z důvodu nepřiměřené velikosti či například neofobie.

Relativně časté (Tab.) je využití takzvané prázdné kontroly. Reakce na predátora se pak v takovém případě srovnává s chováním ptáka v nepřítomnosti jakéhokoliv stimulu. Takovéto experimentální uspořádání však není úplně optimální a neumožňuje vyloučit generalizovanou antipredační odpověď na jakéhokoliv „vetřelce“, což nepochybně snižuje výpovědní hodnotu takovýchto experimentů.

Jako problematické se také jeví použití neživých, obvykle umělých objektů. V případě dravčích siluet slouží jako kontrola různé geometrické tvary odpovídající velikosti (Krätzig 1940, Nice and Ter Pelkwyk 1941, Schleidt et al. 2011). V ostatních pokusech pak byly jako kontrola použity nejrůznější předměty: plastová láhev (Fransson and Weber 1997, McLean et al. 1999, Maloney and McLean 1995, Gentle and Gosler 2001), papírové či plastové krabičky (Knight and Temple 1988, Maloney and McLean 1995, Griffin et al. 2005), židle (Azevedo and Young 2006a,b; Schetini de Azevedo et al. 2012), papírové geometrické tvary (Göth 2001), dřevěný hranol (Baker and Becker 2002) či dětská hračka (Hinde 1960). Hrozí zde dvojí nebezpečí. Objekty mohou být pro testované ptáky zcela nezajímavé a ti na ně budou reagovat méně než by reagovali na neškodného ptáka. Nelze však ani vyloučit, že nový nápadný objekt, především je-li umístěný v blízkosti hnízda, vyvolá neofobní reakci. Sordahl (2009) zjistil, že k neznámým předmětům umístěným v blízkosti hnízda ptáci přistupovali s jistou mírou obezřetnosti, nicméně nikdy na ně neútočili a jejich přítomnost nebránila hnízdícímu páru v návštěvě hnízda.

Zajímavou, avšak nepříliš využívanou, možností je použití neškodného, avšak pro testované ptáky neznámého (ptačího) druhu (Tab.). Takovouto formu kontroly použili ve své studii například Welbergen a Davies (2009), kteří rákosníku obecnému prezentovali vycpanou kukačku a stejně velký model “generalizovaného“ papouška (tmavě zelená svrchní a světle zelená spodní část těla). Veen et al. (2000) pak ve své práci na rákosníku *Acrocephalus sechellensis* použili jako kontrolu vycpaninu sýkory koňadry, což je sice existující pták, ale testovaní rákosníci neměli nikdy možnost se s ní setkat. Pokud by testování ptáci v těchto studiích reagovali obdobným antipredačním chováním na predátora i na kontrolu, naznačovalo by to, že rozlišují nejen predátory od neškodných živočichů ale i neznámé živočichy od známých. Kategorie predátorů či lépe řečeno nebezpečných živočichů by pak byla vymezena nikoliv pozitivně (ti co jsou nebezpeční) ale negativně (ti co nejsou neškodní). Žádný takový efekt se však v dosud prováděných studiích nepotvrdil a zdá se, že ptáci mají spíše obecnou představu, čeho se mají bát, a neznámé stimuly spíše ignorují.

2.2. Pozemní vs. vzdušní predátoři

Jak již bylo uvedeno, soustředilo se studium schopnosti rozpoznávat predátory především na predátory ptačí. Z toho plyne, že se jen nevelké množství prací zabývalo rozlišováním predátorů vzdušných a pozemních (Tab.), přičemž se převážně jednalo o experimentální studie. Nejčastější byla srovnávána reakce na dravé ptáky a šelmy. Experimenty probíhaly v laboratorních podmínkách (Evans et al. 1993a, Göth 2001, Zaccaroni et al. 2007, Binazzi et al. 2010, Sieving et al. 2010, Dessborn et al. 2012, Schetini de Azevedo et al. 2012), nebo na hnízdě (Brown and Hoogland 1986, Knight and Temple 1988, Halupka 1999, Arroyo et al 2001, Kleindorfer et al. 2005), ale i v terénu (Naguib et al. 1999, Rainey et al. 2004, Yorzinski and Vehrenkamp 2009). Nečetné práce pak testovaly schopnost rozlišovat mezi šelmou a krkavcovitými ptáky či racky (Elliot 1985, Bureš and Pavel 2003, Stenhouse et al. 2005), jedna mezi dravcem a hadem (Kleindorfer et al. 1996) a jedna dokonce mezi vránou a hadem (Suzuki 2011). Výsledky těchto studií, až na některé výjimky (Brown and Hoogland 1986, Schetini de Azevedo et al. 2012) potvrzují schopnost testovaných ptáků vzdušné a pozemní predátory rozlišovat. Ve shodě s experimentálními studiemi jsou i studie observační (Byrkjedal 1987, Brunton 1990, Jacobsen and Ugelvik 1992, Amat and Masero 2004, Sordahl 2004, Murphy 2006).

Nejvíce důkazů o schopnosti ptáků rozlišovat mezi pozemním a vzdušným predátorem ale poskytují analýzy varovných hlasů (Evans et al. 1993a, Knight and Temple 1988, Stone and Trost 1991, Suzuki 2011, Naguib et al. 1999, Rainey et al. 2004). Opakovaně v nich bylo prokázáno, že varování na tyto dva typy predátorů se od sebe liší. Ptáci v přítomnosti vzdušných a pozemních predátorů buď produkují varovné hlasy s různou intenzitou (Evans et al. 1993a Naguib et al. 1999, Rainey et al. 2004) či délkou (Stone and Trost 1991), případně používají varovné hlasy naprosto odlišné (Knight and Temple 1988, Suzuki 2011).

Otázkou však je, zda ptáci skutečně rozlišují konkrétní predátory z těchto kategorií nebo pouze směr hrozícího nebezpečí. Metodika většiny studií zabývajících se rozpoznáváním vzdušných a pozemních predátorů neumožňuje obě možné příčiny rozdílu v reakci odlišit, neboť současně testuje obě možnosti. Vzdušný predátor bývá zpravidla buď prezentován jen jako letící silueta nebo je umístěn na vyvýšeném posedu. Oproti tomu pozemní predátoři jsou z logiky věci vždy umístěni na zemi. Hypotézu, že reakce závisí spíše na směru, odkud nebezpečí přichází, než na druhu predátora, podpořila již jedna z prvních studií na toto téma (Gyger et al. 1987), která analyzovala vokalizace kohoutů kura domácího chovaných ve venkovních voliérách. V této práci byla sledována reakce na nejrůznější přirozeně se vyskytující objekty v okolí voliéry. „Ground alarm calls“ byly typickou reakcí na jakékoliv objekty pohybující se po zemi, zatímco objekty pohybující se ve vzduchu vyvolávaly produkci „aerial alarm calls“.

Zajímavé jsou i výsledky Kleindorfer et al. (2005), kteří zjistili, že reakce tří blízce příbuzných druhů rákosníků (*Acrocephalu. melanopogon*, *A. scirpaceus* and *A. arundinaceus*) závisí na pozici vlastního hnízda. Páry, které měli hnízdo nízko nad zemí, vykazovali silnější reakci vůči pozemním predátorům (had; hranostaj). Oproti tomu ptáci s vysoko umístěnými hnízdy byli agresivnější vůči vzdušnému predátorovi (pochop rákosní). Autoři z toho ovšem vyvozují, že ptáci pozemní a vzdušné predátory nejen rozlišují, ale že ve své reakci zohledňují jejich aktuální nebezpečnost.

Potenciální zdroj chybných interpretací skrývá také identifikace varovných hlasů. Palleroni et al. (2005) ukazují, že rozdělení varovných hlasů na „ground“ a „aerial“, může být do značné míry umělé a že ve skutečnosti tato varování možná kódují mnohem více informací, než jen směr nebezpečí. Samci i samice kura domácího v jeho experimentech produkovali „aerial alarm calls“ častěji v reakci na velkého dravce, zatímco „ground alarm calls“ reagovali spíše na menšího dravce. K obdobným výsledkům dospěli Templeton et al. (2005), kteří testovali hlasovou reakci sýkor *Poecile atricapilla* na různě velké vzdušné i pozemní predátory. Varování na jednotlivé predátory se průkazně lišila počtem slabik, vysvětlující proměnnou však nebyl typ predátora, ale pouze jeho velikost.

2.3. Predátoři hnízd vs. predátoři dospělců

Rozlišování ptačích predátorů hnízd od ptačích predátorů dospělců bylo studováno mnohem častěji než rozlišování predátorů vzdušných a pozemních. Důvodem zřejmě je, že se jedná o schopnost, která může podstatnou měrou zvýšit fitness hnízdících ptáků a byla proto v popředí zájmu behaviorální ekologie (Tab.). Dravci a sovy obvykle představují nebezpečí především pro rodiče nebo vyvedená mláďata, zatímco vejce a mláďata na hnízdě ohrožují z ptačích predátorů zejména krkavcovití, a, hlavně u ptáků hnízdících v dutinách, také datlovití. Zástupci obou skupin byly proto také nejčastěji používáni v experimentech.

Ve shodě s předpoklady o výhodnosti rozlišování predátorů hnízd a dospělců jsou výsledky observačních i experimentálních studií (Tab.). Ptáci na specializované predátory hnízd obvykle reagují intenzivněji. Projevuje se to tak, že je napadají častěji či s větší agresivitou (Strnad et al. 2012, Ash 1970, Curio 1975, Gottfried 1979, Patterson et al. 1980, Elliot 1985, Halupka 1999, Hogstad 2005, Nijman 2004, Sordahl 2004). Menší nebezpečí, které od specializovaných predátorů hnízd hrozí dospělým ptákům, se projevuje větší ochotou riskovat. Bránící ptáci se přibližují na menší vzdálenost (Curio and Onnebrink 1995) či zůstávají v blízkosti hnízda (Amat and Masero 2004). Je-li však odpovědí na přítomnost predátora snaha neupozornit na blízkost hnízda, chovají se ptáci vůči predátorům hnízd opatrněji, například výrazně snižují frekvenci krmení (Ghalambor and Martin 2000).

Silnější reakce na specializované predátory hnízd ale nemusí charakterizovat všechny ptačí druhy. Podle studie Ghalambor and Martin (2000) intenzita reakce závisí na life-history testovaných druhů. V jejich experimentech reagoval na predátora hnízd střízlíka *Troglodytes aedon* silněji jen brhlík *Sitta carolinensis*, zatímco v průměru déle žijící druh *Sitta canadensis* se choval opatrněji v přítomnosti predátora dospělců (krahujec *Accipiter striatus*). Důležitým dokladem rozlišování predátorů hnízd od predátorů dospělců jsou také změny v intenzitě obrany v průběhu hnízdění. Predátoři hnízd ohrožují snůšky od samého počátku a intenzita obrany vůči nim zůstává po celou dobu hnízdění stejná (Green et al. 1990). Oproti tomu predátoři dospělců ohrožují především vyvedená mláďata a intenzita obrany vůči nim v průběhu hnízdění vzrůstá (Green et al. 1990, Patterson et al. 1980, Halupka and Halupka 1997).

Specifickou skupinu „predátorů“ hnízd představují hnízdní parazité. Od ostatních se odlišují zejména tím, že jsou nebezpeční pouze v krátké časné fázi hnízdění. To by se mělo odrazit v odpovídajícím načasování antipredačního chování. Testováno bylo především rozpoznávání vlhovce *Molothrus ater* (Robertson and Norman 1977, Smith et al. 1984, Folkers and Lowther 1985, Briskie and Sealy 1989, Hobson and Sealy 1989, Mark and Stutchbury 1994, Gill et al. 1997, Nice and Ter Pelkwyk 1941, Neudorf and Sealy 1992, Bazin and Sealy 1993, Gill and Sealy 1996, Burhans 2001, Gill and Sealy 2004, D’Orazio and Neudorf 2008), ale i různých druhů tropických kukaček (*Urodynamis taitensis* - McLean 1987, *Chrysococcyx lucidus* - Langmore et al. 2012, *Clamator glandarius* - Avilés and Parejo 2006, *Surniculus lugubris* - Duckworth 1997). Ve všech výše zmíněných pracích dokázali testovaní ptáci hnízdního parazita rozpoznat a odpovídajícím způsobem na něj reagovat, což není zas tak překvapivé, vzhledem k tomu, že šlo o druhy dobře odlišitelné od predátorů či neškodných ptáků sloužících jako kontrola.

Zcela osobitou problematikou je, také hojně testované, rozpoznávání kukačky obecné. V mnoha případech bylo sice zjišťováno pouze to, zda na ni ptáci reagují (Edwards et al. 1950, Moksnes et al. 1990, Bártol et al. 2002, Honza et al. 2006, Welbergen and Davies 2009) či její rozlišení od nápadně odlišného predátora (Campobello and Sealy 2010, Yang et al. 2014). Kromě toho však byla velká pozornost věnována pravděpodobně nenáhodné podobnosti její šedé morfy s krahujcem obecným, která je stejná pro lidské i ptačí vidění (Stoddard 2012). Shoda zbarvení obou druhů je tak velká, že bývá kukačka považována za mimika krahujce („cuckoo-hawk mimicry hypothesis“ - Welbergen and Davies 2008). I přes relativně malé rozdíly ve vzhledu jsou schopni kukačku a krahujce rozlišovat rákosník velký (Trnka and Prokop 2012), rákosník obecný (Duckworth 1991, Welbergen and Davies 2008, Welbergen and Davies 2011, Thorogood and Davies 2012), ťuhýk obecný (Ash 1970) či budníček větší (Edwards et al. 1950). Zajímavé srovnání pak přinášejí práce testující ptáky, kteří nejsou hostiteli kukačky. Tyto práce zjistily, že ani sýkory (Davies and Welbergen 2008) ani vrabci (Trnka et al. 2015) nejsou schopni šedou morfu kukačky a krahujce odlišit a na oba reagují se shodnou mírou strachu. Tyto výsledky jsou tedy přesvědčivým důkazem, že se ptáci mohou naučit rozlišovat i velmi podobné nepřátele, pokud k tomu mají dostatečnou motivaci.

2.4. Různé druhy predátorů z téže ekologické gildy

Počet prací studující schopnost ptáků rozlišovat jednotlivé druhy predátorů z téže ekologické gildy není úplně malý (Tab.), nemají však shodnou výpovědní hodnotu, neboť rozlišení v nich předkládaných nebo pozorovaných predátorů je různě náročné. Řada studií porovnává reakce na predátory lišící se navzájem velikostí (Tab.). Ti obvykle představují pro určitou potenciální kořist i odlišnou míru ohrožení. Každý predátor preferuje kořist optimální velikosti, kterou nejefektivněji loví a zpracovává. Zvláště v případě ptačích predátorů optimální velikost kořisti do značné míry určuje jejich vlastní velikost. Možnost separovat takto potravní niky bývá dokonce považována za příčinu výrazného velikostního pohlavního dimorfismu (Kruger 2005), například u některých zástupců rodů *Accipiter* či *Falco.*

Pak se ovšem nabízí možnost, že testovaní ptáci nerozlišují jednotlivé druhy predátorů, ale právě jen jejich velikost. Platí to zejména pro všechny studie zaměřené na variabilitu varovných hlasů, především sýkor. Již Apel (1985) zjistil, že prezentace atrapy of krahujce *Accipiter striatus* vyvolává u sýkory *Poeciele atricapilla* rychlejší varování než atrapy větších predátorů. Toto zjištění bylo následně potvrzeno a rozvedeno v několika voliérových studiích s tímto druhem (Templeton et al. 2005), ale i dalšími severoamerickými sýkorami (*Poecile carolinensis* - Soard and Ritchison 2009, *Baeolophus bicolor* - Courter and Ritchison 2010). Sýkory reagovaly na prezentované predátory různých velikostních kategorií varováním “chick-a-dee“ s různým počtem a typem slabik. Větší, pro drobné pěvce méně nebezpeční dravci, jako například káně *Buteo jamaicensis* vyvolávali varování s větším počtem úvodních “chick“ slabik a menším počtem slabik „dee“, zatímco menší a pro drobné ptáky tedy nebezpečnější ptačí predátoři (např. výreček *Megascops asio*) vyvolávaly varování s malým počtem nebo zcela bez slabik „chick“ avšak s průkazně větším počtem „dee“ slabik (Soard and Ritchison 2009, Courter and Ritchison 2010). Jednoznačné doklady o rozdílných reakcích na predátory shodné velikosti nicméně tyto studie nepřinášejí. Nezdá se tedy, že by varování amerických sýkor přinášelo informace přímo o druhu jimi objeveného predátora.

Podobně nejednoznačné se zdají být i některé experimenty zaměřené na širší okruh reakcí testovaných ptáků. Curio et al. (1983) umisťoval různé živé dravce k hnízdním dutinám sýkor koňader. Mobbing na jednotlivé druhy se lišil minimální vzdáleností, na kterou se sýkory odvážily přiblížit. Nejdál se sýkory držely od krahujce obecného, naopak nejblíže se odvážili přiblížit k puštíku obecnému. Sýkory tedy byly přinejmenším schopny rozlišit dravce od sovy. To je ovšem jednodušší než rozlišit mezi dvěma druhy dravců či sov, neboť není třeba využít druhově specifické znaky, například zbarvení. Sovy jako skupina se od dravců liší celkovým tvarem těla, polohou očí či závojem okolo nich. Schopnost rozlišit dravce a sovy byla prokázána také u sýkory lužní (Kullberg 1998) a americké *Baelophus bicolor* (Sieving et al. 2010) či sojky zlověstné (Griesser 2009). Studie Curio et al. (1983) nicméně také dokládá, že sýkory koňadry reagují odlišně i na dva různé druhy sov. Zatímco k již zmiňovanému puštíku obecnému se odvážily relativně blízko, větší odstup si udržovaly od kulíška nejmenšího. Puštík obecný není výrazně větší než krahujec obecný, oproti tomu kulíšek je nejmenší středoevropský predátor ptáků a jeho nebezpečnost by tak mohla být podceněna. Na rozdíl od puštíka je ovšem kulíšek specializovaným predátorem drobných ptáků, čemuž odpovídá i opatrné chování sýkor.

Schopnost rozlišovat dravce či sovy, lišící se navzájem svou velikostí a zároveň i nebezpečností pro testovaný druh, byla prokázána nejen u různých ptačích druhů, ale i v různých kontextech. Stejně jako výše zmiňované sýkory, reagovaly i sojky zlověstné odlišnou intenzitou mobbingu na atrapy různě nebezpečných dravců a sov umístěných u krmítek Griesser (2009). Několik dalších prací pak přináší stejná zjištění pro různé ptačí druhy studované v terénu a to jak pomocí prezentace atrap (Miller 1952, Altmann 1956, Nocera and Ratcliffe 2009), tak i pouze na základě pozorování spontánních střetů s predátory (Buitron 1983, Winkler 1992). Schopnost rozlišovat zbarvením podobné dravce lišící se nápadně pouze velikostí byla potvrzena i v pokusech s v zajetí odchovanými ptáky (Palleroni et al. 2005). V této studii tři cvičení zástupci rodu *Accipiter*, z různých velikostní kategorií (malý *Accipiter striatus*; středně velký *Accipiter cooperii* a velký *Accipiter gentilis*) přelétali nad výběhem s volně se pohybujícími slepicemi. Silnější reakce, přikrčení se k zemi, se objevovala nejčastěji v přítomnosti velkého dravce, zatímco projev ostražitosti, vzpřímený postoj a načepýření se, byl častější odpovědí na přelet malého dravce. V přítomnosti středně velkého dravce slepice zaujímaly přechodnou pozici. Intenzitu reakce ovlivňovalo to, zda měly v době pokusu kuřata. Kvočny hlídající kuřata byly celkově agresivnější, především pak vůči menším dravcům.

Velmi zajímavé výsledky poskytují také experimenty se siluetami letících dravců. Podstoupili je jak domácí kuři (Evans et al. 1993b) tak i v přírodě odchycení ptáci, konkrétně sýkory modřinky (Klump and Curio 1983) and sýkory lužní (Alatalo and Helle 1990). Oproti experimentům s vycpaninami, respektive živými ptáky, zmíněnými výše, reagovali testovaní ptáci na větší siluety většinou intenzivněji než na menší, konkrétně snížením pohybu a naopak zvýšením frekvence či intenzity varovných hlasů. Autoři to vysvětlují tím, že velikost poskytovala testovaným ptákům informaci o výšce letu prezentovaného dravce. Větší silueta tedy vyvolávala větší strach, protože představovala dravce nízko letícího a pro potencionální kořist nebezpečnějšího. Opačný výsledek přinesla pouze studie Alatalo and Helle (1990), ve které sýkory více varovaly při simulovaném přeletu menší siluety. Autoři tento výsledek vysvětlují tím, že varování je riskantní a proto v případě vysokého stupně nebezpečí jsou sýkory raději zticha a varují, jen když je riziko upozornění na sebe nižší.

Obojí interpretace vyhlíží přesvědčivě, nicméně vede k otázce, proč ve všech výše popsaných pokusech s atrapami, popřípadě živými dravci, testovaní ptáci reagovali na rozdíly ve skutečné velikosti. Odpověď se nabízí dvojí. V pokusech s atrapami mohli ptáci rozlišovat druhy a nikoliv jen velikost predátorů. Proti tomu hovoří jejich mimořádná podobnost. Druhá možná odpověď je zajímavější. Siluety nenabízejí testovaným ptákům žádný jiný znak než velikost, nelze tedy jednoduše zjistit, zda se liší druhovou příslušností, velikostí nebo výškou letu. Potenciální kořist tak z velikosti siluety usuzuje pouze na třetí z možností, což je zřejmě za daných okolností nejjistější parametr pro odhad aktuální nebezpečnosti. Pokud by byly atrapy opatřeny například očima či zobákem nebo pařáty, mohla by jejich obdobně (ne)snadná rozlišitelnost poskytnout informaci o tom, že se pohybují v obdobné výšce a liší se velikostí. Takový předpoklad podporuje studie Grubb (1977), který sledoval reakci lysky *Fulica americana* na různé přirozeně se vyskytující dravce (*Buteo lineatus*, *Haliaeetus leucocephalus*, *Pandion haliaetus*). Přestože dravci létali v různých vzdálenostech a výškách, lysky se bály pouze orla *Haliaeetus leucocephalus*, což je dle autora známý predátor vodních ptáků. Ostatní dravci (včetně letadel) žádný strach nevyvolávali.

I poté, co vyřadíme studie testující rozlišování různě velkých predátorů, zůstává několik dokladů schopnosti rozpoznávat jednotlivé druhy lišící se pouze zbarvením, popřípadě i dalšími druhově unikátními znaky. Asi jako první toto ukázal ve své práci Edwards et al. (1950), který zjistil, že budníček větší reaguje odlišnou intenzitou mobbingu na atrapy dvou stejně velkých, ale různě nebezpečných dravců (krahujec, poštolka), umístěné u jeho hnízda. Schopnost rozlišit tyto dva velikostí se téměř nelišící, ale různé nebezpečí představující dravce byla opakovaně prokázána i v novějších studiích. Ťuhýci (Strnad et al. 2012) i sýkory (Tvardíková and Fuchs 2011, 2012) se vůči nebezpečnějšímu krahujci (specializovanému predátoru drobných ptáků) chovali mnohem opatrněji než vůči poštolce (lovící převážně drobné savce). Přitom výsledky experimentů jednoznačně dokládají, že v obou druzích jak ťuhýci, tak sýkory rozpoznávají predátory.

Další doklady přinášejí studie observační. Tři druhy čejek, které sledoval Walters (1990), vesměs ignorovaly kondory a luňáky a reagovaly na ně jen, když se přiblížili ke kuřatům. Silněji pak reagovaly na karanče, sokoly a krahujcovité dravce, kteří jsou jejich častými predátory. Mimořádnou výpovědní hodnotu mělo chování *Vanellus chilensis*, které úplně ignorovaly rybožravého specialistu *Busarellus nigricollis*, ale na jiné velké dravce (*Buteo albicaudatus*, *B. magnirostris*, *Buteogallus urubitinga*) reagovaly.

3. Vodítka užívaná pro rozpoznání predátorů

Předchozí kapitola přesvědčivě dokládá, že je schopnost rozpoznávat predátory mezi ptáky široce rozšířená a zahrnuje nejen rozlišení predátorů od neškodných živočichů, ale také vzájemné rozlišení jednotlivých skupin a druhů predátorů mezi sebou. To nás přivádí k otázce, jaká vodítka ptáci pro rozpoznávání využívají.

3.1. Nemanipulativní studie

Studie testující schopnost ptáků predátory rozpoznávat, diskutované v předchozí kapitole, nám mohou při hledání odpovědi pomoci jen málo. Ze vzhledu testovaných predátorů a neškodných živočichů použitých jako kontrola se nicméně můžeme pokusit stanovit, které jejich odlišnosti (potenciální rozlišovací znaky) jsou pro rozpoznávání k dispozici a měli bychom proto na ně zaměřit svou pozornost.

Zanedbatelný užitek přinášejí studie testující rozlišování zástupců různých tříd (viz kapitola 1), především pozemních a vzdušných predátorů. Jejich odlišnost je tak velká, že pro rozpoznání může být využito cokoliv, počínaje tělním plánem či pokryvem těla a konče různými znaky lokálními (čenich vs. zobák aj.).

Nejvýznamnějšími a také nejčastěji testovanými ptačími predátory dospělců jsou dravci a sovy. Obě skupiny jsou vzhledově poměrně uniformní. Mají obdobné tělesné proporce (poměrně velká hlava, krk kratší než ocas a krátké nohy) a charakterizuje je i několik poměrně nápadných lokálních znaků (kratší ale silný, hákovitě zahnutý zobák; silné nohy s dlouhými drápy). U sov je navíc doplňují dopředu směřující velké oči se závojem, zatímco u dravců méně nápadný kostěný nadoční hřeben. Všechny tyto znaky mohou být použity k rozlišování zástupců obou skupin od neškodných ptáků, které bylo doloženo celou řadou studií (viz kapitola 2.1.). To ovšem neznamená, že by testovaní ptáci nemohli ve většině z nich použít i znaky jiné, charakteristické pro jednotlivé druhy, především zbarvení. Tato možnost je vyloučena pouze u takových druhů predátorů, se kterými testovaní ptáci nemohli mít předchozí zkušenost. Pro testovaný druh (ťuhýk obecný) nepochybně neznámý luňák rodu *Aviceda* byl ale použit pouze v dosud nepublikované studii Němec et al. (2015). Její výsledky navíc naopak ukazují, že obecné dravčí znaky agresivitu ťuhýků nespouštějí, neboť na luňáka na rozdíl od známých dravců nereagovali.

Určitý doklad toho, že ptáci skutečně obecné znaky dravců pro rozpoznávání využívají, nicméně poskytují studie testující rozlišování krahujce a šedé formy kukačky obecné. Velikostí, tělesnými proporcemi (dlouhý ocas) i zbarvením (vlnkované břicho, žluté oko) se oba druhy téměř neliší. Pokud je přesto testovaní ptáci rozlišovali (viz kapitola 2.3.), mohli k tomu využít nejspíše nápadně odlišný tvar zobáku, popřípadě odlišnou délku a sílu pařátů.

Mnohem méně uniformní vzhled než dravci a sovy mají ptačí predátoři hnízd a to i tehdy, omezíme-li se na nejčastěji testovanou skupinu krkavcovité pěvce. Pomineme-li více méně uniformně černě zbarvené druhy (v Evropě většina zástupců rodu *Corvus*), mohli bychom za společný znak, kromě (v rámci pěvců) nadprůměrné velikosti, považovat jen silný, rovný zobák. Předpokládali bychom tedy, že jejich odlišení (jako skupiny) od neškodných druhů (např. holubů a hrdliček) představuje poměrně obtížnou úlohu. Přesto existuje nepřímý doklad, že jsou toho ptáci schopni. Ťuhýci testovaní v studii Němec a Fuchs (2014), útočili vedle sojky i na jiného drobnějšího zástupce krkavcovitých, ořešníka obecného. Tento druh prakticky nepreduje hnízda (Cramp 1979). Lze proto stěží předpokládat, že polovina testovaných párů, která na něj útočila, s ním měla negativní zkušenost. Pravděpodobnější je, že jej vyhodnotila jako potenciální nebezpečí, přičemž vodítkem jim mohl být jeho relativně mohutný zobák.

Nejjednodušším znakem odlišujícím jednotlivé druhy dravců a sov je nepochybně velikost. Tou se lišila většina predátorů použitých při dešifrování informací sdělovaných ve varovných hlasech sýkor (Tab.). Opět ale nelze vyloučit, že je testovaní ptáci nebyli schopni rozlišovat i na základě dalších znaků. Tak by tomu bylo pouze v případě, že by reagovali shodně na obdobně velké druhy lišící však významně svoji nebezpečností, například z důvodů odlišných potravních preferencí, což ovšem prokázáno nebylo (viz kapitola 2.4.). Velikostí se lišili i zástupci rodu *Accipiter* použití ve studii Palleroni et al. (2005). Ani v jejich případě sice nelze opět použití jiných znaků pro rozlišení vyloučit, jeví se však na prvý pohled jako málo pravděpodobné, neboť zbarvení všech použitých druhů je podobné.

Pouze velikost zřejmě rozhodovala o chování ťuhýků obecných k potenciálním hnízdním predátorům z rodu *Corvus* (Němec a Fuchs 2014), ke kterým se na rozdíl od sojky a ořešníka chovali zcela pasivně. Ti se od všech tří použitých zástupců rodu *Corvus* liší výrazně menší velikostí a tím pádem i větší nadějí na úspěch při útoku na ně. Navíc největší opatrnost projevovali ťuhýci vůči největšímu krkavci. Zajímavé je i to, že oba menší druhy se liší nebezpečností pro vejce respektive mláďata. Zatímco vrána je (stejně jako krkavec) významným predátorem hnízd (Cramp 1979), havran je vyhledává pouze výjimečně (Cramp 1979). To by opět podporovalo předpoklad, že o chování ťuhýků rozhodovala pouze velikost predátorů. Starého havrana lze přitom od vrány, přes uniformní černé zbarvení, odlišit podle lysého kořene zobáku.

Prací testujících schopnost ptáků rozlišovat mezi druhy z téhož taxonu, obdobné velikosti, lišícími se pouze zbarvením, existuje poměrně málo (viz kapitola 2.4.). Asi nejjednoznačnějším případem je rozlišování poštolky a krahujce, které bylo prokázáno jak u sýkor v krmítkových experimentech (Tvardíková a Fuchs 2011, 2012), tak u ťuhýků obecných (Strnad et al. 2012) a budníčků větších Edwards et al. (1950) při obraně hnízda. Tyto druhy mají obdobné tělesné proporce i velikost a nesou typické společné znaky naprosté většiny dravců (zahnutý zobák, pařáty s dlouhými drápy, kostěný val nad očima). Je proto evidentní, že k jejich rozlišení museli testovaní ptáci použít zbarvení. Otázkou ale zůstává jakým způsobem. Poštolka a krahujec se liší celou řadou dílčích prvků zbarvení a to jak barevnými odstíny (např. hnědá vs. šedivá svrchní strana těla), tak i ornamenty (např. podélné stříkance vs. příčné vlnkovaní na prsou a břiše). Odlišnou barvu mají i oči (šedohnědé vs. žluté) a nohy (růžové vs. žluté). Jednotlivé prvky jsou více (např. barva očí) či méně (např. zbarvení svrchní strany těla) nápadné.

Ptáci mohou zbarvení vnímat jako celek, tj. všechny jeho prvky jako více méně rovnocenné, nebo se mohou soustředit jen na jediný nápadný a pro daného predátora unikátní prvek. Tyto možnosti představují jen krajní body gradientu a lze předpokládat, že při rozpoznávání bude obvykle využito více prvků zbarvení než jeden, nikoliv však všechny. Navíc všem sledovaným prvkům nemusí být nepřisouzena stejná důležitost. Důležitou roli bude zřejmě hrát jejich nápadnost a unikátnost pro daný druh predátora.

Například pro rozpoznání krahujce bude nepochybně mít mimořádný význam příčné vlnkování prsou a břicha. Jedná se o prvek nápadný (kontrastní, zaujímající velkou plochu, dobře viditelný u letícího i sedícího ptáka) a unikátní (pomineme-li příbuzného ale mnohem většího jestřába, který je také specializovaným predátorem ptáků, šedou formu kukačky a pěnici vlašskou). Je ovšem otázka, zda by po odstranění vlnkování ptáci krahujce nerozpoznali, nebo zda by naopak po přidání vlnkovaní rozpoznali krahujce v poštolce nebo i zcela neškodném ptačím druhu (například v hrdličce).

3.2. Manipulativní studie

Pokud chceme zjistit, jak „nabídku“ rozpoznávacích znaků testovaní ptáci využívají, musíme s jednotlivými prvky zbarvení predátorů ale i s jejich kombinacemi (včetně dalších znaků) manipulovat. Manipulace může zahrnovat odstranění prvku (např. skvrněni u poštolky nebo vlnkování u krahujce), nebo jeho nahrazení znakem neškodného ptáka (například žluté oko krahujce červeným okem holuba). Manipulovat lze ovšem i jiné znaky než zbarvení, např. dravčí zobák či pařáty, nebo velikost.

Odstraněním potenciálního rozpoznávacího znaku testujeme, zda je pro rozpoznání nezbytný. Pokud testovaní ptáci v takto připraveném stimulu rozpoznají nemodifikovaného predátora (např. krahujce), tj. pokud na něj reagují obdobně intenzivním antipredačním chováním (viz kapitola 1.), není manipulovaný znak pro rozpoznání konkrétního druhu predátora nezbytný. Obdobně, pokud testovaní ptáci v stimulu rozpoznají predátora, tj. pokud na něj reagují intenzivnějším antipredačním chováním než na neškodnou kontrolu (viz kapitola 1.), není manipulovaný znak nezbytný ani pro rozpoznání obecnější kategorie predátorů (např. dravců).

V případě, že potenciální rozpoznávací znak přidáváme na atrapu neškodného ptáka (např. výměnou zobáku či oka holuba za dravčí zobák či oko krahujce, nebo doplněním krahujčího vlnkování na prsa a břicho hrdličky) testujeme, zda příslušné znaky jsou pro rozpoznání konkrétního dravčího druhu či dravce obecně postačující. Pokud testovaní ptáci reagují na upravenou atrapu méně intenzivním antipredačním chováním než na nemodifikovaného predátora, znak k rozpoznání konkrétního druhu predátora (např. krahujce) nepostačuje, a pokud na ni nereagují intenzivnějším antipredačním chováním než na neškodnou kontrolu, nepostačuje ani pro rozpoznání obecnější kategorie predátorů (např. dravců).

Odebírání (náhrada) znaků na atrapě predátora a přidávání (náhrada) znaků na atrapě neškodného živočicha tedy přinášejí odpovědi na odlišné otázky. Pokud bude přitom reakce na atrapu predátora s odebranými (nahrazenými) dravčími (druhovými) znaky silnější než reakce na atrapu neškodného živočicha s přidanými (nahrazenými) dravčími (druhovými) znaky, je zřejmé, že vedle testovaného znaku (kombinace znaků) se při rozpoznávání konkrétního predátora (skupiny predátorů) uplatňují i znaky další.

3.2.1. Siluety

Výzkumu toho, jak ptáci predátory rozpoznávají, byla ve srovnání se výzkumem výsledků tohoto procesu, tedy schopnosti predátory rozpoznávat a hodnotit jejich nebezpečnost věnována behaviorální ekologií mnohem menší pozornost. Významná skupina studií však vznikla již v pionýrském období tohoto oboru.

Jeden ze zakladatelů etologie Konrad Lorenz vyslovil hypotézu, že jakékoli specifické zvířecí chování je vyvoláno specifickým podnětem, který nazval „Auschlöser“, anglicky „releaser“ (Lorenz 1937a,b). Z něj odvodil Tinbergen (1948) pojem “sign stimulus” označující signál (část těla či prvek chování) vyslaný jedním zvířetem, který způsobuje typické chování u druhého zvířete. Takovéto signály pak řídí všechny aspekty života od epigamního chování (Lack 1943; Tinbergen 1948), přes hnízdní chování (Tinbergen 1951) až právě po chování antipredační a tedy i rozpoznávání predátorů, které musí antipredačnímu chování předcházet. Později byly autory zabývajícími se rozpoznáváním predátorů ale jiných živočichů (například sexuálních partnerů) užívány i pojmy “key features” (Marr a Nishihara 1978), nebo “salient features” (Schleidt et al. 2011).

Antipredační chování, které je spontánní a není vázáno na určitou etapu života či roční dobu, nabízelo i jednu z cest, jak podobu a funkci sign stimuli experimentálně studovat. Povaha těch, které spouštějí antipredační chování (a tedy i rozpoznávání predátorů) byla poprvé prokázána v experimentech se siluetami dravců. Při nich byly porovnávány reakce tetřevovitých (*Lagopus* sp., *Tetrao* sp.), krocanů a kuřat kura domácího na siluety ptáků různých tvarů (Goethe 1937, 1940; Krätzig 1940; Lorenz 1939).

Výsledky ukázaly, že o spuštění antipredačního chování rozhodovala relativní délka krku siluety. Pokud bylo siluetou pohybováno takovým směrem, že byl vytvořen dojem krátkého krku vpředu a dlouhého ocasu vzadu (dravec), vyvolávala u testované drůbeže útěkové chování. Pokud bylo touž atrapou pohybováno v opačném směru a jevila se tedy jako pták s dlouhým krkem a krátkým ocasem (husa), antipredační chování se neobjevilo. Ostatní potenciální znaky, tvary křídel či těla siluety, neměly na reakci testovaných ptáků žádný vliv.

Ve své revizi Lorenzových a Tinbergenových experimentů však Schleidt et al. (2011) poznamenávají, že Tinbergen a Lorenz napsali víc prací o „krátkém krku“, ale kreslili v nich různé obrázky, které si navzájem neodpovídaly – není tedy zcela jasné, co kdy bylo použito. Lorenz sám pak podle nich navíc za „spouštěč“ antipredační reakce nepovažoval ani tak „krátký krk“, jako spíš „pomalou relativní rychlost letu“. Samotným autorům této revize (Schleidt et al. 2011) vycházelo, že v zajetí chovaná mláďata krocanů bez zkušenosti z přírody opravdu reagují spíše na siluety podobné dravcům, zatímco volně se pohybující krocani s individuálními zkušenostmi s predátory se bojí prakticky jakéhokoliv přelétajícího objektu.

Přestože se jedná o velmi tradiční téma, nelze zřejmě považovat otázku, zda jsou ptáci schopni podle siluety rozlišit predátory od neškodných ptáků za rozřešenou. Je přitom nepochybné, že by takováto schopnost byla při reálných setkáních s predátory velmi užitečná, neboť by mohla uspíšit a zpřesnit adekvátní reakci, což na jednu stranu zvyšuje šanci na únik a na druhou potlačuje zbytečné časové a energetické ztráty. Další experimenty by tedy mohly přinést zajímavé výsledky. Zaměřit by se měly na zvýšení věrohodnosti atrap predátorů i jejich pohybu. Především by se ale v experimentech měli uplatnit ptáci odchycení v přírodě. Stávající studie pracovaly s jedinci pocházejícími z chovů a navíc se nejčastěji jednalo o domácí drůbež.

3.2.2. Dílčí znaky – zbarvení

V dalších desetiletích studie věnované hledání a ověřování klíčových znaků používaných k rozpoznávání predátorů přibývaly pomalu. Zřejmě nejrozsáhlejší výzkum na toto téma provedl (Curio 1975), který sledoval intenzitu varovné vokalizace (call-rate) lejska černohlavého vůči modifikovaným atrapám ťuhýka obecného. Tento druh pěvce se sice živí převážně velkým hmyzem, je však schopen ulovit i malé obratlovce (Cramp 1979).

V rámci své studie Curio (l.c.) otestoval mnoho dílčích znaků, nejčastěji však různé prvky zbarvení. Nejprve prezentoval atrapy samce ťuhýka s barevnými úpravami černé oční pásky, která je u tohoto predátora asi nejnápadnějším prvkem zbarvení. Nejsilnější varovnou reakci přirozeně vyvolávala u lejsků nemodifikovaná kontrolní atrapa. Reakce na atrapu s červeným očním proužkem se od reakce na kontrolu signifikantně nelišila, naopak atrapa se zeleným proužkem vyvolala velmi výrazný pokles intenzity varování. Dále byl testován vliv kontrastu mezi očním proužkem a zbytkem hlavy. Odebírání sytosti proužku nevyvolalo v reakci lejsků větší změny. Teprve když proužek zcela splynul s podkladem, varovat přestali.

Z těchto výsledků vyplývá, že klíčová je přítomnost nápadného barevného znaku, nikoliv jeho provedení. Nesmí zřejmě ovšem být příliš vzdáleno od reálného vzhledu predátora. Červená respektive červenohnědá barva i různé odstíny šedi jsou v zbarvení ťuhýka zastoupeny, jakýkoliv odstín zelené však nikoliv a proto oční páska této barvy zřejmě jeho rozpoznání nespustí. Samotná přítomnost nemodifikovaného znaku ale také není dostačující, neboť bílá čtverhranná tyčka se stylizovanou oční páskou, postrádající však í tvar ptačího těla, nevyvolávala u lejsků žádnou varovnou reakci. Přestože je tedy přítomnost věrohodně zbarvené oční pásky pro rozpoznání ťuhýka nezbytná, nejedná se o „releaser“, tak jak ho chápal (Lorenz 1937a,b), neboť ten by měl spustit antipredační chování za jakýchkoliv podmínek.

Důležitá je také poloha oční pásky. Lejsci reagovali na atrapu, u níž byl oční proužek posunut z čela na týl a to dokonce o něco silněji než na kontrolní nemodifikovanou atrapu. Ostatní modifikace (páska pod krkem, na břiše, vertikálně na temeni) už vyvolávaly jen velmi slabé varovné reakce. Obdobné výsledky přinesly i prezentace atrap samce ťuhýka s radikálně barevně upraveným tělem. Lejsci reagovali silně pouze na kontrolní nezměněnou atrapu. Když byly z ťuhýka sejmuty všechny prvky zbarvení a černý oční proužek byl ponechán na uniformě bílém těle, intenzita varování dramaticky poklesla. Žádnou reakci pak nevyvolávala jednotně bílá atrapa bez očního proužku.

Výsledky tedy opět ukazují, že oční páska sama pro rozpoznání nepostačuje. Musí být zasazena na správném místě těla a doplněna dalšími prvky zbarvení. Na druhou stranu je oční páska pro rozpoznání nezbytná. Pokud by se lejsek setkal s ťuhýkem bez oční pásky, nevyhodnotil by ho zřejmě jako nebezpečí. To je zajímavé především proto, že ťuhýk poskytuje znak odkazující přímo na jeho potenciální nebezpečnost. V terminologii behaviorální ekologie bychom ho mohli nazvat znakem čestným. Je jím velký a silný, na konci mírně hákovitě zakončený zobák, který by mohl hrát při rozpoznávání stejnou roli jako hákovitý zobák dravců a sov (viz kapitola 3.2.4.). Nicméně všichni evropští ťuhýci (4 druhy) oční pásku mají a není proto zřejmě nezbytné využívat pro rozpoznávání méně nápadné byť „čestné“ znaky.

Jak již bylo uvedeno výše, je charakteristickým barevným znakem nejnebezpečnějšího evropského predátora drobných ptáků, krahujce, tmavé příčné vlnkování na jinak světlé spodině těla. Proto se několik autorů pokusilo testovat jeho význam pro rozpoznávání tohoto dravce potenciální kořistí. V práci Veselý et al. (2016) byly sýkorám na krmítku prezentovány atrapy krahujce s kompletně, nebo částečně modifikovaným zbarvením. Atrapa, která měla charakteristické vlnkování na břiše odstraněno, ale i atrapy zbarvené jako neškodní ptáci (koňadra, červenka) vyvolávaly u sýkor stejný strach jako nemodifikovaný krahujec. Pouze atrapa s umělým fialovo-bílým šachovnicovým vzorem nebyla vnímána jako větší nebezpečí než neškodná kontrola (holub). Tato práce tedy nezbytnost vlnkování na břiše pro rozpoznání of krahujce neprokázala. K shodným výsledkům došli i Davies and Welbergen (2008), kteří na krmítku také prezentovali atrapu of the krahujce zbavenou vlnkování na břiše. Stejně jako v předchozí studii se jí sýkory nebály méně než krahujce nemodifikovaného.

Výsledky experimentů s krahujcem a ťuhýkem obecným se tedy zásadně liší. Zatímco vlnkování na spodní straně těla není pro rozpoznání krahujce nezbytné, oční páska u ťuhýka ano. Vysvětlení se nabízí několik. Především atrapa s odstraněným vlnkováním stále nabízí přinejmenším jeden znak charakteristický pro krahujce – žluté oko. To nemá žádný evropský dravec srovnatelné velikosti. Na prvý pohled se ovšem zdá nepravděpodobné, že by takový detail mohl postačit pro rozpoznání krahujce, nicméně význam barvy očí pro rozpoznávání a to nejen krahujce dokládá více studií (viz kapitola 2.3.).

Nelze ovšem vyloučit, že sýkory v atrapě zbavené vlnkování nerozpoznávaly krahujce ale dravce pro ně neznámého druhu, na kterého reagovaly stejně (obdobně) obezřetně jako na krahujce. Modifikované atrapy nabízely řadu znaků, počínaje tělesnými proporcemi a konče délkou drápů, společných pro všechny evropské dravce. Opatrné chování vůči neznámému predátorovi se jeví pravděpodobným i proto, že ptáci navštěvující krmítko jsou obecně poměrně ostražití a jakýkoliv podezřelý objekt v nich může vyvolat strach (Bonter et al. 2013). Zde se ukazují limity experimentů s netrénovanými ptáky, u nichž lze rozlišování jakýchkoliv „objektů“ prokázat jen tehdy vyvolávají-li odlišné chování. Zajímavé by bylo nabídnout sýkorám přímý výběr mezi modifikovanou a nemodifikovanou atrapou v dvoukrmítkovém experimentů a stálo by za to sledovat také habituaci, které by v případě „neznámého dravce“ měla být rychlejší.

Zajímavé možnosti studia významu vlnkované spodní části těla pro rozpoznávání krahujce nabízí mimořádná podobnost zbarvení šedé formy kukačky obecné zmíněná již v předchozí kapitole. Lze dokonce využít i observační data. Lyon a Gilbert (2013) pozorovali mobbing na kukačku u druhu, který kukačka téměř neparazituje (vlaštovka obecná) nebo který ji vůbec nezná (americký mlynařík *Psaltriparus minimus*). V obou případech si ji podle autorů pletou s krahujcem obecným, či, v případě amerického mlynaříka, s některým místním malým zástupcem rodu *Accipiter*. Také sýkory koňadra a modřinka, další kukačkou neparazitovaní pěvci, na ni podle pozorování Langmore et al. (2012) reagují podobně opatrně jako na krahujce. Liang a Møller (2015) navíc zjistili, že vlaštovky obecné brání hnízdo proti kukačce i krahujci víc v Dánsku než v Číně. Autoři výsledky vysvětlují tak, že se v Číně vyskytuje sympatricky více druhů hnízdních parazitů a pro potenciální hostitele je tedy těžší je rozeznat. Příčinou však by mohlo být i to, že v Dánsku je krahujec hojnější než v Číně a představuje tedy pro vlaštovky známější nebezpečí. Zdá se tedy, že zatímco vlnkování spodní části těla není pro rozpoznání krahujce nezbytné, spolu se žlutým okem postačuje k tomu, aby byl krahujec rozpoznán v neškodné (pro testované druhy) kukačce, přesto že ta se odlišuje přinejmenším zcela odlišným tvarem zobáku a pařátů.

Nicméně, kukačkou běžně parazitovaný rákosník obecný, reagoval v blízkosti hnízda varovnými hlasy na atrapu kukačky mnohem silněji, než na atrapu krahujce i kontrolní neškodný druh (čírka obecná), což ukazuje, že mezi nimi spolehlivě rozlišuje (Welbergen a Davies 2008, 2011). K podobným závěrům došlo i několik dalších prací testujících reakce potenciálních hostitelů kukačky (Edwards et al. 1950; Ash 1970; Duckworth 1991; Thorogood and Davies 2012).

Welbergen and Davies (2011) navíc zjistili, že vlnkování na břiše není pro rozpoznání kukačky nezbytné. Rákosníci obecní varovali na kukačku zbavenou vlnkování více než na hrdličku a krahujce (bez ohledu na jejich modifikaci), což svědčí pro to, že ji rozpoznávali na základě jiného znaku. Pokud jsou tedy ptáci motivováni k tomu, aby mezi kukačkou a krahujcem rozlišovali, mohou tuto schopnost získat.

Jaký znak, mohou ptáci používat pro rozpoznání kukačky testovala studie Trnky et. al. (2012). Rákosníci velcí aktivně napadali atrapu kukačky zbavenou vlnkování, nikoliv však atrapu s hnědýma očima a koutky zobáku. Naopak ale útočili na atrapu hrdličky s kukaččím okem a zobákem. Autoři z toho vyvozují, že nikoliv vlnkování spodní strany těla ale barva očí je klíčovým znak pro rozpoznání kukačky. Zdůvodňují to tím, že je oko u kukačky sedící níž než rákosník lépe viditelné. Lze ovšem navrhnout i jiné vysvětlení. Žluté oko umožňuje rozpoznat i hnědou formu kukačky a je tedy znakem spolehlivějším.

Předchozí závěry nicméně zpochybňuje další výsledek ze studie Welbergen and Davies (2011), který ukazuje, že podobnost šedé formy kukačky s krahujcem ji opravdu chrání před napadením ze strany hostitelských ptáků. Rákosníci obecní si troufali přiblížit na kratší vzdálenost ke kukačce, která měla odstraněno vlnkovaní spodní části těla, než ke kukačce nemodifikované. Naopak, když byla vlnkováním opatřena atrapa kontrolní neškodné hrdličky zahradní, přibližovali se k ní rákosníci méně než k atrapě nemodifikované..

Rozpor se studií Trnka et al. (2012) může ale být jen zdánlivý. Testovaní ptáci řešili dvě rozdílné úlohy: rozpoznávání kukačky, které absence vlnkování téměř nezhoršuje, a rozpoznání krahujce, které vlnkování „zlepšuje“, ovšem takovým způsobem, že je rozpoznán i v jiných druzích ptáků.

Ani u rákosníků obecných však není efekt vlnkování univerzální. K atrapě krahujce s odstraněným vlnkováním spodní strany těla se přibližovali se stejnou opatrností jako ke krahujci nemodifikovanému (Welbergen and Davies 2011). Tento výsledek se shoduje s výše popsanými studiemi na sýkorách a i vysvětlení bude zřejmě obdobné. Rákosníci buď rozpoznávají krahujce podle jiných znaků, k čemuž se přiklánějí autoři, nebo krahujce sice nerozpoznávají, vůči atrapě však zachovávají opatrnost, neboť ta nese všechny obecné dravčí znaky a může být vyhodnocena jako neznámý a potenciálně nebezpečný dravčí druh. Rozhodnout by mohlo jen přímé srovnání (nejlépe v dvoukrmítkovém uspořádání) s nemodifikovaným krahujcem. Výsledky experimentů může navíc ovlivnit i jejich uspořádání. Trnka a Prokop (2012) zjistili, že rákosníci velcí sice napadají kukačku intenzivněji než krahujce, avšak jen když byly atrapy obou vetřelců prezentovány současně. Pokud byly prezentovány samostatně, pouze s neškodnou kontrolou, intenzita útoků se v důsledku častějšího napadání krahujce průkazně nelišila.

Autoři se domnívají, že rákosníci velcí jsou díky svým tělesným dispozicím mimořádně agresivní a při obraně hnízda generalizují nebezpečnost kukačky na všechny vetřelce. V takovém případě by se však intenzita útoků na kukačku a krahujce neměla lišit ani při současné prezentaci. Pokud rákosníci velcí útočí intenzivněji jen na samostatně prezentovaného krahujce, je přinejmenším stejně validním vysvětlením, že negeneralizují nebezpečnost kukačky ale její vzhled, tedy že krahujce, pokud jej s ní nemohu přímo porovnat, rozpoznávají jako kukačku. Příčinou nižší schopnosti rákosníků velkých rozlišovat šedou formu kukačky od krahujce ovšem může být jejich lepší schopnost zahánět od hnízda jakékoliv vetřelce a tedy i menší zvýhodnění ptáků, kteří si rozpoznání osvojí.

Vedle těchto dvou se nabízí ještě jedno vysvětlení – rákosníci kukačku a krahujce za všech okolností rozlišují, v jednotlivých pokusných uspořádáních se však pokoušejí přednostně zahnat aktuálně nebezpečnějšího z obou vetřelců. Kukačku upřednostňují před hrdličkou i krahujcem, krahujce jen před hrdličkou. Takovouto schopnost optimalizovat obranné chování při střetnutí se dvěma predátory prokázala u ťuhýka obecného Syrová et al. (2016). Určité světlo by do problému mohlo přinést, kdyby byl opakován s dravcem nepodobným kukačce, například s poštolkou.

Trnka a Grim (2013) testovali i reakci rákosníka velkého na hnědou formu kukačky. Ti na ni útočili mnohem intenzivněji než na neškodnou hrdličku, takže v ní nepochybně rozpoznávali nebezpečí. Je ovšem otázkou jaké, neboť intenzita útoků byla nižší než na šedou formu a nelišila se průkazně od intenzity útoků na krahujce a poštolku. Získání přesnější odpovědi by vyžadovalo manipulaci jak se znaky hnědé formy kukačky (zbarvení) tak i poštolky (obecně se vyskytující znaky dravců) a také testování na dalších lokalitách, s odlišným zastoupením obou forem kukačky.

Při hodnocení všech experimentů testujících rozpoznávání kukačky a její rozlišování od krahujce, je konečně třeba mít na paměti, že prezentované výsledky těchto i dalších studií zachycují „střední hodnotu“ reakce, ta ovšem nejenže nemusí mít normální rozdělení, ale nemusí být a zřejmě nebývá (např. Beránková et al. 2014) ani „spojitá“. Jednotliví ptáci buď stimuly rozpoznají a (více či méně) reagují, nebo nerozpoznají a (více či méně) nereagují.

Rozdíly v „schopnosti“ stimuly rozpoznat může způsobovat větší či menší zkušenost, kterou s nimi mají, nebo odlišná personalita (z pohledu behaviorální psychologie asi odlišné kognitivní schopnosti).

Stejně tak je třeba zohlednit, že žádný z experimentů netestuje schopnost rozpoznávat predátora ale jen schopnost rozlišit jej od jiného „objektu“ což se ale projeví jen tehdy, pokud jej považuje za menší či větší nebezpečí a reaguje na něj slaběji či silněji. (viz kapitola 1). Absence rozdílu v reakcích tedy nemusí znamenat, že testovaný pták predátora nerozpoznává. Taková situace může nastat zvláště tehdy, porovnáváme-li reakce na různé predátory (nebo na predátora a hnízdního parazita).

Na základě výsledků stávajících experimentů lze shrnout, že ptáci nápadné dílčí prvky zbarvení pro rozpoznávání predátorů (a hnízdních parazitů) nepochybně využívají. Nemusejí však být nezbytné ani postačující. Pokud chybí, nebo jsou nespolehlivé, mohou je nahradit jiné, alespoň na prvý pohled, méně nápadné znaky. Naopak, pokud takovéto „doplňkové“ znaky chybí, nebo nemají správnou podobu, nemusí přítomnost nápadných prvků zbarvení sama o sobě postačovat.

Výsledek zřejmě závisí na různých okolnostech. V případě rozlišování krahujce od šedé formy kukačky, se lze setkat se záměnou krahujce za kukačku i kukačky za krahujce. Tento potenciální mimetický komplex ale představuje spíše výjimku. Pokud se určitý barevný prvek (ale i jiný dílčí znak) vyskytuje u všech zástupců nějaké skupiny, představujících obdobné nebezpečí, jako třeba oční páska evropských ťuhýků nebo typický zobák dravců, a lze se tedy na ně spolehnout, k selhání v rozpoznání obvykle nedochází. Ťuhýk ovšem nesmí být zelený a dravec pravidelně károvaný. Netrénovaní ptáci se při rozpoznávání predátorů tedy chovají obdobné jako holubi v experimentech studie Aust a Huber (2001), trénovaní rozpoznávat lidskou postavu. Významným klíčovým znakem pro ně byly mimo jiné šaty, musely se však nacházet na „objektu“ více či méně podobném lidské postavě.

3.2.3. Dílčí znaky – velikost

Také význam tělesné velikosti pro rozpoznání různých druhů predátorů naznačovaný i nemanipulativními studiemi (viz kapitola 3.1) byl testován cíleně. Evans et al. (1993b) konfrontovali naivní kuřata s různě velkými siluetami dravců promítanými na monitoru na stropě ubikace. Velké siluety vyvolávaly nejintenzivnější varovnou vokalizaci, v závislosti na velikosti promítané siluety se ale měnilo i další chování. Při projekci malé siluety byla rozpoznatelná jen oční fixace kuřat na dravce a sledování siluety otáčením hlavy. Siluety prostřední velikosti vyvolaly mírné přikrčení, při promítání největších dravců se kuřata přikrčila tak silně, že se tělem dotýkala podlahy. Autoři ovšem interpretují tento výsledek tak, že kuřata vnímali velikost jako ukazatel výšky letu a reagovali silněji na bližšího predátora.

Různě velké atrapy jestřába použili Klump a Curio (1983) pro testování v přírodě odchycených sýkor modřinek. Atrapy byly přesouvány na laně ve výšce 4 m nad voliérou. Na atrapu v normální velikosti reagovali sýkory hlasitou varovnou vokalizací a inhibicí pohybu trvající až tři minuty. Zmenšená atrapa vyvolala u sýkor tichý, krátký varovný hlas „seet“ a způsobila inhibici pohybu na méně než 1 min. Obdobně jako v předchozí studii se autoři domnívají, že sýkory vnímaly různě velké atrapy spíše jako různě vzdálené predátory a tomu přizpůsobily antipredační odezvu. Možná je ale i opačná interpretace, podle které sýkory rozpoznaly pravou velikost atrap a reagovaly ve skutečnosti silněji na malého než na velkého dravce. Tomu by odpovídalo použití varování typu „seet“ pro „vzdálenou“ siluetu, které ovšem sýkory používají jako signál akutního nebezpečí (Ficken et al. 1978; Smith 1991; Templeton and Greene 2007). V malém jestřábovi by v takovém případě ale rozpoznávaly spíše krahujce. Ten se zbarvením od jestřába téměř neliší a sýkory jsou jeho typickou kořistí (Cramp 1979). Obdobně by šlo polemizovat se závěry předchozí studie, neboť pro kura domácího naopak představují větší nebezpečí velcí dravci (např. jestřáb). Rozhodnout o významu velikosti pro rozlišení různých druhů predátorů nicméně výše uvedené ani další obdobně koncipované studie nemohou. Při prezentaci letících atrap nelze nikdy jednoznačně odlišit, zda velikost atrapy odkazuje na tělesné rozměry nebo na vzdálenost. Bylo by třeba experiment navrhnout tak, aby se testovaný pták ocitl v jednoznačně definované vzdálenosti od predátora a tedy použít atrapu sedící. S takovými pracoval jen Curio (1975). V jeho experimentech zmenšená atrapa ťuhýka obecného s nezměněným zbarvením vyvolávala obdobnou reakci lejsků černohlavých jako atrapa nemodifikovaná.

3.2.4. Dílčí znaky – oči a zobák

Mnohé druhy dravců a sov mají velmi nápadné oči, kontrastní vůči zbarvení hlavy. Navíc se často v okolí oka nachází výrazně zbarvená holá kůže, která jeho nápadnost ještě podtrhuje. Bylo také opakovaně prokázáno, že jsou ptáci schopni poznat, zda se na ně predátor dívá a tedy, zda jím jsou bezprostředně ohroženi. Watve et al. (2002) zjistili, že pro vlhu *Merops orientalis* je významné, jaký úhel svírá pohled očí člověka s přímkou vedoucí k jejímu hnízdu, zatímco úhel svíraný mezi tělem a hnízdem význam nemá. Podobné poznatky získali Carter et al. (2008), když otestovali vliv přímého pohledu člověka na krmící se špačky obecné. Pokud byl pohled „lidského predátora“ odvrácený, špačci se vrátili k hledání potravy a zkonzumovali jí více v kratším čase.

Není proto překvapivé, že přítomnost i barva očí jsou často považovány za „sign stimuli“ umožňující rozpoznání různých druhů predátorů a jejich význam byl experimentálně testován. Většina studií je ovšem staršího data, což může být příčinou ne zcela konzistentních výsledků.

Nice a TerPelkwyk (1941) testovali reakci strnada *Melospiza melodia* na různě modifikované kartonové modely puštíka *Strix varia* se závěrem, že pro rozpoznání atrapy jako sovy je sice hlava nejdůležitější, nicméně pouhá nepřítomnost očí strach z atrapy nesnižuje. Naopak Smith and Graves (1978) ukázali, že nepřítomnost hlavy, nebo i jenom očí na atrapě výra silně snižuje intenzitu mobbingu ze strany vlaštovek obecných. Scaife (1976) v experimentech s naivními kuřaty zjistil, že antipredační chování (ústup do úkrytu) vyvolává atrapa poštolky zbavená očí stejně jako atrapa kiwiho, na níž byly žluté (modifikované) oči poštolky přeneseny. Obě tyto atrapy ovšem vyvolávaly slabší reakci než poštolka se žlutýma očima.

Curio (1975) se ve své komplexní studii vedle zbarvení zabýval i významem očí. Atrapa ťuhýka postrádající oči nevyvolávala u lejsků žádnou antipredační reakci. V pokusech s kulíškem, lejsci atrapu po zakrytí jednoho oka peřím prakticky ignorovali. Když však byly zakryty obě oči, začali na ni reagovat, byť nárůst aktivity nebyl signifikantní a nedal se srovnat s reakcí na nemodifikovaného kulíška. Autor tento nárůst vysvětluje obnovením symetrie atrapy. Pokud byly oči kulíška přeneseny na atrapu ťuhýka, zvýšily intenzitu antipredačního chování lejsků ve srovnání s jejich reakcí na ťuhýka nemodifikovaného. Pokud ovšem byly obě oči umístěny na stejné straně hlavy, intenzita reakce klesala. Konečně, na atrapu kulíška s trojúhelníkovitýma očima reagovali lejsci téměř stejně silně jako na kontrolní nezměněnou atrapu. Význam očí pro rozpoznávání kukačky (Trnka et al. 2012) byl již diskutován v kapitole 3.2.2.

Dalším charakteristickým znakem dravců a sov je hákovitý zobák, který jim umožňuje porcovat kořist. Proto jej lze terminologií behaviorální ekologie označit jako „honest signal“, neboť až na nepatrné výjimky nechybí žádnému zástupci obou skupin. Oproti očím jsou tvar a barva zobáku dravců i sov poměrně uniformní. Lze proto předpokládat, že se mohou uplatnit spíše při rozpoznání příslušnosti k oběma skupinám vzdušných predátorů než k rozlišení různých druhů. Také studie testující význam tohoto potenciálního klíčového znaku jsou staršího data a jejich závěry je nutno přijímat s určitou opatrností.

V experimentech Curia (1975) nezměnilo prodloužení zobáku ťuhýka reakci testovaných lejsků, v případě kulíška však způsobila obdobná modifikace částečné snížení intenzity jejich antipredačního chování. Smith and Graves (1978) zjistili, že atrapa výra bez zobáku vyvolává u vlaštovek mnohem slabší mobbing než atrapa nemodifikovaná. Gill et al. (1997) prokázali klíčový význam zobáku při rozpoznávání hnízdního parazita vlhovce *Molothurus ater*. Připevnili na jeho atrapu zobák špačka, který je, podobně jako zobák of the vlhovce, tmavý, avšak delší a tenčí. Lesňáčci *Dendroica petechia* reagovali mnohem silněji na nemodifikovanou atrapu s původním zobákem.

Beránková et al. (2014) předkládali sýkorám v laboratorních podmínkách atrapy holuba a krahujce se vzájemně vyměněnýma očima a zobáky. Přítomnost holubích očí na krahujci snížila míru strachu, který vzbuzoval, nicméně, přítomnost očí krahujce nezvýšila míru strachu z holuba. Naopak přítomnost holubího zobáku nesnížila strach z krahujce, ale přítomnost krahujčího zobáku zvýšila strach z holuba. Tento výsledek odpovídá tomu, že zobák slouží sýkorám jako obecný znak dravce, zatímco žluté oko jako druhově specifický znak krahujce. Proto žluté oko na holubovi jeho „nebezpečnost“ nezvyšuje (nemá žádný další znak krahujce) zatímco absence na krahujci ano (postrádá významný druhově specifický znak). Obdobně pak krahujčí zobák zvyšuje „nebezpečnost“ holuba (žádný z ostatních znaků, které nabízí, není s příslušností k dravcům v nápadném rozporu) zatímco absence na krahujci nikoliv (má všechny druhově specifické znaky).

Odlišný přístup volila starší studie (Edwards et al. 1950), která se zabývala rozpoznáváním kukačky a manipulovala celou hlavou. Výsledky jsou z dnešního pohledu překvapivé. Testovaní budníčci větší torzo kukačky zbavené hlavy nenapadali, oproti tomu však samotná oddělená hlava u nich vyvolala intenzivní mobbingovou reakci. Tento výsledek je ve shodě s pionýrskými etologickými studiemi (např. Lack 1940, 1943), zaměřenými na rozpoznávání sexuálních partnerů a soků. Zdá se však být v rozporu s novějšími výsledky, které ukazují, že klíčové znaky fungují jen, nacházejí-li se v kontextu znaků ostatních. Je až překvapivé, že tyto experimenty dosud nenašly pokračovatele, neboť hodnověrné testování efektu izolovaných klíčových znaků je nepochybně nezbytným krokem v porozumění rozpoznávacích procesů u netrénovaných ptáků.

Rozporuplné výsledky přinášejí i ostatní studie. O příčinách lze jen spekulovat. Můžeme je hledat v testovaných ptácích (zkušení vs. naivní), různé nebezpečnosti použitých predátorů (např. kulíšek vs. výr), sledovaných parametrech chování, ale i odlišném významu testovaných znaků u různých predátorů, což naznačují výsledky studií zaměřených na rozpoznání kukačky a krahujce (kapitola 3.2.2) ale výsledky Beránkové et al. (2014). Zajímavá je v tomto ohledu konečně studie Gill et al. (1997). Rozhodující význam zobáku, který není v žádném případě unikátní, pro rozpoznání vlhovce *Molothrus ater* může být dán tím, že tento uniformně zbarvený hnízdní parazit nenabízí jiné znaky pro odlišení od středně velkých pěvců. Každopádně by význam očí i zobáku pro rozpoznávání skupin a druhů predátorů zasluhoval další pozornost. Především by bylo žádoucí důsledně testovat, nakolik jsou pro rozpoznání nejen nezbytné ale i postačující.

3.2.5. Kombinace dílčích znaků

Studie rozebírané v předchozích kapitolách ukazují, že efekt jednotlivého, byť i velmi nápadného znaku obvykle závisí na kontextu znaků ostatních. Asi nejhezčí ukázku poskytuje díky značné pozornosti, která jí byla věnována, vlnkovaná spodní strana těla krahujce obecného a kukačky obecné. Pokud chceme význam kontextu poznat přesněji, musíme manipulovat více znaky současně, což umožní testovat cíleně a soustavně jejich různé kombinace

Beránková et al. (2015) prezentovali sýkorám modifikované atrapy krahujce. Ty se lišily celkovým zbarvením a velikostí. Byly testovány dvě sady – v přirozené velikosti krahujce a zmenšené na velikost sýkory koňadry. Atrapy byly prezentovány jako sedící dravci, takže možnost, že by je sýkory vnímaly jako různě vzdálené exempláře týchž forem, mohla být vyloučena. Atrapz neslz zbarvení: 1) nemodifikovaného krahujce, 2) holuba (neškodný pták velikosti krahujce), 3) červenky (neškodný pták velikosti sýkory koňadry), 4) sýkory koňadry. Sýkory projevovaly strach v přítomnosti obou atrap zbarvených jako krahujec. Pokud bylo zachováno zbarvení, velikost tedy nehrála žádnou roli. Podobně oba dravci zbarvení jako great tit nevyvolávali žádný strach. Zde naopak konspecifické zbarvení eliminovalo přítomnost obecných dravčích znaků (zobák, drápy) i přítomnost specificky zbarveného krahujčího oka. Vliv velikosti se projevil pouze u atrap zbarvených jako červenka a holub, kde atrapy v nepřirozené velikosti (velká červenka, malý holub) vyvolávaly více strachu, než atrapy velikostně nemodifikované. Velikost tedy hrála roli jen u atrap zbarvených jako ptáci, s nimiž se sýkory mohou setkat, kteří však pro ně za normální okolnosti nejsou zajímaví.

Pokud byly tyto druhy prezentovány v „nesprávné“ velikosti, přitáhly zřejmě pozornost sýkor zachované dravčí respektive krahujčí znaky.

Němec et al. (in prep.) otestovali současně význam potenciálních obecných klíčových znaků dravce (zahnutý zobák, dlouhé drápy, oko s kostěným supraorbitálním hřebenem) a druhově specifického zbarvení peří pro rozpoznání poštolky ťuhýky bránícími své hnízdo. Klíčové dravčí znaky zůstaly u jedné sady atrap (vyrobených z plyše) dravčí. U druhé sady byly zaměněny za holubí (oko bez supraorbitálního hřebene, tenčí rovný zobák, růžové nohy s krátkým, rovnými drápy). 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 luňáka *Aviceda leuphotes*. Jako kontroly sloužily vycpaniny poštolky (pro ověření věrohodnosti plyšových atrap) a holuba. Pokud byly na normálně zbarvené plyšové atrapě poštolky ponechány klíčové znaky dravce (původní zobák, oko a pařáty), byla tato atrapa považovaná ťuhýky za poštolku a ti na ní útočili stejně intenzivně jako na poštolku vycpanou. S o něco nižší intenzitou pak útočili na atrapu zjednodušenou, zatímco na atrapu ve zbarvení „Aviceda“ byť i s klíčovými znaky dravce napadali již jen minimálně. Naproti tomu pokud byly klíčové znaky nahrazeny holubími, ťuhýci neútočili na žádnou z atrap, bez ohledu na její zbarvení. Ani v případě atrapy s nezměněným zbarvením poštolky, nejevili ťuhýci o ni zájem, a dokonce v její přítomnosti krmili mláďata. Ťuhýci tedy druhově specifické zbarvení rozpoznávali a to i v dosti pozměněné podobě, ovšem jen tehdy pokud měla atrapa současně obecné znaky dravce. Naopak samotné klíčové znaky dravce agresivní reakci nevyvolaly. Zdá se tedy, že rozpoznání poštolky probíhá ve dvou stupních. V prvém je na základě obecných znaků rozpoznán dravec, ve druhém na základě specifických znaků konkrétní druh. Tento závěr ovšem platí za předpokladu, že ťuhýci útočí jen na známé druhy dravců.

3.3. Závěr

Na prvý pohled působí na čtenáře výsledky prací z této kapitoly jako nepřehledná změť, z které není možné učinit obecný závěr. O nějaké shrnutí bychom se však měli pokusit. Je zřejmé, že ptáci nápadné dílčí znaky pro rozpoznávání predátorů využívají. Mohou být dokonce pro rozpoznání nezbytné, obvykle však pro rozpoznání nepostačují. Nejedná se tedy o „ausloser“ v přísném slova smyslu, tak jak je definoval (Lorenz 1937a,b). Nemají stejný absolutní efekt, jako měl například chomáč červeného peří v pokusech, které konal Lack (1940) s vnitrodruhovým rozpoznáváním u červenky.

Jinými slovy častěji není predátor bez nápadného znaku jako predátor rozpoznán než neškodný druh s nápadným znakem ano. Při povrchním zamyšlení je tento rozdíl poněkud překvapivý. Pokud není nápadný znak pro rozpoznání postačující, neměl by být ani nezbytný. Nicméně hypotézu, jak by mohl probíhat rozpoznávací proces odpovídající zjištěným rozdílům, navrhnout lze. V případě dravce (například krahujce) bez druhově specifického nápadného znaku by mohl vypadat takto: „Tento pták je dravec, ale nemá vlnkované břicho, krahujec to tedy není“. V případě neškodného ptačího druhu (například hrdličky) s druhově specifickým nápadným znakem dravce (například krahujce) by hodnocení znělo: „Toto není ne dravý pták, není tedy třeba věnovat pozornost jeho zbarvení“. Takovýto proces by vysvětloval pokusy Němce et al. (in prep.), v nichž ťuhýci nereagovali na poštolku s holubím okem, zobákem a pařáty. Nevěnovali tedy pozornost jejímu druhově specifickému zbarvení, přestože je nepochybně znali.

Stávající výsledky zároveň ukazují, že izolovaný efekt nápadných znaků ovlivňuje míra jejich specifičnosti. Znaky obecné (například společné znaky dravců) jej mají větší než znaky speciální (například druhově specifické zbarvení poštolky). Holub s dravčím zobákem vzbuzoval jistou míru strachu (ovšemže nižší než nemodifikovaný krahujec), zatímco holub s krahujčím okem nikoliv. To dává smysl. Všichni ptáci se během života pravděpodobně setkávají s pro ně dosud neznámými ptačími druhy. Společné dravčí znaky představují užitečné vodítko pro jejich zařazení do kategorie „dravec“, zbarvení, které je druhově velmi proměnlivé, takovýmto znakem není a to ani tehdy, podobá-li se zbarvení nějakého dravce nebo naopak zbarvení neškodného ptáka.

Literatura

Abrahams M.V., Dill L.M. (1989): A Determination of the Energetic Equivalence of the Risk of Predation. Ecology 70: 999-1007.

Adams J.L., Camelio K.W., Orique M.J., Blumstein D.T. (2006): Does information of predators influence general wariness? Behavioral Ecology and Sociobiology 60:742-747.

Adriaensen F., Dhont A. A., Van Dongen S., Lens L., Matthysen E. (1998): Stabilizing selection on blue tit fledgling mass in the presence of sparrowhawks. Proceedings of the Royal Society of London series B-Biological Sciences 265: 1011-1016.

Aizaki K., Yusa Y. (2010): Learned Predator Recognition in a Freshwater Snail, Pomacea canaliculata. Malacologia 52:21-29.

Alatalo R.V., Helle P. (1990): Alarm calling by individual willow tits, *Parus montanus*. Animal Behaviour 40:437-442.

Albano N., Santiago-Quesada F., Masero J.A., Sanchez-Guzman J.M., Mostl E. (2015): Immunoreactive cortisone in droppings reflect stress levels, diet and growth rate of gull-billed tern chicks. General and Comparative Endocrinology 213:74-80.

Altmann S.A. (1956): Avian mobbing behavior and predator recognition. Condor 58:241-253.

Amat J.A., Masero J.A. (2004): Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Animal Behaviour 67:293-300.

Amat J.A., Carrascal L.M., Moreno J. (1996): Nest defence by Chinstrap Penguins *Pygoscelis antarctica* in relation to offspring number and age. Journal of Avian Biology 27:177-179.

Amo L., Galván I., Tomás G., Sanz J.J. (2008): Predator odour recognition and avoidance in a songbird. Functional Ecology 22:289-293.

Amo L., López-Rull I., Pagán I., García C.M. (2015): Evidence that the house finch (*Carpodacus mexicanus*): uses scent to avoid omnivore mammals. Revista Chilena de Historia Natural 88.

Andersson M., Wiklund C.G., Rundgren H. (1980): Parental defence of offspring: model and an example. Animal Behaviour 28:536-542.

Apel K.M. (1985): Antipredator behavior in the Blackcapped Chickadee (*Parus atricapillus*). Dissertation, University of Wisconsin.

Arnold K.E. (2000): Group Mobbing Behaviour and Nest Defence in a Cooperatively Breeding Australian Bird. Ethology 106:385-393.

Arnold J.M., Ordonez R., Copeland D.A., Nathan R., Scornavacchi J.M., Tyerman D.J., Oswald S.A. (2011): Simple and inexpensive devices to measure heart rates of incubating birds. Journal of Field Ornithology 82:288-296.

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.

Ash J. (1970): Observations on a decreasing population of red-backed shrikes. British Birds 63:185-205.

Astheimer L.B., Buttemer W.A., Wingfield J.C. (1994): Gender and seasonal differences in the adrenocortical response to ACTH challenge in an Arctic passerine, *Zonotrichia leucophrys gambelii*. General and Comparative Endocrinologyinol 94:33-43.

Aust U., Huber L. (2001): The role of item- and category-specific information in the discrimination of people versus nonpeople images by pigeons. Animal Learning & Behavior 29:107-119.

Aust U., Huber L. (2002): Target-defining features in a “people-present/people-absent” discrimination task by pigeons. Animal Learning & Behavior 30:165-176.

Avilés J.M., Parejo D. (2006): Nest defense by Iberian azure-winged magpies (*Cyanopica cyanus*): do they recognize the threat of brood parasitism? Ethology Ecology & Evolution 18:321-333.

Azevedo C.S., Young R.J. (2006a): Behavioural responses of captive-born greater rheas Rhea Americana Linnaeus (Rheiformes, Rheidae): submitted to antipredator training. Revista Brasileira de Zoologia 23:186-193.

Azevedo C.S., Young R.J. (2006b): Do captive-born greater rheas Rhea Americana Linnaeus (Rheiformes, Rheidae): remember antipredator training? Revista Brasileira de Zoologia 23:194-201.

Baker M.C., Becker A.M. (2002): Mobbing calls of black-capped chickadees: effects of urgency on call production. The Wilson Bulletin 114:510-516.

Barash D.P. (1975): Evolutionary aspects of parental behavior: distraction behavior of the Alpine Accentor. The Wilson Bulletin 87:367-373.

Barash D.P. (1976): Mobbing Behavior by Crows: the Effect of the „Crow-In-Distress" Model. Condor 70:120

Bártol I., Karcza Z., Moskát C., Røskaft E., Kisbenedek T. (2002): Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. Journal of Avian Biology 33:420-425.

Bautista L.M., Lane S.J. (2000): Coal tits increase evening body mass in response to tawny owl calls. Acta ethologica 2:105-110.

Bazin R.C., Sealy S.G. (1993): Experiments on the responses of a rejector species to threats of predation and cowbird parasitism. Ethology 94:326-338.

Bažant M. (2009): How birds judge the risk of predation during winter nourishment experiments – meaning of the movement of the model. BSc. thesis in Czech, University of South Bohemia.

Beauchamp G. (2001): Should vigilance always decrease with group size? Behavioral Ecology and Sociobiology 51:47-52.

Beránková J., Veselý P., Sýkorová J., Fuchs R. (2014): The role of key features in predator recognition by untrained birds. Animal cognition 17:963-971.

Beránková J., Veselý P.., Fuchs R. (2015): The role of body size in predator recognition by untrained birds. Behavioural processes 120:128-134.

Betts M.G., Halley A.S., Doran P.J. (2005): Avian Mobbing Response is Restricted by Territory Boundaries: Experimental Evidence from Two Species of Forest Warblers. Ethology 111:821-835.

Binazzi R., Zaccaroni M., Nespoli A., Massolo A., Dessi-Fulgheri F. (2011): 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.

Blancher P.J., Robertson R.J. (1982): Kingbird aggression: does it deter predation? Animal Behaviour 30:929–930.

Bonter D.N., Zuckerberg B., Sedgwick C.W., Hochachka W.M. (2013): Daily foraging patterns in free-living birds: exploring the predation - starvation trade-off. Proceedings of the Royal Society of London series B-Biological Sciences 280:20123087

Bosque C., Molina C. (2002): Communal breeding and nest defense behavior of the Cayenne Jay (*Cyanocorax cayanus*): Journal of Field Ornithology 73:360–362.

Breuner C.W., Delehanty B., Boonstra R. (2013): Evaluating stress in natural populations of vertebrates: total CORT is not good enough. Functional Ecology 27:24-36.

Briskie J.V., Sealy S.G. (1989): Changes in nest defense against a brood parasite over the breeding cycle. Ethology 82:61-67.

Brown C.R., Hoogland J.L. (1986): Risk in mobbing for solitary and colonial swallows. Animal Behaviour 34:1319–1323.

Brunton D.H. (1986): Fatal antipredator behaviour of killdeer. The Wilson Bulletin 98:605-607.

Brunton D.H. (1990): The effects of nesting stage, sex, and type of predator on parental defense by Killdeer (*Charadrius vociferous*): testing models of avian parental defense. Behavioral Ecology and Sociobiology 26:181-190.

Brunton D.H. (1997): Impacts of predators: center nests are less successful than edge nests in a large nesing colony of lest terns. Condor 99:372-380.

Brunton D. (1999): “Optimal” colony size for least terns: an intercolony study of opposing selective pressures by predators. Condor 101:607-615.

Buitron D. (1983): Variability in the responses of Black-billed Magpies to natural predators. Behaviour 78:209-236.

Bump S.R. (1986): Yellow-headed blackbird nest defense: aggressive responses to marsh wrens. Condor 88:328-335.

Bureš S., Pavel V. (2003): Do birds behave in order to avoid disclosing their nest site? Bird Study 50:73-77.

Burger J., Gochfeld M., Saliva J.E., Gochfeld D., Gochfeld D., Morales H. (1989): Antipredator behaviour in nesting zenaida doves (*Zenaida aurita*): parental investment or offspring vulnerability? Behaviour 65:129-143.

Burger J., Gochfeld M. (1992): Experimental Evidence for Aggressive Antipredator Behavior in Black Skimmers (*Rynchops niger*). Aggressive Behavior 18:241-248.

Burger J., Shealer D.A., Gochfeld M. (1993): Defensive Aggression in Terns: Discrimination and Response to Individual Researchers. Aggressive Behavior 19:303-311.

Burhans D.E. (2000): Avoiding the Nest: Responses of Field Sparrows to the Threat of Nest Predation. Auk 117:803-806.

Burhans D.E. (2001): Enemy recognition by field sparrows. The Wilson Bulletin 113:189-193.

Butler P.J., Green J.A., Boyd I.L., Speakman J.R. (2004): Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. Functional Ecology 18:168-183.

Byrkjedal I. (1987): Antipredator behavior and breeding success in Greater Golden-Plover and Eurasian Dotterel. Condor 89:40-47.

Campobello D., Sealy S.G. (2010): Enemy recognition of reed warblers (*Acrocephalus scirpaceus*): threats and reproductive value act independently in nest defence modulation. Ethology 116:498-508.

Cannicci S., Morino L., Vannini M. (2001): Behavioural evidence for visual recognition of predators by the mangrove climbing crab *Sesarma leptosoma*. Animal Behaviour 63:77-83.

Canoine V., Hayden T.J., Rowe K., Goymann W. (2002): The stress response of European stonechats depends on the type of stressor. Behaviour 139:1303-1311.

Canty N., Gould J.L. (1995): The hawk/goose experiment: sources of variability. Animal Behaviour 50:1091-1095.

Carere C., Groothuis T.G.G., Mostl E., Daan S., Koolhaas J.M. (2003): Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. Hormones and behavior 43:540-548.

Caro T. (2005): Antipredator defenses in birds and mammals. The University of Chicago Press, Chicago

Carrascal L.M., Alonso C.L. (2006): Habitat use under latent predation risk. A case study with wintering forest birds. Oikos 112: 51-62

Carrascal L.M., Polo V. (1999): Coal tits, Parus ater, lose weight in response to chases by predators. Animal Behaviour 58: 281-285

Carter J., Lyons N.J., Cole H.L., Goldsmith A.R. (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.

Cavanagh P.M., Griffin C.R. (1993): Response of nesting common terns and laughing gulls to flyovers by large gulls. The Wilson Bulletin 105:333-338.

Cawthorn J.M., Morris D.L., Ketterson E.D., Nolan V. (1998): Influence of experimentally elevated testosterone on nest defence in Darkeyed Juncos. Animal Behaviour 56:617-621.

Chávez-Zichinelli C.A., Gomez L., Ortiz-Pulido R., Lara C., Valdez R., Romano M.C. (2014): Testosterone levels in feces predict risk-sensitive foraging in hummingbirds. Journal of Avian Biology 4:501-506.

Chu M. (2001): Heterospecific responses to scream calls and vocal mimicry by phainopeplas (*Phainopepla nitens*): in distress. Behaviour 138:775-787.

Cibulková A., Veselý P., Fuchs R. (2014): Importance of conspicuous colours in warning signals? The Great tit's (*Parus major*): point of view. Evolutionary Ecology 28:427-439.

Clinchy M., Zanette L., Charlier T.D., Newman A.E.M., Schmidt K.L., Boonstra R., Soma K.K. (2011): Multiple measures elucidate glucocorticoid responses to environmental variation in predation threat. Oecologia 166:607-614.

Clode D., Birks J.D.S., Macdonald D.W. (2000): The influence of risk and vulnerability on predator mobbing by terns (Sterna spp.): and gulls (Larus spp.). Journal of Zoology 252:53-59.

Cockrem J.F., Silverin B. (2002): Sight of a predator can stimulate a corticosterone response in the great tit (*Parus major*). General and Comparative Endocrinology 125:248–255.

Cockrem J.F. (2013): Individual variation in glucocorticoid stress responses in animals. General and Comparative Endocrinology 181:45-58.

Conner L.M., Rutledge J.C., Smith L.L. (2010): Effects of Mesopredators on Nest Survival of Shrub-Nesting Songbirds. Journal of Wildlife Managent 74:73-80.

Conkling T.J., Pope T.L., Smith K.N., Mathewson H.A., Morrison M.L., Wilkins R.N., Cain J.W. (2012): Black-capped vireo nest predator assemblage and predictors for nest predation. Journal of Wildlife Managent 76:1401-1411.

Conover M.R. (1987): Acquisition of Predator Information by Active and Passive Mobbers in Ring-Billed Gull Colonies. Behaviour 102:41-57.

Conover M.R., Perito J.J. (1981): Response of starlings to distress calls and predator models holding conspecific prey. Zeitschrift für Tierpsychologie 57:163-172.

Cook N.J. (2012): Review: Minimally invasive sampling media and the measurement of corticosteroids as biomarkers of stress in animals. Canadian Journal of Animal Science 92:227-259.

Cordero P.J., Senar J.C. (1990): Interspecific nest defence in European Sparrows: different strategies to deal with a different species of opponent? Ornis Scan 21:71-73.

Courter J.R., Ritchison G. (2010): Alarm calls of tufted titmice convey information about predator size and threat. Behavioral Ecology 21:936-942.

Cox W.A., Pruett M.S., Benson T.J., Chiavacci S.J., Thompson F.R. III (2012): Development of Camera Technology for Monitoring Nests. USGS Northern Prairie Wildlife Research Center, Paper 250.

Cramp S. ed (1979): The Birds of the Western Palearctic, Volume 2: Hawks to Bustards. Oxford University Press, Oxford

Cresswell W., Butler S., Whittingham M.J., Quinn J.L. (2009): Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. Behaviour 146:795-813.

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. (1976): The ethology of predation. Springer, Berlin

Curio E., Ernst U., Vieth W. (1978): Cultural transmission of enemy recognition: one function of mobbing. Science 202:899-901.

Curio E., Klump G., Regelmann K. (1983): An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? Oecologia 60:83-88.

Curio E., Onnebrink H. (1995): Brood defense and brood size in the Great Tit (*Parus major*): a test of a model of unshared parental investment. Behavioral Ecology 6:235-241.

Curio E., Regelmann K. (1985): The behavioural dynamics of Great Tits (*Parus major*): approaching a predator. Zeitschrift für Tierpsychologie 69:3-18.

Curio E., Regelmann K. (1986): Predator harassment implies a real deadly risk: a reply to Hennessy. Ethology 72:75-78.

Cutler T.L., Swann D.E. (1999): Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571-581.

D’Orazio K.A., Neudorf D.L.H. (2008): Nest defense by Carolina Wrens. Wilson Journal of Ornithology 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.

Davies N.B., Welbergen J.A. (2008): Cuckoo - hawk mimicry? An experimental test. Proceedings of the Royal Society B: Biological Sciences 275:1817-1822.

Davies Z.G., Fuller R.A., Dallimer M., Loram A., Gaston K.J. (2012): Household Factors Influencing Participation in Bird Feeding Activity: A National Scale Analysis. Plos One 7:e39692.

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.

Dessborn L., Englund G., Elmberg J., Arzél C. (2012): Innate responses of mallard ducklings towards aerial, aquatic and terrestrial predators. Behaviour 149:1299-1317.

Deviche P., Gao S., Davies S., Sharp P.J., Dawson A. (2012): Rapid stress-induced inhibition of plasma testosterone in free-ranging male rufous-winged sparrows, *Peucaea carpalis*: Characterization, time course, and recovery. General and Comparative Endocrinology 177:1-8.

Dickens M.J., Bentley G.E. (2014): Stress, captivity, and reproduction in a wild bird species. Hormones and behavior 66:685-693.

Duckworth J.W. (1997): Mobbing of a drongo cuckoo *Surniculus lugubris*. Ibis 139:190-192.

Dufty A.M., Crandall M.B. (2005): Corticosterone secretion in response to adult alarm calls in American Kestrels. Journal of Field Ornithology 76:319-325.

Dunn E.H., Tessaglia D.L. (1994): Predation of birds at feeders in winter. Journal of Field Ornithology 65:8-16.

East M. (1981): Alarm calling and parental investment in the robin (*Erithacus rubecula*). Ibis 123:223-230.

Edelaar P., Wright J. (2006): Potential prey make excellent ornithologists: adaptive, flexible responses towards avian predation threat by Arabian Babblers *Turdoides squamiceps* living at a migratory hotspot. Ibis 148:664-671.

Edwards G., Hosking E., Smith S. (1950): Reactions of some passerine birds to a stuffed cuckoo. II. A Detailed Study of the Willow Warbler. British Birds 43:144-150.

Eggers S., Griesser M.., Ekman J. (2005): Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). Behavioral Ecology 16:309-315.

Ekman J., Eggers S., Griesser M.., Tegelström H. (2001): Queuing for preferred territories: delayed dispersal of Siberian Jays. Journal of Animal Ecology 70:317-324.

Elgar M.A .(1989): Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biological Reviews of the Cambridge Philosophical Society 64:13-33.

Elliot R.D. (1985): The effects of predation risk and group size on the anti-predator responses of nesting lapwings *Vanellus vanellus*. Behaviour 92:169-187.

Ely C.R., Ward D.H., Bollinger K.S. (1999): Behavioral correlates of heart rates of free-living Greater White-fronted Geese. Condor 101:390-395.

Enstipp M.R., Andrews R.D., Jones D.R. (1999): Cardiac responses to first ever submergence in double-crested cormorant chicks (Phalacrocorax auritus). Comp Biochem Phys A 124:523-530.

Evans C.S., Evans L., Marler P. (1993a): On the meaning of alarm calls: functional reference in an avian vocal system. Animal Behaviour 46:23-28.

Evans C., Macedonia J., Marler P. (1993b): 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.

Ficken M.S., Hailman E.D., Hailman J.P. (1994): The chick-a-dee call system of the Mexican chickadee. Condor 96:70-82.

Ficken M.S., Ficken R.W., Witkin S.R. (1978): Vocal repertoire of the black-capped chickadee. Auk 34-48.

Filiater T.S., Breitwisch R., Nealen P.M. (1994): Predation on northern cardinals nests: Does choice of nest site matter? Condor 96:761-768.

Fisher R.J., Wiebe K.L. (2006): Investment in nest defense by Northern flickers: effects of age and sex. Wilson Journal of Ornithology 118:452-460.

Flasskamp A. (1994): The adaptive significance of avian mobbing. An experimental test of the move on hypothesis. Ethology 96:322-333.

Fluck E., Hogg S., Mabbutt P.S., File S.E. (1996): Behavioural and Neurochemical Responses of Male and Female Chicks to Cat Odour. Pharmacology Biochemistry and Behavior 54:85-91.

Folkers K.L., Lowther P.E. (1985): Responses of nesting red-winged blackbirds and yellow warblers to brown-headed cowbirds. Journal of Field Ornithology 56:175-177.

Forbes M., Clark R., Weatherhead P., Armstrong T. (1994): Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. Behavioral Ecology and Sociobiology 34:79-85.

Frankenberg E. (1981): The adaptive significance of avian mobbing IV. "alerting others" and "perception advertisement" in blackbirds facing an owl. Zeitschrift für Tierpsychologie 55:97-118.

Fransson T., Weber T.D. (1997): Migratory fuelling in blackcaps (*Sylvia atricapilla*): under perceived risk of predation. Behavioral Ecology and Sociobiology 41:75-80.

Freeberg T.M., Lucas J.R. (2002): Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. Animal Behaviour 63:837-845.

Friesen L.E., Casbourn G., Martin V., Mackay R.J. (2013): Nest predation in an anthropogenic landscape. Wilson Journal of Ornithology 125:562-569.

Fuchs E. (1977): Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. Ornis Scand 8:17-32.

Fuller R.A., Warren P.H., Armsworth P.R., Barbosa O., Gaston K.J. (2008): Garden bird feeding predicts the structure of urban avian assemblages. Diversity and Distributions 14:131-137.

Gaddis P. (1980): Mixed flocks, accipiters, and antipredator behavior. Condor 82:348-349.

Gentle L.K., Gosler A.G. (2001): Fat reserves and perceived predation risk in the great tit, *Parus major*. Proceedings of the Royal Society of London series B-Biological Sciences 268:487–491.

Gérard A., Jourdan H., Millon A., Vidal E. (2015): Anti-predator behaviour in a procellariid seabird: Wedge-tailed shearwaters do not respond to the odour of introduced ship rats: Anti-predator behaviour in seabird. Austral Ecol 40:775-781.

Ghalambor C.K., Martin T.E. (2000): Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Gill S.A., Grieef P.M., Staib L.M., Sealy S.G. (1997): Does nest defence deter or facilitate cowbird parasitism? A test of the nesting-cue hypothesis. Ethology 103:56-71.

Gill S.A., Neudorf D.L., Sealy S.G. (1997): Host responses to cowbirds near the nest: cues for recognition. Animal Behaviour 53:1287-1293.

Gill S.A., Sealy S.G. (1996): Nest Defence by Yellow Warblers: Recognition of a Brood Parasite and an Avian Nest Predator. Behaviour 133:263-282.

Gill S.A., Sealy S.G. (2004): Functional reference in an alarm signal given during nest defence: seet calls of yellow warblers denote brood-parasitic brown-headed cowbirds. Behavioral Ecology and Sociobiology. 56:71-80.

Gilson W.D., Kraitchman D.L. (2007): Cardiac Magnetic Resonance Imaging in Small Rodents using Clinical 1.5T and 3.0T Scanners. Methods 43:35-45.

Gluckman T.L., Mundy N.I. (2013): Cuckoos in raptors’ clothing: barred plumage illuminates a fundamental principle of Batesian mimicry. Animal Behaviour 86:1165-1181.

Gochfeld M. (1984): Antipredator behavior: aggressive and distraction displays of shorebirds. In: Burger J, Olla BL (eds): Behavior of marine animals 5. Plenum Press, New York

Godard R.D., Bowers B.B., Wilson C.M. (2007): Eastern bluebirds Sialia sialis do not avoid nest boxes with chemical cues from two common nest predators. Journal of Avian Biology 38:128-131

Goethe F. (1937): Beobachtungen und Untersuchungen zur Bioiogie der Silbermöwe (Larus a. argentatus Pontopp.): auf der Vogelinsel Memmertsand. Journal of Ornithology 85:1-119.

Goethe F. (1940): Beobachtungen und Versuche über angeborene Schreckreaktionen junger Auerhühner. Zeitschrift für Tierpsychologie 4:165-167.

Goławski 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.

Goławski 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 57:403-410.

Göth A. (2001): Innate predator-recognition in Australian brush-turkey (*Alectura lathami*, Megapodiidae): hatchlings. Behaviour 138:117-136.

Gottfried B.M. (1979): Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. Condor 81:25l-257.

Goymann W. (2012): On the use of non-invasive hormone research in uncontrolled, natural environments: the problem with sex, diet, metabolic rate and the individual. Methods in Ecology and Evolution 3:757-765.

Green R., Carr W., Green M. (1968): The hawk-goose phenomenon: further confirmation and a search for the releaser. The Journal of Psychology 69:271-276.

Green R.E., Hirons G.J.M., Kirby J.S. (1990): The effectiveness of nest defence by black-tailed godwits *Limosa limosa*. Ardea 78:405-413.

Greig-Smith P.W. (1980): Parental investment in nest defence by stonechats (*Saxicola torquata*): Animal Behaviour 28:604-619.

Griesser M. (2003): Nepotistic vigilance behavior of Siberian jay parents. Behavioral Ecology 14:246-250.

Griesser M. (2008): Referential calls signal predator behavior in a group living bird species. Currrent Biology 18:69-73.

Griesser M. (2009): Mobbing calls signal predator category in a kin group-living bird species. Proceedings of the Royal Society of London series B-Biological Sciences 276:2887-2892.

Griffin A.S. (2004): Social learning about predators: a review and prospectus. Animal Learning & Behavior 32:131-140.

Griffin A.S. (2008): Social learning in Indian mynahs, *Acridotheres tristis*: the role of distress calls. Animal Behaviour 75:79-89

Griffin A.S., Evans C.S., Blumstein D.T. (2001): Learning specificity in acquired predator recognition. Animal Behaviour 62:577–589

Griffin A.S., Savani R.S., Hausmanis K., Lefebvre L. (2005): Mixed-species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*. Animal Behaviour 70:507-515.

Griggio M., Matessi G., Pilastro A. (2003): Male Rock Sparrow (*Petronia petronia*): nest defence correlates with female ornament size. Ethology 109:659-669.

Grim T. (2005): Host Recognition of Brood Parasites: Implications for Methodology in Studies of Enemy Recognition. Auk 122:530-543

Grubb T.C. Jr (1977): Discrimination of aerial predators by American coots in nature. Animal Behaviour 25:1065-1066.

Guillory H.D., LeBlanc D.J. (1975): Mobbing and other interspecific aggression by Barn Swallows. The Wilson Bulletin 87:110-112.

Gunn J.S., Desrochers A., Villard M.A., Bourque J. (2000): Playbacks of mobbing calls of black-capped chickadees as a method to estimate reproductive activity of forest birds. Journal of Field Ornithology 71:472-483.

Gyger M., Marler P., Pickert R. (1987): Semantics of an avian alarm cal system: the male domestic fowl, *Gallus domesticus*. Behaviour 102:15-40.

Hagelin J.C., Jones IL, Rasmussen LEL (2003): A tangerine-scented social odour in a monogamous seabird. Proceedings of the Royal Society of London series B-Biological Sciences 270:1323-1329.

Hagelin J.C., Jones I.L. (2007): Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? Auk: 124:741-761.

Hakkarainen H., Korpimäki E. (1994): Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. Animal Behaviour 48:843-849.

Hakkarainen H., Yli-Tuomi I., Korpimäki E., Ydenberg R. (2002): Provisioning response to manipulation of apparent predation danger by parental pied flycatchers. Ornis Fennica 79:139-144.

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.

Halupka K., Halupka L. (1997): The influence of reproductive season stage on nest defence by meadow pipits (*Anthus pratensis*). Ethology Ecology & Evolution 9:89-98.

Hamer K.C., Furness R.W. (1993): Parental investment and brood defense by male and female Great Skuas *Catharacta skua*: the influence of food-supply, laying date, body size and body condition. Journal of Zoology 230:7-18.

Harkin A., O'Donnell J.M., Kelly J.P. (2002): A study of VitalView ™ for behavioural and physiological monitoring in laboratory rats. Physiology & Behavior 77:65-77.

Harvey P.H., Greenwood P.J. (1978): Anti-predator defence strategies: some evolutionary problems. In: Krebs JR, Davies N.B. (eds.): Behavioural Ecology: an evolutionary approach. Blackwell, Oxford.

Hauser M.D., Caffrey C. (1994): Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*. Animal Behaviour 48:1469-1471.

Hauser M.D., Wrangham R.W. (1990): Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. Ethology 86:116-130.

Hill G.E. (1986): The function of distress calls given by tufted titmice (*Parus bicolor*). Animal Behaviour 34:590-598.

Hilton G.M., Cresswell W., Ruxton G.D. (1999): Intraflock variation in the speed of escape-flight response on attack by an avian predator. Behavioral Ecology 10:391-395.

Hinde R.A. (1960): Factors governing the changes in strength of a partially inborn response as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). III . The interaction of short-term and long-term incremental and decremental effects. Proceedings of the Royal Society of London series B-Biological Sciences 153:398-420.

Hinsley S.A., Bellamy P.E., Moss D. (1995): Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. Ibis 137:418-420.

Hobson K.A., Sealy S.G. (1989): Responses of yellow warblers to the threat of Cowbird parasitism. Animal Behaviour 38:510-519.

Hobson K.A., Bouchart M.L., Sealy S.G. (1988): Reponses of naïve Yellow Warblers to a novel nest predator. Animal Behaviour 36:1823-1830.

Hogstad O. (1993): Nest defence and physical condition in Fieldfare *Turdus pilaris*. Journal of Ornithology 134:25-33.

Hogstad O. (1995): Alarm calling by willow tits, *Parus montanus*, as mate investment. Animal Behaviour 49:221-223.

Hogstad O. (2005): Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition. Ibis 147:375-380.

Hollander F.A., Van Overveld T., Tokka I., Matthysen E. (2008): Personality and Nest Defence in the Great Tit (*Parus major*). Ethology 114:405-412.

Holway D.A. (1991): Nest-site selection and the importance of nest concealment in the black-throated blue warbler. Condor 93:575-581.

Hölzer C., Bergmann H-H., McLean I.G. (1996): Training captive-raised, naive birds to recognise their predator. In: Ganslosser U, Hodges JK, Kaumanns W (eds): Research and captive propagation. Filander Verlag, Fürth

Honza M., Šicha V., Procházka P., Ležalová R. (2006): Host nest defense against a color-dimorphic brood parasite: great reed warblers (*Acrocephalus arundinaceus*): versus common cuckoos (*Cuculus canorus*). Journal of Ornithology 147:629-637.

Honza M., Šulc M., Jelínek V., Požgayová M., Procházka P. (2014): Brood parasites lay eggs matching the appearance of host clutches. Proceedings of the Royal Society of London series B-Biological Sciences 281:20132665

Jacobsen O.W., Ugelvik M. (1992): Antipredator behavior of breeding *Eurasian wigeon*. Journal of Field Ornithology 63:324-330.

Jansson C., Ekman J., von Brömssen A. (1981): Winter Mortality and Food Supply in Tits *Parus* spp. Oikos 37:313-322.

Jenni-Eiermann S., Helfenstein F., Vallat A., Glauser G., Jenni L. (2015): Corticosterone: effects on feather quality and deposition into feathers. Methods in Ecology and Evolution 6:237-246.

Johnson-Delaney C.A. (2003): Use of the vetronics CardioStore for avian ECG. 24th Annual Conference and Expo of the Association-of-Avian-Veterinarians, Pittsburgh, PA, Aug 26-28, 2003. Také Flight in Pittsburgh, Proceedings, Pages: 19-21.

Johnstone C.P., Reina R.D., Lill A. (2012): Interpreting indices of physiological stress in free-living vertebrates. Journal of Comparative Physiology B 182:861-879.

Kagawa H., Suzuki K., Takahasi M., Okanoya K. (2014): Domestication changes innate constraints for birdsong learning. Behavioural processes 106:91-97.

Kleindorfer S., Hoi H., Fessl B. (1996): Alarm calls and chick reactions in the moustached warbler, *Acrocephalus melanopogon*. Animal Behaviour 51:1199-1206.

Kleindorfer S., Fessl B., Hoi H. (2003): The role of nest site cover for parental nest defence and fledging success in two *Acrocephalus warblers*. Avian Science 3:21-29.

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.

Klump G.M., Curio E. (1983): Reactions of Blue Tits *Parus caeruleus* to Hawk Models of Different Sizes. Bird Behavior 4:78-81.

Knight R.L., Temple S.A. (1986a): Methodological problems in studies of avian nest defence. Animal Behaviour 34:561-566.

Knight R.L., Temple S.A. (1986b): Nest defense in the American goldfinch. Animal Behaviour 34:879-897.

Knight R.L., Temple S.A. (1986c): Why does intensity of avian nest defence increase during the nesting cycle? Auk 103:318-327.

Knight R.L., Temple S.A. (1988): Nest-defense behavior in the red-winged blackbird. Condor 90:193-200.

Koivula K, Rytkönen, Orell M. (1995): Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate willow tits. Ardea 83:397-404.

Krams I. (2000): Length of feeding day and body weight of great tits in a single and a two-predator environment. Behavioral Ecology and Sociobiology 48:147-153.

Krams I. (2001): Communication in crested tits and the risk of predation. Animal Behaviour 61:1065-1068.

Krams I., Krama T., Igaune K. (2006): Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? Journal of Avian Biology 37:131-136.

Krätzig H. (1940): Untersuchungen zur Lebensweise des Moorschneehuhns (*Lagopus l. lagopus L.*): während der Jugendentwicklung. Journal of Ornithology 88:139-165.

Kruger O. (2005): The evolution of reversed sexual size dimorphism in hawks, falcons and owls: A comparative study. Evolutionary Ecology 19:467-486.

Kruuk H. (1964): Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus*). Behaviour. Supplement 11:1-129.

Kruuk H. (1976): The biological function of gulls' attraction towards predators. Animal Behaviour 24:146-153.

Kullberg C. (1998): Spatial niche dynamics under predation risk in the Willow Tit *Parus montanus*. Journal of Avian Biology 29:235-240.

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.

Lack D. (1943): The life of the robin. Whiterby, London

Lack D. (1954): The Natural Regulation of Animal Numbers. Clarendon Press, Oxford

Lane J. (2006): Can non-invasive glucocorticoid measures be used as reliable indicators of stress in animals? Animal Welfare 15:331-342.

Langmore N.E., Feeney W.E., Crowe-Riddell J., Luan H., Louwrens K.M., Cockburn A. (2012): Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. Behavioral Ecology 23:798-805.

Leger D.W., Carrol L.F. (1981): Mobbing calls of the Phainopepla. Condor 83:377-380.

Lemmetyinen R. (1971): Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators. Ornis Fennica 48:13-24.

Liang W., Møller A.P. (2015): Hawk mimicry in cuckoos and anti-parasitic aggressive behavior of barn swallows in Denmark and China. Journal of Avian Biology 46:216-223.

Lilliendahl K. (1997): The effect of predator presence on body mass in captive greenfinches. Animal Behaviour 53:75-81.

Lima S.L. (1993): Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. The Wilson Bulletin 105:l-47.

Lima S.L. (1995): Back to the basics of anti-predatory vigilance: the group size effect. Animal Behaviour 49:11-20.

Lima S.L., Dill L.M. (1990): Behavioral decisions made under the risk of predation - A review and prospectus. Canadian Journal of Zoology 68:619-640.

Lind J., Jongren F., Nilsson J., Alm D.S., Strandmark A. (2005): Information, predation risk and foraging decisions during mobbing in great tits *Parus major*. Ornis Fennica 82:89-96.

Londoño G.A., García D.A., Sánchez Martínez M.A. (2015): Morphological and Behavioral Evidence of Batesian Mimicry in Nestlings of a Lowland Amazonian Bird. The American Naturalist 185:135-141.

Lorenz K. (1937a): The companion in the bird's world. Auk 54:245-273.

Lorenz K. (1937b): Über die Bildung des Instinktbegriffes. Naturwissenschaften 25:289–300.

Lorenz K. (1939): Vergleichende verhaltensforschung. Verhandlungen der Deutschen Zoologischen Gesellschaft Zoologischer Anzeiger, Supplementband 12: 69–102.

Lyon B.E., Gilbert G.S. (2013): Rarely Parasitized and Unparasitized Species Mob and Alarm Call to Cuckoos: Implications For Sparrowhawk Mimicry By Brood Parasitic Cuckoos. Wilson Journal of Ornithology 125:627-630.

Magrath R.D., Pitcher B.J., Gardner J.L. (2007): A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. Behavioral Ecology 18:944-951.

Magrath R.D., Haff T.M., Horn A.G., Leonard M.L. (2010): Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. Advances in the Study of Behavior 41:187-253.

Maloney R.F., McLean I.G. (1995): Historical and experimental learned predator recognition in free-living New-Zealand robins. Animal Behaviour 50:1193-1201.

Mark D., Stutchbury B.J. (1994): Response of a forest-interior songbird to the threat of cowbird parasitism. Animal Behaviour 47:275-280.

Marr D., Nishihara H.K. (1978): Representation and recognition of spatial-organization of 3-dimensional shapes. Proceedings of the Royal Society of London series B-Biological Sciences 200:269-294.

Martín J., de Neve L., Polo V., Fargallo J.A., Soler M. (2006): Health-dependent vulnerability to predation affects escape responses of unguarded chinstrap penguin chicks. Behavioral Ecology and Sociobiology 60:778-784.

Martin T.E. (1993a): Nest predation among vegetation layers and habitat types: Revising the dogmas. The American Naturalist 141:897-913.

Martin T.E. (1993b): Nest predation and nest sites. BioScience 43:523-532.

Martin T.E., Roper JJ (1988): Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51-57.

Mathot K.J., van den Hout P.J., Piersma T. (2009): Differential responses of red knots, *Calidris canutus*, to perching and flying sparrowhawk, *Accipiter nisus*, models. Animal Behaviour 77:1179-1185.

McLean I.G. (1987): Response to a dangerous enemy: should a brood parasite be mobbed? Ethology 75:235-245.

McLean I.G., Hölzer C., Studholme B.J. (1999): Teaching predator-recognition to a naive bird: implications for management. Biological Conservation 87:123-130.

McLean I.G., Lundie-Jenkins G., Jarman P.J. (1996): Teaching an endangered mammal to recognise predators. Biological Conservation 75:51-62.

McLean I.G., Rhodes G. (1991): Enemy recognition and response in birds. Current Ornithology 8:173-211.

McLean I.G., Smith J.N.M., Stewart K.G. (1986): Mobbing behaviour, nest exposure, and breeding success in the american robin. Behaviour 96:171-185.

McNicholl M.K. (1973): Habituation of aggressive responses to avian predators by tems. Auk 90:902-904.

McPhail L.T., Jones D.R. (1998): The relationship between power output and heart rate in ducks diving voluntarily. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 120:219-225.

Meilvang D., Moksnes A., Røskaft E. (1997): Nest predation, nesting characteristics and nest defence behaviour of Fieldfares and Redwings. Journal of Avian Biology 28:331-337.

Melvin K.B., Cloar F.T. (1969): Habituation of responses of quail (*Colinus virginianus*): to a Hawk (*Buteo swainsoni*): Measurement through an 'innate suppression' technique. Animal Behaviour 17:468-473.

Melzack R., Penick E., Beckett A. (1959): The problem of innate fear of the hawk shape: an experimental study with mallard ducks. Journal of Comparative and Physiological Psychology 52:69-698.

Miller L. (1952): Auditory recognition of predators. Condor 54:89-92.

Minderman J., Lind J., Cresswell W. (2006): Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. Journal of Animal Ecology 75:713-723.

Moksnes A., Røskaft E., Braa A.T., Korsnes L., Lampe H.T., Pedersen H.C. (1990): Behavioural responses of potential hosts towards artificial Cuckoo eggs and dummies. Behaviour 116: 64-89.

Montgomerie R.D., Weatherhead P.J. (1988): Risks and Rewards of Nest Defence by Parent Birds. The Quarterly Review of Biology 63:167-187.

Moore E.L., Mueller H.C. (1982): Cardiac responses of domestic chickens to hawk and goose models. Behavioural Processes 7:255-258.

Mueller H.C., Parker P.G. (1980): Naive ducklings show different cardiac response to hawk than to goose models. Behaviour 74:101-113.

Müller M., Pasinelli G., Schiegg K., Spaar R., Jenni L. (2005): Ecological and social effects on reproduction and local recruitment in the red-backed shrike. Oecologia 143:37-50.

Murphy T.G. (2006): Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail. Behavioral Ecology 17:547-553.

Murray L. (2015): Success and Predation of Bird Nests in Grasslands at Valley Forge National Historical Park. Northeastern Naturalist 22:10-19.

Naguib M., Janik V., Clayton N., Zuberbühler K. (2009): Vocal Communication in Birds and Mammals. Academic Press.

Naguib M., Mundry R., Ostreiher R., Hultsch H., Schrader L., Todt D. (1999): Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. Behavioral Ecology 10:636-640.

Nealen P.M., Breitwisch R. (1997): Northern cardinal sexes defend nests equally. The Wilson Bulletin 109:269-278.

Němec M., Fuchs R. (2014): Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. Acta ethologica 17:149-154.

Němec M., Syrová M., Dokoupilová L., Veselý P., Šmilauer P., Landová E., Lišková S., Fuchs R. (2015): Surface texture plays important role in predator recognition by Red-backed Shrikes in field experiment. Animal cognition 18:259-268.

Němec M., Součková T., Fuchs R. (unpublished): The red-backed shrike *Lanius collurio* recognize the predator due local, not due global features.

Neudorf D.L., Sealy S.G. (1992): Reactions of Four Passerine Species to Threats of Predation and Cowbird Parasitism: Enemy Recognition or Generalized Responses? Behaviour 123:84-105.

Nice M.M., Ter Pelkwyk J. (1941): Enemy recognition by the song sparrow. Auk 58:195-214.

Nijman V. (2004): Seasonal variation in naturally occurring mobbing behaviour of drongos (Dicruridae): towards two avian predators. Ethology Ecology & Evolution 16:25-32.

Nilsson S.G. (1984): The evolution of nest site selection among hole-nesting birds: The importance of nest predation and competition. Ornis Scand 15:167-175.

Nocera J.J., Ratcliffe L.M. (2009): Migrant and resident birds adjust antipredator behavior in response to social information accuracy. Behavioral Ecology 21:121-128.

Olendorf R., Robinson S.K. (2000): Effectiveness of nest defence in the Acadian Flycatcher *Empidonax virescens*. Ibis 142:365-371.

Orchinik M. (1998): Glucocorticoids, Stress, and Behavior: Shifting the Timeframe. Hormones and behavior 34:320-327.

Owen R.B. (1969): Heart rate, a measure of metabolism in the blue-winged teal. Comparative Biochemistry and Physiology 31:431-436.

Palestis B.G. (2005): Nesting Stage and Nest Defense by Common Terns. Waterbirds 28:87-94.

Palleroni A., Hauser M., Marler P. (2005): Do responses of galliform birds vary adaptively with predator size? Animal cognition 8:200-210.

Patterson T.L., Petrinovich L., James D.K. (1980): Reproductive value and appropriateness of response to predators by White-crowned Sparrows. Behavioral Ecology and Sociobiology 7:227-231.

Pavel V., Bureš S. (2001): Offspring age and nest defence: test of the feedback hypothesis in the meadow pipit. Animal Behaviour 61:297-303.

Peluc S.I., Sillett T.S., Rotenberry J.T., Ghalambor C.K. (2008): Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Poiani A., Yorke M. (1989): Predator harassment: More evidence on the deadly risk. Ethology 83:167-169.

Pravosudov V.V., Grubb T.C.J. (1998): Management of fat reserves in tufted titmice, Baelophus bicolor, in relation to risk of predation. Animal Behaviour 56:49-54.

Quinn J.L., Cresswell W. (2005): Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. Behaviour 142:1383-1408.

Quinn J.L., Cole E.F., Bates J., Payne R.W., Cresswell W. (2012): Personality predicts individual responsiveness to the risks of starvation and predation. Proceedings of the Royal Society of London series B-Biological Sciences 279:1919-1926.

Radford A.N., Blakey J.K. (2000): Intensity of nest defence is related to offspring sex ratio in the Great Tit *Parus major*. Proceedings of the Royal Society of London series B-Biological Sciences 267:535-538.

Rainey H.J., Zuberbuhler K., Slater P.J.B. (2004): The responses of Black-casqued Hornbills to predator vocalisations and primate alarm calls. Behaviour 141:1263-1277.

Randler C. (2006): Disturbances by dog barking increase vigilance in coots *Fulica atra*. European Journal of Wildlife Research 52:265-270.

Redondo T. (1989): Avian Nest Defence: Theoretical Models and Evidence. Behaviour 111:161-195.

Redondo T., Carranza J. (1989): Offspring reproductive value and nest defense in the magpie (*Pica pica*). Behavioral Ecology and Sociobiology 25:369-378.

Remeš V. (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.

Reudink M.W., Nocera J.J., Curry R.L. (2007): Anti-predator responses of Neotropical resident and migrant birds to familiar and unfamiliar owl vocalizations on the Yucatan peninsula. Ornitologia Neotropical 18:543-552.

Riclefs R.E. (1969): An analysis of nesting mortality in birds. Smithsonian contributions to zoology 9:1-48.

Robb G.N., McDonald R.A., Chamberlain D.E., Reynolds S.J., Harrison T.H.E., Bearhop S. (2008a): Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters 4:220-223.

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

Robertson R.J., Norman R.F. (1977): The function and evolution of aggressive host behaviour toward the Brown-Headed Cowbird (*Molothrus ater*). Canadian Journal of Zoology 55:508-518.

Rodriguez-Prieto I., Fernández-Juricic E., Martín J., Regis Y. (2009): Antipredator behavior in blackbirds: habituation complements risk allocation. Behavioral Ecology 20:371-377.

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

Roth T.C., Cox J.G., Lima S.L. (2008): The Use and Transfer of Information About Predation Risk in Flocks of Wintering Finches. Ethology 114:1218-1226.

Rothstein S.I. (1990): A Model System for Coevolution: Avian Brood Parasitism. Annual Review of Ecology and Systematics 21:481-508.

Rytkönen S. (2002): Nest defence in great tits Parus major: support for parental investment theory. Behavioral Ecology and Sociobiology 52:379-384.

Rytkönen S., Koivula K., Orell M. (1990): Temporal increase in nest defence intensity of the willow tit (*Parus montanus*); parental investment or methodological artefact? Behavioral Ecology and Sociobiology 27:283-286.

Rytkönen S., Orell M., Koivula K., Soppela M. (1995): Correlation between two components of parental investment: nest defence intensity and nestling provisioning effort of willow tits. Oecologia 104:386-393.

Sansom A., Lind J., Cresswell W. (2009): Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. Behavioral Ecology 20:1168-1174.

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.

Schaller G.B., Emlen Jr J.T. (1962): The ontogeny of avoidance behaviour in some precocial birds. Animal Behaviour 10:370-381.

Schetini de Azevedo C., Young R.J., Rodrigues M. (2012): Failure of captive-born greater rheas (*Rhea americana*, Rheidae, Aves): to discriminate between predator and nonpredator models. Acta ethologica 15:179-185.

Schleidt W., Shalter M.D., Moura-Neto H. (2011): The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. Journal of Comparative Psychology 125:121-133.

Scheuerlein A., Van't Hof T.J., 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.

Shalter M.D. (1978): Mobbing in the Pied Flycatcher: effect of experiencing a live owl on responses to a stuffed facsimile. Zeitschrift für Tierpsychologie 47:173-179.

Shedd D.H. (1982): Seasonal variation and function of mobbing and related antipredatory behviors of the American robin (*Turdus migratorius*). Auk 99:342-346.

Shedd D.H. (1983): Seasonal variation in mobbing intenstity in the Black-capped chickadee. The Wilson Bulletin 95:343-348.

Shields W.M. (1984): Barn swallow mobbing: Self-defence, collateral kin defence, group defence, or parental care? Animal Behaviour 32:132-148.

Siegel-Causey D., Hunt Jr. G.L. 1981. Colonial defense behavior in Double-crested and Pelagic Cormorants. Auk 98:522-531.

Sieving K.E., Hetrick S.A., Avery M.L. (2010): The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. Oikos 119:264-276.

Simmons K.E.L. (1955): The nature of the predator reactions of waders towards humans, with special reference to the role of the aggressive-, escape- and brooding-drives. Behaviour 8:130-173.

Skutch A.F. (1949): Do tropical birds rear as many young as they can nourish? Ibis 91:430-458.

Smith E.L. (1970): Cactus Wrens attack Ground Squirrel. Condor 72:363-364.

Smith S.M. (1997): The black-capped chickadee. Behavioral ecology and natural history. Cornell University Press, Ithaca, New York

Smith J.M., Graves H.B. (1978): Some factors influencing mobbing behaviour in barn swallows Hirundo rustica. Behavioral Biology 23:355-372.

Smith J.N.M., Arcese P., McLean I.G. (1984): Age, experience, and enemy recognition by wild song sparrows. Behavioral Ecology and Sociobiology 14:101-106.

Soard C.M., Ritchison G. (2009): "Chick-a-dee" calls of Carolina chickadees convey information about degree of threat posed by avian predators. Animal Behaviour 78:1447-1453.

Sordahl T.A. (1990): The risks of avian mobbing and distraction behavior: an anecdotal review. The Wilson Bulletin 102:349-352.

Sordahl T.A. (2004): Field evidence of predator discrimination abilities in American Avocets and Black-necked Stilts. Journal of Field Ornithology 75:376-385.

Stenhouse I.J., Gilchrist H.G., Montevecchi W.A. (2005): An experimental study examining the anti-predator behaviour of Sabine's gulls (*Xema sabini*): during breeding. Journal of ethology 23:103-108.

Stoddard M.C. (2012): Mimicry and masquerade from the avian visual perspective. Current Zoology 58:630-648.

Stone E., Trost C.H. (1991): Predators, risks and context for mobbing and alarm calls in black-billed magpies. Animal Behaviour 41:633-638.

Storch S., Gremillet D., Culik B.M. (1999): The telltale heart: A non-invasive method to determine the energy expenditure of incubating great cormorants *Phalacrocorax carbo carbo*. Ardea 87:207-215.

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.N. (2011): Parental alarm calls warn nestlings about different predatory threats. Currrent Biology 21:R15–R16.

Suzuki T.N. (2012): Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. Animal Behaviour 84:53-57.

Syrová M., Němec M., Veselý P., Landová E., Fuchs R. (unpublished): Facing a clever predator demands clever responses - red-backed shrike (*Lanius collurio*): vs. black-billed magpie (*Pica pica*)

Templeton C.N., Greene E., Davis K. (2005): Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size. Science 308:1934-1937.

Templeton C.N., 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.

Thorogood R. and Davies N.B. (2012): Cuckoos Combat Socially Transmitted Defenses of Reed Warbler Hosts with a Plumage Polymorphism. Science 337:578-580.

Tilgar V., Saag P., Kulavee R., Mand R. (2010): Behavioral and physiological responses of nestling pied flycatchers to acoustic stress. Hormones and behavior 57:481-487.

Tillmann J.E. (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.

Tinbergen N. (1948): Social releasers and the experimental method required for their study. The Wilson Bulletin 60:6-51.

Tinbergen N. (1951): The Study of Instinct. Clarendon Press, New York

Trail P.W. (1987): Predation and antipredator behaviour at Guianan Cock-of-the-rock leks. Auk 104:496-507.

Trnka A., Prokop P. (2012): The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. Animal Behaviour 83:263-268.

Trnka A., Prokop P., Grim T. (2012): Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites. PLoS One 7:e37445.

Trnka A., Trnka M., Grim T. (2015): Do rufous common cuckoo females indeed mimic a predator? An experimental test. Biological Journal of the Linnean Society 116:134-143.

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.

Tvardíková K., Fuchs R. (2010): Tits use amodal completion in predator recognition: a field experiment. Animal cognition 13:609-615.

Tvardíková K., Fuchs R. (2011): Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behavioral Ecology and Sociobiology 65:727-733.

Tvardíková K., Fuchs R. (2012): Tits recognize the potential dangers of predators and harmless birds in feeder experiments. Journal of ethology 30:157-165.

van den Hout P.J., Piersma T., Dekinga A., Lubbe S.K., Visser G.H. (2006): Ruddy turnstones Arenaria interpres rapidly build pectoral muscle after raptor scares. Journal of Avian Biology 37:425-430.

van den Hout P.L., Mathot K.J., Maas L.R.M., Piersma T. (2010): Predator escape tactics in birds: linking ecology and aerodynamics. Behavioral Ecology 21:16-25.

van der Veen I.T. (1999): Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citronella*). Behavioral Ecology 10:545-551.

Van Dongen S., Lens L., Matthysen E. (2001): Developmental instability in relation to stress and fitness in birds and moths studied by the Laboratory of Animal Ecology of the University of Antwerp. Belgian Journal of Zoology 131:59-64.

Van Hout A.J.M., Eens M., Darras V.M., Pinxten R. (2010): Acute stress induces a rapid increase of testosterone in a songbird: Implications for plasma testosterone sampling. General and Comparative Endocrinology 168:505-510.

Veen T., Richardson D.S., 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.

Veselý P., Buršíková M., Fuchs R. (2016): Birds at the Winter Feeder do not Recognize an Artificially Coloured Predator. Ethology 122: 1-8

Walters J.R. (1990): Anti-Predatory Behavior of Lapwings: Field Evidence of Discriminative Abilities. The Wilson Bulletin 102:49-70.

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.

Weatherhead P.J. (1989): Nest defence by song sparrows: methodological and life history considerations. Behavioral Ecology and Sociobiology 25:129-136.

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

Weidinger K. (2010): Foraging behaviour of nest predators at open-cup nests of woodland passerines. Journal of Ornithology 151:729-735.

Weisman R.G., Spetch M.L. (2010): Determining when birds perceive correspondence between pictures and objects: a critique. Comparative Cognition & Behavior Reviews, 5, 117-131.

Welbergen J.A., Davies N.B. (2008): Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. Animal Behaviour 76:811-822.

Welbergen J.A., Davies N.B. (2009): Strategic variation in mobbing as a front line of defense against brood parasitism. Currrent Biology 19:235-240.

Welbergen J.A., Davies N.B. (2011): A parasite in wolf’s clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behavioral Ecology 22:574-579.

Whittingham M.L., Butler S.J., Quinn J.L., Cresswell W. (2004): The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. Oikos 106:377-385.

Wiklund C.G. (1990): The adaptive significance of nest defence by merlin, *Falco columbarius*, males. Animal Behaviour 40:244-253.

Winkler D.W. (1992): Causes and consequences of variation in parental defence behaviour by tree swallows (*Tachycineta bicolor*). Condor 94:502-520.

Winkler D.W. (1994): Anti-predator defence by neighbours as a responsive amplifier of parental defence in tree swallows. Animal Behaviour 47:595-605.

Wong S. (1999): Visual predator recognition in Australian brush-turkey (*Alectura lathami*): hatchlings. In: Dekker RWRJ, Jones DN, Benshemesh J (eds): Proceedings of the Third International Megapode Symposium, Nhill, Australia, December 1997. Zoologische Verhandelingen, Leiden

Yang C., Wang L., Cheng S-J., Hsu Y-C., Liang W., Møller A.P. (2014): Nest defenses and egg recognition of yellow-bellied prinia against cuckoo parasitism. Naturwissenschaften 101: 727-734.

Ylönen H., Eccard J.A., Jokinen I., Sundell J. (2006): Is the antipredatory response in behaviour reflected in stress measured in faecal corticosteroids in a small rodent? Behavioral Ecology and Sociobiology 60:350-358.

Yorzinski J.L., Vehrencamp S.L. (2009): The effect of predator type and danger level on the mob calls of the American crow. Condor 111:159-168.

Zaccaroni M., Ciuffreda M., Paganin M., Beani L. (2007): Does an early aversive experience to humans modify antipredator behaviour in adult Rock partridges. Ethology Ecology & Evolution19:193-200.

Článek I.

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 Fennicaica 89:206-215.

Ornis Fennica 89:206–215. 2012

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

Martin Strnad, Michal Němec, Petr Veselý* & Roman Fuchs

M. Strnad & R. Fuchs, Faculty of Sciences, Charles University, Albertov 6, 128 43 Praha 2, Czech Republic
M. Němec, R. Fuchs & P. Veselý, Faculty of Science, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic. *Corresponding author's e-mail petr-vesely@seznam.cz*

Received 21 December 2011, accepted 11 April 2012

We studied the ability of Red-backed Shrikes to adjust their nest defence to the potential threat posed to defending adults and their nests. We presented mounts of two raptor species which prey 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 potential threat to the nest. The proportion of mobbing events resulting in physical contact (mobbing intensity) declined from the most mobbed species, Jay to the Kestrel, to the Sparrowhawk, which was considered most dangerous to adult shirkes. The Red-backed Shrikes appeared to adjusted their mobbing intensity by assessing the potential threat to themselves. Our results show the importance of a differentiation between mobbing intensity 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 2006) when this behaviour is used to avoid nest predation (Biermann & 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 & Krams 2005; Krams *et al.* 2007).

Like other forms of parental investment, predator mobbing is both time and energy consuming (Collias & Collias 1978, Dale *et al*. 1996, Scheuerlein *et al*. 2001); thus, the defending birds should adjust their mobbing behaviour according 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 a 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 & Temple 1986a, Sordahl 1990, Duckworth 1991, Jacobsen & Ugelvik 1992, Dale *et al.* 1996, Arroyo *et al*. 2001, Amat & Masero 2004, Hogstad 2005), owls vs. birds of prey (Arroyo *et al*. 2001), terrestrial vs. aerial predators (Bures & Pavel 2003, Hogstad 2005, Kleindorfer *et al*. 2005, Sordahl 1990) and predators vs. parasites (Duckworth 1991; Welbergen & Davies 2011; Trnka & Prokop 2012). Nevertheless, the danger presented by predators may differ significantly even within a specific guild: for example, a bird-capturing raptor is expected to represent a bigger threat for defending birds (and potentially for fledglings) than does a small mammal-catching raptor. In order for the defending birds to respond adequately to these predators, they should have the ability to discriminate between particular predator species and not only groups of predators. This ability has not been tested in the above-mentioned studies. 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, so that the ability of a defending bird to discriminate between particular predator species could be tested. We examined the nest-defence behaviour in a 30-g passerine, the Red-backed Shrike (*Lanius collurio*) as a good experimental model species with which to study defence behaviour, as it vigorously defends its nest, even against humans (Gotzman 1967, Tryjanowski & Golawski 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 the nest contents of Red-backed Shrikes (Lefranc 1993).

The Sparrowhawk is specialized on small birds (Opdam 1978, Simeonov 1984, Frimer 1989, Kropil & Sladek 1990, Varga & Rekasi 1993, Zawadzka & Zawadzki 2001, Bujoczek & 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 (Korpimäki 1986, Vanzyl 1994, Salata-Pilacinska & 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 was identified as more of a nest predator than Jay by Groom (1993) and Chiron and Julliard (2007), including the Red-backed shrike (Roos & Part 2004). However, the true relative levels of predation by these two species on nests is unknown. 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 according to the apparent threat to the nest content. Mobbing frequency should be lower towards the two raptors than towards the two corvids, and within corvids, Jay should be mobbed less often than Magpie. (2) The intensity of mobbing behaviour is adjusted according to the threat perceived by the defending birds to themselves. Mobbing intensity should therefore 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 & Worfolk 1997). The Red-backed Shrike is mainly 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% (Simek 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 & Worfolk 1997). All of the tested predator species are roughly equally abundant at our experimental localities (Stastny *et al*. 2010). Between 2002 and 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 & Rhodes 1992, Halupka 1999, Rytkönen 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 the 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. 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 recorded as a reaction value of zero. The minimum time interval until the presentation of the next dummy was one hour. To check for habituation or positive reinforcement, which may affect the defence behaviour significantly (Knight & 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 only light wind.

Two types of behaviour were included in the statistical analyses: (1) Mobbing frequency, i.e., the total number of mobbing events (where the bird flies over the mount, decreases its flight altitude and sometimes strikes the mount) accomplished by a tested bird during a 20-min trial; and (2) Mobbing intensity, i.e., the occurrence of mobbing events with physical contact (the bird hits the mount during the mobbing event, usually with its bill), contrary to non-physical mobbing.

2.3. Statistical analyses

A positive correlation in the mobbing frequency was found between males and females of the same

Table 1. Pair-wise test results for the total number of mobbing events performed by Red-backed Shrikes to particular mounts. Test (*t*) values are shown down and left, and respective *p* values are shown up and right. Probabilities are Bonferroni adjusted.

	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	–

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 (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 intensity. 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 strength. 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

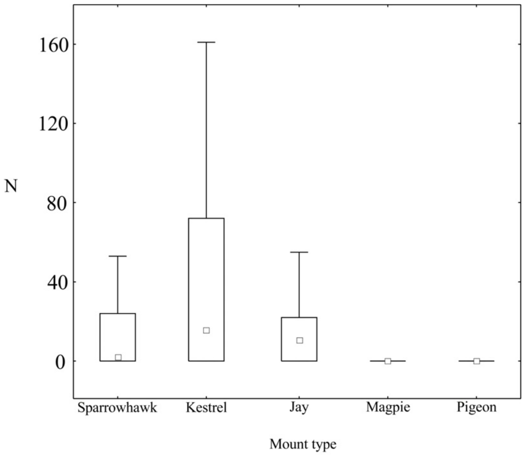


Fig. 1. Numbers of all mobbing events performed by particular shrike pairs towards particular mount types during 20-min study trials.

Table 2. The dependence of mobbing frequency in the Red-backed Shrike on mount type and shrike sex. Mobbing events with and without physical contact, performed by males and females to particular mount pairs, are tested. Probabilities are Bonferroni adjusted.

Comparison	*t*	df	*p*
Male/Female × Sparrowhawk/Kestrel	0.59	153	0.56
Male/Female × Sparrowhawk/Jay	0.74	153	0.46
Male/Female × Sparrowhawk/Magpie	0.89	153	0.37
Male/Female × Sparrowhawk/Pigeon	–1.02	153	0.31
Male/Female × Kestrel/Jay	0.16	153	0.88
Male/Female × Kestrel/Magpie	0.31	153	0.76
Male/Female × Kestrel/Pigeon	–0.44	153	0.66
Male/Female × Jay/Magpie	0.15	153	0.88
Male/Female × Jay/Pigeon	–0.28	153	0.78
Male/Female × Magpie/Pigeon	–0.13	153	0.90

Table 3. Pair-wise comparisons of the proportion of mobbing events with physical contact over all mobbing events (mobbing intensity), performed towards particular mounts. Test (*t*) values are shown down and left, *p* values are shown up and right. Probabilities are Bonferroni adjusted.

	Jay	Kestrel	Sparrowhawk
Jay	–	>0.01	>0.01
Kestrel	6.02	–	>0.01
Sparrowhawk	8.77	4.68	–

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 strength

The age of nestlings and the order of presentations did not significantly affect the mobbing strength ($t = 1.17$, 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 made contact more often during the mobbing behaviour than did females ($t = –3.08$, df = 2292, $p > 0.01$; Fig. 2) but this difference was significant only for Sparrowhawk and Kestrel (Table 4, Fig. 4).

Table 4. The dependence of mobbing intensity in the Red-backed Shrike on mount type and shrike sex. Mobbing events with and without physical contact, performed by males and females to particular mount pairs, is tested. Probabilities are Bonferroni adjusted.

Comparison	*t*	df	*p*
Male/Female × Jay/Kestrel	2.79	2,292	0.01
Male/Female × Jay/Sparrowhawk	2.46	2,292	0.01
Male/Female × Kestrel/Sparowhawk	0.36	2,292	0.72

4. Discussion

We did not find clear evidence for the hypothesis that the frequency of mobbing behaviour would be adjusted according to the apparent threat to the nest contents. While the Jay was mobbed equally as often as both raptors, the Magpie was mobbed at a rate equal to the control pigeon. Thus, nest predators (Jay and Magpie as a category) were not mobbed more often than predators of adult birds (Sparrowhawk and Kestrel). 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 contents, given the quite different responses to Magpie and Jay. When shrikes mobbed the predator, the frequency of this behaviour appeared more or less equal towards each species. 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 mobbing intensity would be adjusted to the threat to the defending birds – received some support. Mobbing intensity, in terms of occurrence of mobbing events

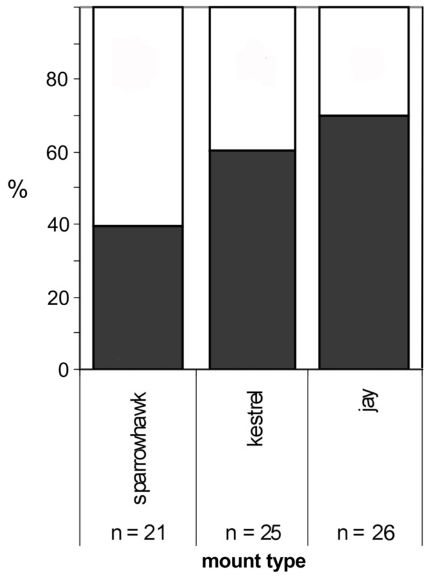


Fig. 2. Proportion of attacks with (black parts of columns) and without (white parts) physical contact, performed by Red-backed Shrikes towards particular mount types. Sample size is shown under each column (total *n* = 36). Only regularly-attacked dummies were included, i.e., Magpie and pigeon were excluded from this comparison. Total numbers of attacks were 419 for Sparrowhawk, 1,316 for Kestrel and 643 for Jay.

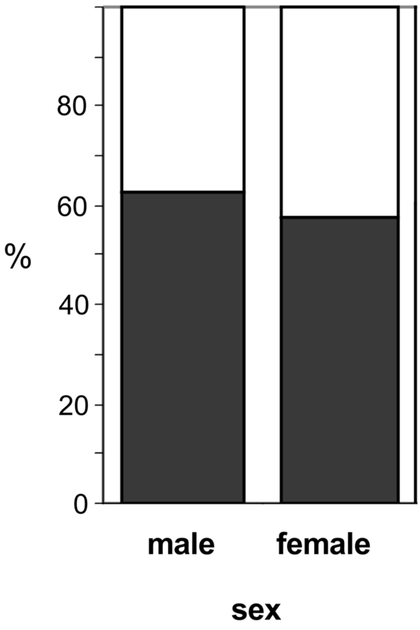


Fig. 3. Proportion of attacks with (black parts of columns) and without (white parts) physical contact performed by Red-backed Shrikes towards all mount types pooled. Sample sizes were 1,411 for males and 872 for females.

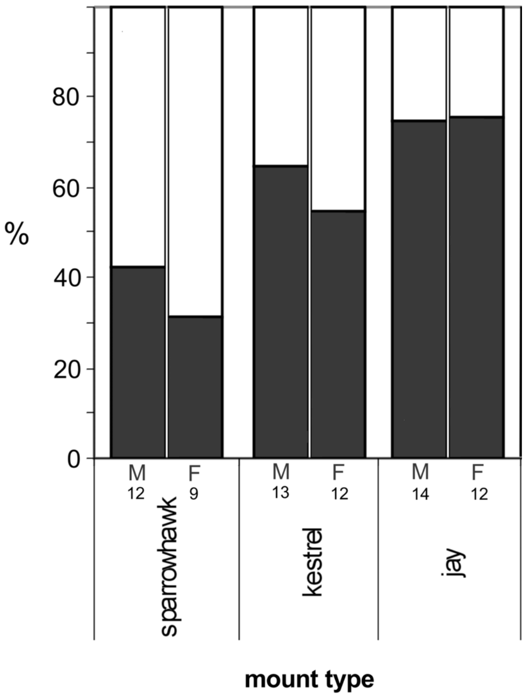


Fig. 4. Proportion of attacks (black parts of columns) and without (white parts) physical contact performed by Red-backed Shrikes towards particular mount types. Numbers under sex (M = male, F = female) show the number of included birds out of a total of 18. Only regularly-attacked dummies were included, i.e., Magpie and pigeon were excluded from this comparison. Numbers of all attacks were 428 for Sparrowhawk (M = 297, F = 131), 1,323 for Kestrel (M = 828, F = 495) and 551 for Jay (M = 287, F = 264).

with physical contact, upon the three regularly-mobbed predators steeply decreased from Jay through Kestrel to 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 the 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 & Ugelvik 1992, Amat & Masero 2004, Hogstad 2005, Dale *et al*. 1996). 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 intensity 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 intensity 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 & Fernandez 2011), 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 response by Red-backed Shrikes towards the Magpie, in contrast to the frequent mobbing events upon the Jay. The former apparently represents a similar if not bigger threat to the nest, compared to the Jay (Chiron & Julliard 2007). The Magpie is larger and apparently more frequently preys upon adult birds than the Jay (Tatner 1983, Cramp 2000), 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 & 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 is known to prey on birds' nests (Chiron & Julliard 2007), may well have *a priori* experience of mobbing, and use this information to search the area after a mobbing event for 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 & Krams 2005, Krams *et al.* 2007), so the zero activity in the presence of a Magpie, demonstrated here, may reflect optimal behaviour as regards the 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 which might have returned to prey on the nests. Nevertheless, such an explanation assumes that the Magpie is a more skilled and/or specialized nest predator than the Jay,, yet no studies have truly compared the relative effects of the share of Jays and Magpies on nest predation.

Our experiment suggests small differences in the sex-related difference in mobbing frequency for the Red-backed Shrike, which partly contradicts 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 & 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 frequency as the female (Lefranc & Worfolk 1997). The observed, strong correlation in the mobbing frequency between male and female has been shown rarely and only in birds with vigorous nest defence (Hogstad 2005), though nest defence may be more easily achieved if both partners participate.

Mobbing intensity (strikes on the model 'predator') differed between males and females. Male attacks were more acute than female ones, but only in case of predators of adult birds (Sparrowhawk and Kestrel), suggesting an important difference between mobbing intensity and mobbing frequency. Higher risk-taking by males may also be explained by the generally higher aggression of males, possibly caused by higher levels of testosterone (Wacker *et al.* 2010). However, Montgomerie and Weatherhead (1988) proposed there were different allocations of energy in sexes with different abilities to raise the offspring unaided, as in the Red-backed Shrike (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 & Worfolk 1997) which may more often cause furtive behaviour and therefore lower their activity during the nest defence.

Acknowledgements. We are grateful to Christopher Ray Steer for language corrections. We thank the Academy of Sciences of the Czech Republic (IAA601410803), the Czech Science Foundation (206/08/H044) and the Ministry of Education, Youth and Sport of the Czech Republic (MSM 6007665801) for financial support. The authors were granted with license permitting the experimentation with animals (Czech Animal Welfare Commission No. 489/01).

Pikkulepinkäinen säätelee saalistajaan kohdistamaansa häirinnän voimakkuutta muttei panostamaansa 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 varislintulajeja (harakka ja närhi) sekä kontrollilajia (kesykyyhky). Pikkulepinkäiset hätistivät säännöllisesti varpus- ja tuulihaukkaa sekä närheä, mutteivät harakkaa tai kesykyyhkyä. 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 (oletetusti suurempi varis- kuin petolinnuilla). Päinvastoin fyysisen kontaktin sisältävien hätistely-yrityksien osuus väheni närhestä ja tuulihaukasta varpushaukkaan, vaikka viime mainittua pidettiin tässä vaarallisimpana. Pikkulepinkäiset saattoivat säädellä hätistelyn voimakkuutta arvioimalla itseensä kohdistunutta uhkaa. Tuloksemme kertovat hätistelyn voimakkuuden ja ajallisen panostuksen erottamisen merkityksestä pesäpuolustuksen tutkimuksessa.

References

Amat, J. A. & Masero, J. A. 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, C. G. & Rundgren, H. 1980: Parental defence of offspring: model and an example. — Animal Behaviour 28: 536–542.

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.

Biermann, G. C. & Robertson, R. J. 1981: An increase in parental investment during the breeding season. — Animal Behaviour 29: 487–489.

Brunton, D. H. 1986: Fatal antipredator behaviour of killdeer. — Wilson Bulletin 98: 605–607.

Bujoczek, M. & Ciach, M. 2009: Seasonal changes in the avian diet of breeding sparrowhawks *Accipiter nisus*: how to fulfil the offspring's food demands? — Zoological Study 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, T. 2005: Antipredator defenses in birds and mammals. — The University of Chicago Press Chicago.

Chiron, F. & Julliard, R. 2007: Responses of songbirds to magpie reduction in an urban habitat — Journal of Wildlife Management 71: 2624–2631.

Collias, N. E. & Collias, E. C. 1978: Group territory, dominance, co-operative breeding in birds, and a new factor. — Animal Behaviour 26: 308–309.

Cramp, S. 2000: Birds of the Western Palearctic. — Oxford University Press.

Curio, E., Klump, G. & Regelmann, 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.

Duckworth, J. W. 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. An experimental test of the move on hypothesis. Ethology 96: 322–333.

Frimer, O. 1989: Food and predation in suburban sparrowhawks *Accipiter nisus* during the breeding season. — Dansk Ornitologisk Forenings Tidsskrift 83: 35–44.

Glutz von Blotzheim UN, Bauer KM & Bezzel E 1971: Handbuch der Vogel Mittel europas. Band 4: Falconiformes. Akademische Verlagsges., Frankfurt am Main. (In German with English summary).

Golawski, A. 2007: Seasonal and annual changes in the diet of the Red-backed Shrike *Lanius collurio* in farmland of Eastern Poland. — Belgian Journal of Zoology 137: 215–218.

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

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.

Jacobsen, O. W. & Ugelvik, M. 1992: Antipredator behavior of breeding Eurasian wigeon. — Journal of Field Ornithology 63: 324–330.

King, D. I. 1999: Mortality of an adult Veery incurred during the defense of nestlings. — 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, R. L. & Temple, S. A. 1986a: Nest defense in the American goldfinch. — Animal Behaviour 34: 879–897.

Knight, R. L. & Temple, S. A. 1986b: Why does intensity of avian nest defence increase during the nesting cycle? — Auk 103: 318–327.

Korpimaki, 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.

Krams, I., Krama, T., Igaune, K. & Mand, R. 2007: Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. — Behavioral Ecology 18: 1082–1084.

Kropil, R. & Sladek, J. 1990: Contribution to the knowledge of food of some birds of prey and owls in Slovakia Biologia. — Biologia 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 shrikes of the world. — Pica Press, Sussex.

Lima, S. L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. – Biological Reviews 84: 485–513.

McLean, I. G. & Rhodes, G. 1992: Enemy recognition and response in birds. — In Current Ornithology (ed. Power, D. M.): 173–211. Plenum, New York.

Nijman, V. 2004: Seasonal variation in naturally occurring mobbing behaviour of drongos (Dicruridae) towards two avian predators. — Ethology Ecology and Evolution 16: 25–32.

Opdam, P. 1978: Feeding ecology of a sparrow hawk population *Accipiter nisus.* — Ardea 66: 137–155.

Overskaug, K., Sunde, P. & Stuve, G. 2000: Intersexual differences in the diet composition of Norwegian raptors. — Ornis Norvegica 23: 24–30.

Pavel, V. 2006: When do altricial birds reach maximum of their brood defence intensity? – Journal of Ethology 24: 175– 179.

Pettifor, R. A. 1990: The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. — Animal Behavior 39: 821–827.

Polakova, S. & Fuchs, R. 2006: Where to breed? Advice for Eurasian Blackbirds in Ceske Budejovice, Czech Republic. — Journal of Ornithology 147 Suppl. 1: 231–231.

Roos, S. & Part, 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. — Behavioural Ecology and Sociobiology 52: 379–384.

Salata-Pilacinska, B. & Tryjanowski, P. 1998: Diet composition of the kestrel *Falco tinnunculus* L. and the long-eared owl *Asio otus* (L.) coexisting in farmland of the Mazowiecka Lowland (Poland). — Przeglad Przyrodniczy 9: 95–100.

Scheuerlein, A., Van't Hof, T. J. & 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 Ser. B 268: 1575–1582.

Serra, C. & Fernandez, G.J. 2011: Reduction of nestlings' vocalizations in response to parental alarm calls in the Southern House Wren, *Troglodytes musculus*. — Journal of Ornithology 152: 331–336.

Shedd, D. H. 1982: Seasonal variation and function of mobbing and related antipredator behaviors of the American Robin (*Turdus migratorius*). — Auk 99: 342–346.

Shedd, D.H. 1983: Seasonal variation in mobbing intensity in the Black-capped Chickadee. — Wilson Bulletin 95: 343–348.

Simek, J. 2001: Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*). — Ornis Fennica 78: 61–71.

Simeonov, S. D. 1984: On the diets and the numbers of the hawks (genus Accipiter) in Bulgaria. — Ekologiya (Sofia) 13: 83–95.

Smith, J. M. & Graves, H. B. 1978: Some factors influencing mobbing behaviour in barn swallows *Hirundo rustica.* — Behavioral Biology 23: 355–372.

Sordahl, T. A. 1990: The risk of avian mobbing and distraction behavior: an anecdotal review. — Wilson Bulletin 102: 349–352.

Šťastný, K., Bejček, V. & Hudec, K. 2010: Atlas hnízdního rozšíření ptáků v ČR + Ptačí oblasti ČR — Aventinum, Praha. (In Czech with English summary)

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.

Tryjanowski, P. & Golawski, 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.

Vanzyl, A. J. 1994: Comparison of the diet of the common kestrel *Falco tinnunculus* in South Africa and Europe. — Bird Study 41: 124–130.

Varga, Z. & Rekasi, J. 1993: Food and population dynamics of birds of prey. — Aquila a Madartani Intezet Evkonyve 100: 123–136.

Wacker, D. W., Coverdill, A. J., Bauer, C. M. & Wingfield, J. C. 2010: Male territorial aggression and androgen modulation in high latitude populations of the Sooty, *Passerella iliaca sinuosa*, and Red Fox Sparrow, *Passerella iliaca zaboria*. – Journal of Ornithology 151: 79–86.

Welbergen, J. A. & Davies, N. B. 2011: A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. — Behavioral Ecology 22: 574–579.

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 (Warsaw) 36: 25–31.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. 2009: Mixed effects models and extensions in ecology with R. — Springer, New York.

Článek II.

Němec M., Fuchs R. (2014): Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. Acta Ethologica 17:149-154.

acta ethol (2014) 17:149–154
DOI 10.1007/s10211-013-0175-z

ORIGINAL ARTICLE

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

Michal Němec · Roman Fuchs

Received: 31 August 2013 / Revised: 30 October 2013 / Accepted: 7 November 2013 / Published online: 19 November 2013

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, and the raven being the largest corvid of all. The jay, crow, and raven are habitual nest predators, 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 asses not only the dangerousness of the intruder but also the potential advantageousness, or otherwise, of active defense.

Keywords 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 (Söderström et al. 1998; Schaefer 2004; Bolton et al. 2007). The defense of nests against corvids has thus been investigated in many experimental studies (see Caro 2005 for review). Of the European corvids, the hooded crow—*Corvus cornix* (Meilvang et al. 1997; Hogstad 2004; Csermely et al. 2006), carrion crow—*Corvus corone* (Röell and Bossema 1982), 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 (Knight and Temple 1988; Hatch 1997; Förschler 2002), 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; Hogstad 2004; Olendorf and Robinson 2008). 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 sparrow hawk (*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: Firstly, shrikes

M. Němec (✉) · R. Fuchs
Faculty of Science, University of South Bohemia, Branišovská 31,
37005 České Budějovice, Czech Republic
e-mail: majkl.mn@gmail.com

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. Secondly, shrikes are physically 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.

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 eggs and nestlings only (the jay, crow, and raven); and (3) the small corvid, which is dangerous for eggs and nestlings only (the jay).

Methods

Study area

The study took place in the Doupov 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 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/km^2; Němec, personal observation).

Study species

The red-backed shrike 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 Goławski 2004; Strnad et al. 2012). Nevertheless, nest predation is the most common cause of nest failure of the red-backed shrike (Tryjanowski et al. 2000; Roos 2002).

Five corvid species differing in size as well as in threat to nest content were used as intruders in our experiment. Average male's weights of Czech populations (Hudec 1983) show that the jay (170 g) and nutcracker (165 g) are the smallest of the five, the rook (560 g) and crow (515 g) are middle-sized, and the raven (1,330 g) being the largest corvid of all. 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 predators (Andrén 1992; Schaefer 2004; Weidinger 2009), whereas the rook plunders nests only rarely (Holyoak 1968; Kalotás 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 nonthreatening control species (the pigeon). From 2005 through 2007, we examined 25 nests containing nestlings aged between 5 and 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 aberrant plumage 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 1 h from the experimenter disappearance from shrikes' territory. Each trial (the presentation of one dummy) lasted 20 min from the appearance of at least one parent. If the parents did not appear within 20 min, 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. The experimenter abided quietly behind the camera during dummy presentation. All experiments took place between 10:00 a.m. and 18:00 p.m., 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. We also recorded feeding of nestlings events during presentation of each dummy. 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 (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, $p \ll 0.001$), we decided to use pair identity as a random factor in both of the statistical models described below. Tryjanowski and Goławski (2004) used the same method for analysis of similar data with the red-backed shrike.

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 2,783 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's honestly significant difference (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. 2011).

Results

The number of attacks

Twenty of 25 tested shrike pairs attacked at least one of the tested intruders. Only the intruder species (LME ANOVA: $F_{5,\ 264}=32.028$, $p \ll 0.001$) 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's HSD post hoc test and pertain to Fig. 1.

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: $F_{5,\ 2,752}=88.889$ $p \ll 0.001$). The sex of the parent was not significant (LME ANOVA: $F_{1,\ 2,752}=0.906$, $p=0.341$). 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's HSD post hoc test and pertain to Fig. 2.

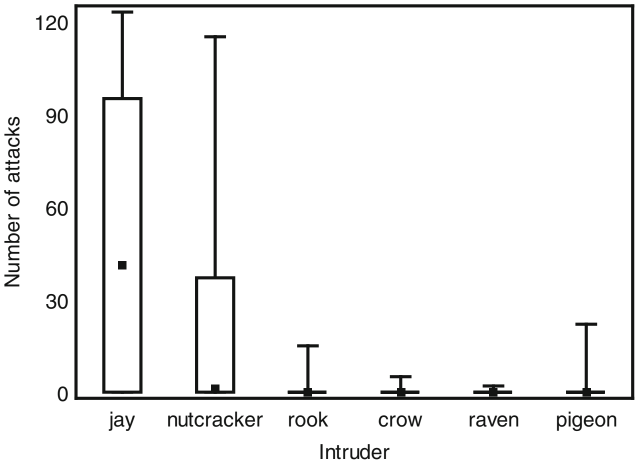


Fig. 1 Number of attacks executed by nesting pairs of the red-backed shrike ($n=25$) against intruders presented individually close to shrikes nest. The *filled-in square* within each box-and-whisker drawing represents the median; the *vertical span of the box* represents the range from the lower to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

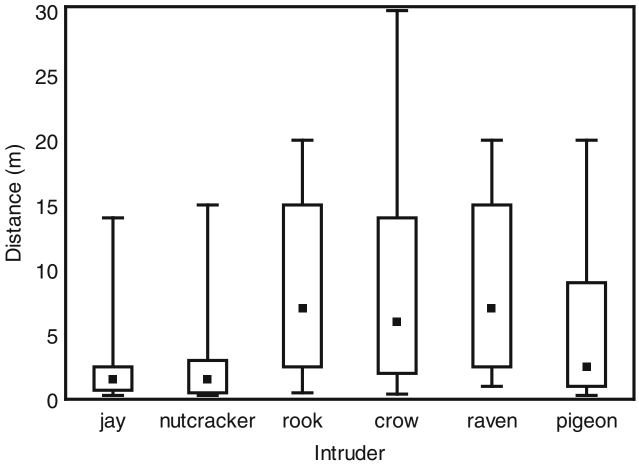


Fig. 2 The distances of sitting individuals of the red-backed shrike after each change of their position during the presence of the intruder close to their nests (n =2,783). The *filled-in square* within each box-and-whisker drawing represents the median; the *vertical span of the box* represents the range from the lower to upper quartile; the *range of whiskers* represents the 5 and 95 % percentiles

The feeding of nestlings

No case of nestlings feeding occurred within any corvid species presentations. In total, 22 cases of feeding were recorded within all presentations of pigeon.

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 (Strnad et al. 2012) where shrikes attacked even raptors, including sparrow hawk which is specialized predator of small adult passerines, including shrikes (Götmark and Post 1996). 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 nonattacked 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). On the other hand, study of the red-backed shrike's response to human intruder (Tryjanowski and Goławski 2004) found that more aggressive parents have higher breeding success than quieter individuals. However, in case of a predator which was selected for plundering nests (and cannot be chased away from the nest), the strategy of more aggressive nest defense would lower the breeding success. Therefore, the ability to recognize predators, to which the active defense is ineffective may evolved in shrikes.

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 nonvocal 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 sparrow hawk (*A. 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 pygmy owl (*Glaucidium perlatum*). However, the pygmy owl is much more dangerous than the tawny owl, since small passerines prevail in the pygmy 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.

Acknowledgments This study was supported by the Grant agency of the University of South Bohemia (159/2013/P).

Ethical note Experiments carried out in this research comply with the current laws of the Czech Republic. Authors are licensed for catching and ringing birds (Bird Ringing Centre Prague no. 1068—Michal Němec), for animal experimentation (Czech Animal Welfare Commission no. 489/01—Roman Fuchs), and for conducting experiments with shrikes (Ministry of Education, Youth and Sports, license no. 13842/2011-30—Roman Fuchs).

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. Northwest Nat 91:23–29. doi:10.1898/NWN09-01.1

Bolton M, Butcher N, Sharpe F et al (2007) Remote monitoring of nests using digital camera technology. J Field Ornithol 78:213–220. doi:10.1111/j.1557-9263.2007.00104.x

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 et al (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. Ital J Zool 73:125–128

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk? Oecologia 60:83–88

Development Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

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, Sθgaard 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

Ehrlich PR, McLaughlin JF (1988) Scrub jay predation on starlings and swallows: attack and interspecific defense. 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. Anim Behav 46:1–11. doi:10.1006/anbe.1993.1156

Feare C, Dunnet G, Patterson I (1974) Ecological studies of the Rook (*Corvus frugilegus* L.) in North-East Scotland: food intake and feeding behaviour. J Appl Ecol Vol 11:867–896

Förschler MI (2002) Predation strategy of the Eurasian Jay *Garrulus glandarius* and antipredator response by the Citril Finch Serinus citrinella. Rev Catalana d'Ornitologia 19:41–43

Götmark F, Post P (1996) Prey selection by sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. Phil Trans R Soc Lond B 351:1559–1577. doi:10.1098/rstb.1996.0141

Gottfried BM (1979) Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. Condor 81:251–257. doi:10.2307/1367626

Hatch MI (1997) Variation in song sparrow nest defense: individual consistency and relationship to nest success. Condor 99:282–289. doi:10.2307/1369934

Hendricks P, Schlang S (1998) Aerial attacks by common ravens, *Corvus corax*, on adult feral pigeons, *Columba livia*. Can Field Nat 112:702–703

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. Br 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 Vol 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 Ornithol 38:27–31. doi:10.3161/068.038.0107

Klicka J, Winker K (1991) Observations of ravens preying on adult kittiwakes. 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 Behav 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*. Behav Ecol 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. Behav Ecol 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 Ornithol 46:55–63. doi:10.3161/000164511X589938

Lockie JD (1956) The food and feeding behaviour of the jackdaw, rook and carrion crow. J Anim Ecol 25:421–428

Meilvang D, Moksnes A, Røskaft E (1997) Nest predation, nesting characteristics and nest defence behaviour of fieldfares and redwings. J Avian Biol 28:331–337. doi:10.2307/3676947

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.2000.tb04432.x

Opermanis O, Mednis A, Bauga I (2001) Duck nests and predators: interaction, specialisation and possible management. Wildl Biol 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

Röell A, Bossema I (1982) A comparison of nest defence by jackdaws, rooks, magpies and crows. Behav Ecol Sociobiol 11:1–6. doi:10.1007/BF00297658

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

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

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

StatSoft, Inc. (2011) Electronic statistics textbook, WEB: http://www.statsoft.com/textbook/. StatSoft, Tulsa, OK

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 Fenn 89:206–215

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. J Ethol 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 Fenn 77:137–141

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

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. Pol J Ecol 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*. Belg J Zool 138:85–89

Článek III.

Syrová M., Němec M., Veselý P., Landová E., Fuchs R. (2016): Facing a Clever Predator Demands Clever Responses - Red-Backed Shrikes (*Lanius collurio*) vs. Eurasian Magpies (*Pica pica*). PLoS ONE 11(7): e0159432

PLOS | ONE

RESEARCH ARTICLE

Facing a Clever Predator Demands Clever Responses - Red-Backed Shrikes (*Lanius collurio*) vs. Eurasian Magpies (*Pica pica*)

Michaela Syrová[1,2], Michal Němec[1], Petr Veselý[1]*, Eva Landová[3], Roman Fuchs[1]

1 Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice, 37005, Czech Republic, **2** Department of Ethology, Institute of Animal Science in Prague, Přátelství 815, Prague – Uhříněves, 10400, Czech Republic, **3** Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 1594/7, Praha – Nové Město, 12800, Czech Republic

* petr-vesely@seznam.cz

Abstract

Red-backed shrikes (*Lanius collurio*) behave quite differently towards two common nest predators. While the European jay (*Garrulus glandarius*) is commonly attacked, in the presence of the Eurasian magpie (*Pica pica*), shrikes stay fully passive. We tested the hypotheses that this passive response to the magpie is an alternative defense strategy. Nesting shrikes were exposed to the commonly attacked European kestrel (*Falco tinnunculus*) in a situation in which i) a harmless domestic pigeon, ii) a commonly attacked European jay, and iii) a non-attacked black-billed magpie are (separately) presented nearby. The kestrel dummy presented together with the magpie dummy was attacked with a significantly lower intensity than when it was presented with the other intruders (pigeon, jay) or alone. This means that the presence of the magpie inhibited the shrike's defense response towards the other intruder. These results support our previous hypotheses that shrikes use an alternative defense strategy in the magpie's presence. We hypothesize that the magpie is able to associate the active defense of the shrikes with the close proximity of a nest and that shrikes try not to draw the magpie's attention to the nest. The reason why this strategy is not used against the jay remains unanswered as jays as well as magpies show very similar cognitive and foraging skills enabling them to individuate the nest presence according to active parental defense.

Introduction

Predator recognition and categorization is an essential cognitive ability enabling the optimization of antipredator behavior [1][2]. Prey species may ignore the presence of a less dangerous predator [3], while it must choose the appropriate antipredator behavior towards the specialized predators of adults or nests [4][5][6][7].

The red-backed shrike (*Lanius collurio*) shows a vigorously active nest defense behavior towards various predators and nest parasites [8][9] including humans [10]. In our previous

Citation: Syrová M, Němec M, Veselý P, Landová E, Fuchs R (2016) Facing a Clever Predator Demands Clever Responses - Red-Backed Shrikes (*Lanius collurio*) vs. Eurasian Magpies (*Pica pica*). PLoS ONE 11(7): e0159432. doi:10.1371/journal.pone.0159432

Editor: Csaba Moskát, Hungarian Academy of Sciences, HUNGARY

Received: February 1, 2016

Accepted: July 1, 2016

Published: July 25, 2016

Data Availability Statement: The data on the numbers of swoops performed towards particular intruders have been deposited in the Dryad Digital Repository, datadryad.org (DOI: 10.5061/dryad.0nv00).

Funding: This work was supported by the Grant agency of the University of South Bohemia, 151/2016/P, https://www.jcu.cz/science-and-research. The funder supported the data collection and preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

study [8] we tested shrikes' responses to two corvid nest predators (Eurasian magpie *Pica pica* and European jay *Garrulus glandarius*). While the jay was commonly attacked, in the presence of a magpie shrikes stayed fully passive; despite the threat represented by both corvid species being equal at first sight. They are both common nest predators of similar size [11]. Although, there is evidence of differences in the intensity of defense responses towards various birds of prey (e.g. [8][12]), owls (e.g. [13]), or corvids (e.g. [14]), such a qualitative difference in the antipredator response towards two members of the same predator guild has never been shown.

In our previous study, we suggested that a likely explanation for the passive response of the shrikes to the magpie is that it is a strategy designed not to draw attention to their nest rather than an absence of interest [8]. There is little evidence for such behavior (e.g. [15][16][17]) because it is not easy to show that the absence of response is an alternative strategy. A more often described alternative antipredator strategy is some form of *distraction display* ([18][19][20][21][22][23][24][25]; summarized in [2]).

In the present study, we tried to test the hypothesis that magpies are not attacked by shrikes, because they use an alternative antipredatory strategy against it. We exposed shrikes to a magpie together with another commonly attacked predator. This situation induced a multiple predator conflict (indexed as MPC hereafter). An MPC constitutes a situation in which a specific defense response towards one predator may put the prey at greater risk of being threatened by the other predator [26][27][28]. In this case, the best solution of the MPC is to choose the response optimal for the more dangerous predator (reviewed [29]). If the goal of the shrikes's passive behavior in the presence of a magpie is not to draw attention to the nest, an active response to another predator in the presence of the magpie would be counterproductive. Assuming the shrikes regard the magpie as a greater danger than any other predator, the best solution of MPC would be passive behavior.

We exposed the shrikes to two pairs of intruders: a European kestrel (*Falco tinnunculus*, a commonly attacked, less dangerous predator of fledglings and adults) with a magpie (a non-attacked nest predator) and with a jay (a commonly attacked nest predator). We tested the hypothesis presuming that the shrikes' passive behavior is an alternative defense strategy and that shrikes consider the magpie as a greater danger than predators which are usually attacked. In this case the shrikes would attack the kestrel less in the presence of the magpie than in the presence of jay or a harmless bird species (control).

Methods

Study area

The study took place in the Doupov mountains, near the town of Karlovy Vary (Western Bohemia; 50°10´N, 13°9´E), the Czech Republic. Experiments were conducted during the breeding season (from early June to late July) in the years 2011 and 2012 and between 10:00 and 18:00.

Study species

The studied species, the red-backed shrike, is a medium sized passerine bird. However it uses active mobbing, including physical attacks, as an important part of its antipredator behavior [8][10].

We chose the dummy of a small bird of prey, adult female European kestrel, as the intruder immediately endangering the nest. The kestrel was the most attacked predator by the red-backed shrikes in our previous study [8].

The dummies of a magpie, jay, and domestic pigeon were chosen as the bystander intruders, which represent only a potential danger. The magpie and the jay are also similarly sized [11] and known as the common predators of passerine nests [30][31][32]. The domestic pigeon is a harmless jay- or magpie-sized bird. In our previous study [8], the red-backed shrikes attacked the jay intensively, while attacks against the magpie and the domestic pigeon occurred only exceptionally. Shrikes are familiar with all of these intruders ([33]; personal observation).

Experimental design

Every pair of shrikes was successively tested in four trials: 'the kestrel with the magpie', 'the kestrel with the jay', 'the kestrel with the domestic pigeon', and 'the kestrel alone' (without the second intruder). The sequence of these trials was random. We did not show any effects of the order of presentation on shrike responses (Linear mixed effect model—indexed as LMM hereafter, $F_{242,3} = 0.17$, $p = 0.99$; Fig 1).

All dummies were placed in an upright position with their wings folded. The kestrel was placed 1m away from the nest on a 1.5 m high pole, facing the nest. The second intruder (magpie, jay, or domestic pigeon) was installed 10 m from the nest, also on a 1.5 m high pole facing the nest. We chose this distance on the basis of our previous research [34] showing that shrikes only seldom attack the jay 10m away from nest. We used four different dummy specimens of each species to avoid a bias caused by the dummy identity. All dummies were stuffed by the same taxidermist in the same position. The dummy identity had no effect on shrikes' responses (kestrel: LMM, $F_{242,3} = 1.27$, $p = 0.86$; magpie: LMM, $F_{242,3} = 0.97$, $p = 0.92$; jay: LMM, $F_{242,3} = 2.34$, $p = 0.71$; pigeon: LMM, $F_{242,3} = 0.11$, $p = 0.99$). The defense behavior was taped on DV Camera (Panasonic HC-V510).

Each trial (presentation of dummies) lasted 20 minutes. The time interval between the trials was one hour allowing shrikes to calm down and supply food to their brood. During the years 2011 and 2012 we examined 20 nests with nestlings at an age of between 5 to 15 days. Female

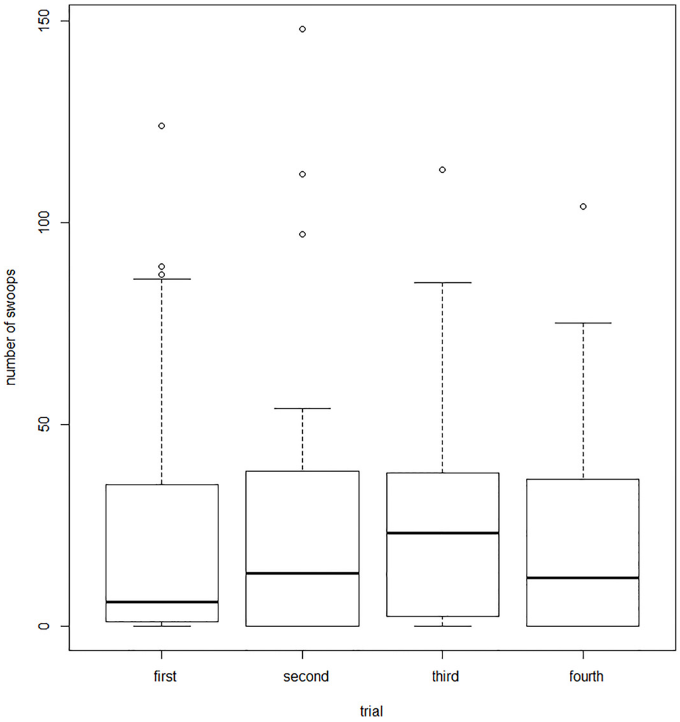


Fig 1. Number of swoops performed by shrikes against the kestrel dummies in particular trials. Line in the middle refers to median, box shows 25–75% of data, whiskers show 10–90% of data and dots are outliers.

doi:10.1371/journal.pone.0159432.g001

and male behaviors were analyzed separately. We recorded the occurrence of any swoops both with and without physical contact.

Statistical analyses

We created linear mixed effect models (LMM) with the random slope model arrangement (random factor 'individual ID' nested in the random factor 'pair ID') to assess the effect of predictor variables (command lmer in R package lme4 [35]). The response variable was the *number of swoops* performed by each individual tested shrike against the kestrel dummy during one trial. In order to meet the demands of normal distribution these data were transformed by logarithmic transformation [log (no of swoops + 1)].

The main categorical predictor variable, the *type of bystander*, had the following four values: jay, magpie, pigeon, none. Other categorical predictors in the model were the *sex of the shrike* (values 'male' and 'female') and the *order of the trial* within the sequence (values 'first', 'second', 'third', 'fourth'). There was also one continuous predictor variable: the *age of the nestlings*.

The effects of the predictor variables were evaluated using a likelihood ratio test based on Gaussian distribution and partial F-test. The Tukey HSD post-hoc tests were used to evaluate the differences among the levels of categorical predictors.

To rank the models, AICc values were computed, and from these the difference in AICc (ΔAICc) was calculated by subtracting the lowest AICc from all others. From this, as measures of strength of evidence for each model, the relative likelihood (exp (0.5/ΔAICc)) and the probability or Akaike weight (relative likelihood/sum of all relative likelihoods*10) were computed [36]. The models are shown in Table 1. The results of the model with the highest Akaike weight are presented in Results (marked with bold font in Table 1). All statistical analyses were computed in R 3.2.1 (R Development Core Team 2015).

Ethical note

This study was conducted in accordance with the valid laws and regulations of the Czech Republic; in compliance with the Ethic Committee of the Faculty of Science, University of South Bohemia, which approved this study. Behavioral experiments on the wild birds were enabled by accreditation no. 13842/2011-30 and a license permitting experimentation with animals no. CZ01629 offered by the Ministry of the Agriculture of the Czech Republic. We have observed that our activities influenced neither the life of the tested birds nor the fate of their nests. Moreover the density of nesting shrikes in the tested populations has been stable for the last 5 years.

Table 1. Model selection for the response variable from linear mixed effect models.

Response variable	Model	AICc	ΔAICc	Relative likelihood	Akaike weight
Log (no. swoops+1)	Intercept	385.74	32.7	1.02	0.58
	Bystander	353.04	0	1	0.57
	Age	386.63	33.59	1.01	0.58
	Sex	387.34	34.30	1.01	0.58
	Bystander+age	**354.13**	**1.09**	**1.58**	**0.90**
	Bystander+sex	354.63	1.59	1.37	0.78
	Age+sex	388.22	35.18	1.01	0.58
	Bystander+age+sex	355.7	2.66	1.21	0.69

Bold type indicates the best models, which were determined based on relative AICc values (ΔAICc) and computed relative likelihood and Akaike weights. Intruder—the type of the intruder, order—the trial order within the sequence, age—the age of the nestlings, sex—the sex of the parent shrike.

doi:10.1371/journal.pone.0159432.t001

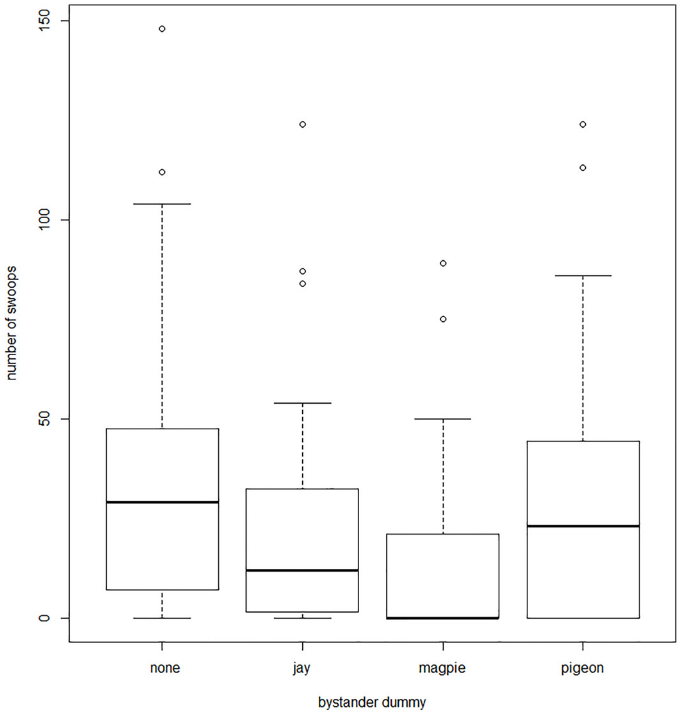


Fig 2. Number of swoops performed by shrikes against the kestrel dummies presented together with three bystander dummies (jay, magpie, pigeon) or alone during the 20-minutes lasting trial. Line in the middle refers to median, box shows 25–75% of data, whiskers show 10–90% of data and dots are outliers.

doi:10.1371/journal.pone.0159432.g002

Results

Only the *type of bystander* affected the number of swoops the shrikes performed against the kestrel (Fig 2, Table 2). Post hoc Tukey HSD tests showed that the kestrel presented with the magpie bystander was attacked less than kestrel presented together with the jay (z = -3.21, p<0.01), pigeon (z = -3,82, p<0.01) or alone (z = -6,21, p<<0.01). The *number of swoops* towards the kestrel in other trials did not differ (Tukey HSD test; kestrel with jay x kestrel with pigeon: z = -0.29, p = 0.98; kestrel with jay x kestrel alone: z = -2.53, p = 0.08; kestrel with pigeon x kestrel alone: z = -2.10, p = 0.10).

Discussion

In concordance with our hypothesis, the kestrel dummy presented together with the magpie dummy was attacked with a significantly lower intensity than when it was presented with the other intruders (pigeon, jay) or alone. This means that the presence of the magpie inhibited the shrikes' defense response towards the other intruder.

Table 2. Factors influencing intensity of mobbing (number of swoops) performed by shrikes against the kestrel (LMM).

	numDF	denDF	F-value	p-value
Intruder type	3	242	31.27	<0.01
Age of nestling	1	242	0.08	0.91

doi:10.1371/journal.pone.0159432.t002

Our new results further show that 1) shrikes are able to solve the MPC arisen from the co-occurrence of a predator, towards which the active nest defense is effective; and a predator, towards which the active nest defense is not effective; 2) shrikes are able to solve this MPC although the predator towards which the active nest defense is effective represents a greater threat than the predator towards which the active nest defense is not effective.

Our results support the hypothesis that the passive behavior of shrikes in the presence of magpies is not an expression of indifference but an alternative defense strategy, and that shrikes perceive the magpie as being more dangerous than the kestrel. The results also concur with (but do not corroborate) our previous hypothesis [8] presuming that shrikes choose an alternative defense strategy against a magpie because active defense may draw attention to the nest. There is evidence for the suppression of active nest defense as an alternative antipredator strategy in birds ([37][38]), though the number of such studies is in striking contradiction to the fact that there is broad evidence in the literature that mobbing can attract a predator`s attention [39][40][41][42][43][44][45][46].

Unfortunately, based on our results, we cannot explain why shrikes consider active defense risky against a magpie and not against a jay. It has been proven in other bird species that they commonly drive jays away from the nest ([38][47][48], but see [49]), while in presence of a magpie parents avoid any interaction with it [50][51]. Nevertheless, in these studies, there are no comparisons with responses to other predators. There are a few alternative explanations for the different responses of shrikes towards jays and magpies which can be meditated.

Firstly, a magpie may devote greater effort to searching for nests. When compared to the diet of the jay, the diet of magpies is biased towards vertebrate prey including adult birds, small mammals, reptiles, and carrion [52][53]. Moreover, it has been documented that magpie predation can affect the nest success and density of songbirds [31][54][55][56][57], including shrikes [58]. Nevertheless, there is no evidence that magpies, rather than jays, are able to individuate the presence of the nest according to other signals e.g. the excitement of parents. It has been shown that predators have the ability to be attracted to the nest by parents' alarm calls [44][45][46], but in such cases the predators are assumed to have developed spatial cognition and sometimes, to some extent, memory. Both these cognitive skills are quite well developed in magpies and jays. In general Corvids are more successful in mental and cognitive tests than other bird groups [59][60]. In laboratory tests the performance of jays and magpies in terms of long-term spatial memory (magpies [61], jays [62]) or object permanence (magpies [63], jays [64][65]) was almost equal.

Another parameter which eases the searching of predators for nests is the social system of magpies and jays [59][66][67]. Both of them live in family groups (magpie [30][68][69], jay [70]) and are able to obtain information in a social context [70][71][72][73][74][75].

Altogether, the difference between magpies and jays in terms of their ability to individuate the presence of a nest based on parental excitement is very small, at least from the human point of view.

Another potential explanation may reside in the different experience of shrikes with jays and magpies, probably in terms of evolutionary history rather than individually. Jays and magpies are ecologically very similar, both congregate in open landscape with fragmented forests, although jays are more specialized to forests and magpies to the open landscape [76]. Shrikes may thus have more evolutionary experience with the magpie, as they both are probably primarily birds of open habitats with scattered shrubs and trees.

This brings us to the question of how shrikes have obtained the ability to suppress active nest defense behavior. We may hypothesize several scenarios leading to the acquisition of such a skill: 1) The shrikes' behavior activated in the magpie's presence is inborn, this ability was selected only against the magpie, because the magpie has a longer co-evolution with the red-backed shrikes. Shrikes displaying the alternative strategy have a significant evolutionary advantage, while shrikes showing active nest defense have been selected out of the population. 2) The shrikes' behavior activated in the magpie's presence is based on the individual experience of particular birds. This presumes the development of a good long-term memory or a specialized, episodic-like memory [77]. The occurrence of an episodic-like memory or a what-where-when memory [78] has never been shown in shrikes. Nevertheless, shrikes are known for their impaling behavior—storing prey on thorns within their territory [79][80], which probably places some demands on their spatial memory skills. 3) The shrikes' behavior activated in the magpie's presence is transferred from parents to their offspring or from other shrikes in the population. This explanation also presupposes quite high cognitive abilities in shrikes, which must be involved in the shrike's antipredator behavior, because the magpie represents a cognitively well-developed adversary. Thus, the two cognitively developed species in mutual combat may represent an interesting model system for the study of the cognitive abilities of birds.

Our results did not show any effect of the order of the dummy presentation. This suggests that there was no reinforcement during the course of four trials. This is seemingly in contrast to our previous results [81], showing that imperfect dummy is attacked more when presented after a perfect one as a results of priming. As the dummies of kestrel in our experiments were equally perfect, we did not show any such effects. Nevertheless, both these results show no effect of habituation, shrikes were always very active, despite the daytime or the time spent attacking the dummies.

Taken together, the existing scientific knowledge finds only small differences in the cognitive abilities and foraging mode of magpies and jays but shrikes respond to their presence with a completely different (and proper) strategy. The behavior of shrikes suggests that the magpie is a more dangerous predator than the jay and this presents new challenges to our understanding of the shrike's motivation in choosing such different antipredatory strategies in response to such seemingly similar predators.

Acknowledgments

We thank Christopher Mark Steer for his proofreading and Daniel Frynta and two anonymous referees for their helpful comments on the manuscript. We also thank the Hradiště Military Training Area Regional Office for allowing us to conduct experiments within their training area.

Author Contributions

Conceived and designed the experiments: MS RF. Performed the experiments: MS MN. Analyzed the data: PV MN. Wrote the paper: MS PV RF EL.

References

1. Kelley JL, Magurran AE. Learned predator recognition and antipredator responses in fishes. Fish Fish. 2003; 4(3): 216–226.
2. Caro TM. Antipredator defenses in birds and mammals. Chicago: University of Chicago Press; 2005.
3. Treves A. Theory and method in studies of vigilance and aggregation. Anim Behav. 2000; 60: 711–722. PMID: 11124869
4. Jacobsen OW, Ugelvik M. Antipredator behaviour of breeding Eurasian wigeon. J Field Ornithol. 1992; 63: 324–330.
5. Dale S, Gustavsen R, Slagsvold T. Risk taking during parental care: A test of three hypotheses applied to the pied flycatcher. Behav Ecol Sociobiol. 1996; 39: 31–42.

6. Amat JA, Masero JA. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Anim Behav. 2004; 67: 293–300.
7. Hogstad O. Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition. Ibis. 2005; 47: 375–380.
8. Strnad M, Němec M, Veselý P, Fuchs R. 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. 2012; 89: 206–215.
9. Lovaszi P, Moskat C. Break-down of arms race between the red-backed shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). Behaviour. 2004; 141: 245–262.
10. Tryjanowski P, Golawski A. Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size and stage of breeding season. J Ethol. 2004; 22: 13–16.
11. Cramp S, Perrins CM. Handbook of the Birds of Europe the Middle East and North Africa. The birds of the Western Palearctic Vol. VIII—Crows to Finches. Oxford, New York: Oxford University Press; 1994.
12. Curio E, Klump G, Regelmann K. An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? Oecologia. 1983; 60: 83–88.
13. Reudink MW, Nocera JJ, Curry RL. Anti-predator responses of Neotropical resident and migrant birds to familiar and unfamiliar owl vocalizations on the Yucatan Peninsula. Ornitol Neotrop. 2007; 18: 543–552.
14. Csermely D, Casagrande S, Calimero A. Differential defensive response of common kestrels against a known or unknown predator. Ital J Zool. 2006; 73: 125–128.
15. Lima SL. Nonlethal effects in the ecology of predator-prey interactions. Bioscience. 1998; 48: 25–34.
16. Sih A, Englund G, Wooster D. Emergent impacts of multiple predators on prey. Trends Ecol Evol. 1998; 13: 350–355. PMID: 21238339
17. Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM et al. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos. 2010; 119: 610–621.
18. Simmons KEL.Distraction-display in the Kentish Plover. Brit Birds. 1951; 44: 181–187.
19. Armstrong EA. The distraction displays of the Little Ringed Plover and territorial competition with the Ringed Plover. Brit Birds. 1952; 45: 55–59.
20. Armstrong EA. Distraction display and the human predator. Ibis. 1956; 98: 641–654.
21. Kilham L. Reproductive Behavior of White-Breasted Nuthatches: I. Distraction Display, Bill-Sweeping, and Nest Hole Defense. Auk. 1968; 85: 477–492.
22. Barash DP. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bull. 1975; 87: 367–373.
23. Brunton DH. Fatal antipredator behavior of a Killdeer. Wilson Bull. 1986; 98: 605–607.
24. Byrkjedal I. Antipredator behavior and breeding success in Greater Golden-Plover and Eurasian Dotterel. Condor. 1987;40–47.
25. Sordahl TA. The risks of avian mobbing and distraction behavior: an anecdotal review. Wilson Bull. 1990; 102: 349–352.
26. Soluk DA, Collins NC. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. Oikos. 1988; 52: 94–100.
27. Krupa JJ, Sih A. Fishing spiders, green sunfish, and a stream-dwelling water strider: male-female conflict and prey responses to single versus multiple predator environments. Oecologia. 1998; 117: 258–265.
28. Ahlgren J, Brönmark C. Fleeing towards death—leech-induced behavioural defences increase freshwater snail susceptibility to predatory fish. Oikos. 2012; 121: 1501–1506.
29. Relyea RA. How prey respond to combined predators: a review and an empirical test. Ecology. 2003; 84: 1827–1839.
30. Birkhead T. The Magpies: The Ecology and Behaviour of Black-billed and Yellow-billed Magpies. London: Academic Press; 1991.
31. Tatner P. The diet of urban magpies *Pica pica*. Ibis. 1983; 125: 90–107.
32. Chiron F, Julliard R. Responses of songbirds to magpie reduction in an urban habitat. J Wildlife Manage. 2007; 71: 2624–2631.
33. Šťastný K, Bejček V, Hudec K. Atlas hnízdního rozšíření ptáků v České republice. Praha: Nakladatelství Aventinum; 2006.
34. Falkenauerová A. Antipredation behavior of the red-backed shrike (Lanius collurio). Bachelor Thesis, University of South Bohemia. 2008. Available: https://wstag.jcu.cz/portal/studium/prohlizeni.html?pc_pagenavigationalstate=H4sIAAAAAAAAAGNgYGBkYDMyMjA2txBmZADxOIpLEktSvVMrwTwRXUsjI2Njc6AKMwtTE3MzC2MTC6AMAwDRBK_4OgAAAA**

35. Bates D, Maechler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw. 2015; 67(1): 1–48.

36. Burnham K, Anderson D, Huyvaert K. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 2011; 65(1): 23–35.

37. Schmidt E. Die Sperbergrasmücke: *Sylvia nisoria*. Ziemsen: Wittenberg Lutherstadt; 1981.

38. Goodwin D. The reactions of some nesting passerines towards live and stuffed jays. Brit Birds. 1953; 6: 193–200.

39. Skutch AF. Do tropical birds rear as many young as they can nourish? Ibis. 1949; 91: 430–455.

40. Latimer W. A comparative study of the songs and alarm calls of some *Parus* species. Z Tierpsychol. 1977; 45: 414–433.

41. Shalter MD. Effect of spatial context on the mobbing behaviour of pied flycatchers to a predator model. Anim Behav. 1978; 26: 1219–1221.

42. Klump GM, Shalter MD. Acoustic behaviour of birds and mammals in the predator context. Z Tierpsychol. 1984; 66: 189–226.

43. Yasukawa K. Costs and benefits of a vocal signal: the nestassociated 'chit' of the female red-winged blackbird, *Agelaius phoeniceus*. Anim Behav. 1989; 38: 866–874.

44. Krams I. Communication in crested tits and the risk of predation. Anim Behav. 2001; 61: 1065–1068.

45. Krama T, Krams I. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. Behav Ecol. 2004; 16: 37–40.

46. Krams I, Krama T, Igaune K, Mänd R. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. Behav Ecol. 2007; 18: 1082–1084.

47. Weidinger K. Nest predators of woodland open-nesting songbirds in central Europe. Ibis. 2009; 151: 352–360.

48. Förschler M. Predation strategy of the European Jay *Garrulus glandarius* and antipredator response by the Citril Finch *Serinus citronella*. Revista Catalana d`Ornitologia. 2002; 19: 41–43.

49. Schaefer T. 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. 2004; 51: 170–177.

50. Klvaňová A, Horáková D, Exnerová A. Nest defence intensity in House Sparrows *Passer domesticus* in relation to parental quality and brood value. Acta Ornithol. 2011; 46: 47–54.

51. Drachmann J, Broberg MM, Søgaard P. 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. 2002; 49: 35–41.

52. Holyoak D. A comparative study of the food of some British Corvidae. Bird Study. 1968; 15: 147–153.

53. Krištín A. Nahrungsanspruche der Nestlinge *Pica pica* L. und *Passer montanus* L. in der Windbrechern der Schuttinsel. Folia Zool. 1988; 37: 343–356.

54. Møller AP. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. Oikos. 1988; 53: 215–221.

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

56. Stoate C, Thomson DL. Predation and songbird populations. In: Aebischer NJ, Evans AD, Grice PV, Vickery JA, editors. Ecology and Conservation of Lowland Farmland Birds. Tring: British Ornithologists Union; 2000. pp. 134–139.

57. Gooch S, Baillie SR, Birkhead TR. Magpie *Pica pica* and songbird populations. Retrospective investigation of trends in population density and breeding success. J. Appl. Ecol. 1991; 28: 1068–1086.

58. Roos S, Pärt T. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). J Anim Ecol. 2004; 73: 117–127.

59. Lefebrve L, Reader SM, Sol D. Brains, Innovations and Evolution in Birds and Primates. Brain Behav Evolut. 2004; 63: 233–246.

60. Emery NJ, Clayton NS. The mentality of crows—convergent evolution of intelligence in corvids and apes. Science. 2004; 306: 1903–1907. PMID: 15591194

61. Zinkivskay A, Nazir F, Smulders TV. What–Where–When memory in magpies (*Pica pica*) Anim Cogn. 2009; 12: 119–125. doi: 10.1007/s10071-008-0176-x PMID: 18670793

62. Clayton NS, Krebs JR. Memory in food-storing birds: from behaviour to brain. Curr Opin Neurobiol. 1995; 5: 149–154. PMID: 7620301

63. Pollok B, Prior H, Güntürkün O. Development of object permanence in food-storing magpies (*Pica pica*). J Comp Psychol. 2000; 114: 148–157. PMID: 10890586

64. Shaw RC, Plotnik JM, Clayton NS. Exclusion in corvids: The performance of food-caching Eurasian jays (*Garrulus glandarius*). J Comp Psychol. 2013; 127: 428. doi: 10.1037/a0032010 PMID: 23668696

65. Zucca P, Milos N, Vallortigara G. Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). Anim Cogn. 2007; 10: 243–258. PMID: 17242935

66. Healy SD, Krebs JR. Food storing and the hippocampus in Corvids amount and volume are correlated. P Roy Soc Lond B. 1992; 248: 241–245.

67. Prior H, Schwarz A, Güntürkün O. Mirror-Induced Behavior in the Magpie (*Pica pica*): Evidence of Self-Recognition. PLoS Biol 2008; 6: e202. doi: 10.1371/journal.pbio.0060202 PMID: 18715117

68. Holyoak D. Territorial and feeding behaviour of the magpie. Bird study. 1974; 21(2): 117–128.

69. Vines G. A socio-ecology of magpies *Pica pica*. Ibis. 1981; 123: 190–202.

70. Díaz JA, Asensio B. Effects of group size and distance to protective cover on the vigilance behaviour of Black-billed magpies *Pica pica*. Bird Study. 1991; 38: 38–41.

71. Lee WY, Lee S, Choe JC, Jablonski PG. Wild birds recognize individual humans: experiments on magpies, *Pica pica*. Anim Cogn. 2011; 14: 817–825. doi: 10.1007/s10071-011-0415-4 PMID: 21614521

72. Cheke LG, Clayton NS. Eurasian jays (*Garrulus glandarius*) overcome their current desires to anticipate two distinct future needs and plan for them appropriately. Biol Letters. 2012; 8: 171–175.

73. Shaw RC, Clayton NS. Eurasian jays, *Garrulus glandarius*, flexibly switch caching and pilfering tactics in response to social context. Anim Behav. 2012; 84: 1191–1200.

74. Shaw RC, Clayton NS. Careful cachers and prying pilferers: Eurasian jays (*Garrulus glandarius*) limit auditory information available to competitors. P Roy Soc B. 2013; 280: 20122238.

75. Legg EW, Clayton NS. Eurasian jays (*Garrulus glandarius*) conceal caches from onlookers. Anim Cogn. 2014; 17: 1223–1226. doi: 10.1007/s10071-014-0743-2 PMID: 24638877

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

77. Allen TA, Fortin NJ. The evolution of episodic memory. P Natl Acad Sci USA. 2013; 110: 10379–10386.

78. Skov-Rackette SI, Miller NY, Shettleworth SJ. What-where-when memory in pigeons. J Exp Psychol Anim B. 2006; 32: 345–358.

79. Yosef R, Pinshaw B. Impaling in true shrikes (Laniidae): A behavioral and ontogenetic perspective. Behav Process. 2005; 69: 363–367.

80. Morelli F, Bussière R, Goławski A, Tryjanowski P, Yosef R. Saving the best for last: Differential usage of impaled prey by red-backed shrike (*Lanius collurio*) during the breeding season. Behav Process. 2015; 119: 6–13.

81. Němec M, Syrová M, Dokoupilová L, Veselý P, Šmilauer P, Landová E et al. Surface texture plays important role in predator recognition by red-backed shrikes in field experiment. Anim. Cogn. 2015; 18: 259–268. doi: 10.1007/s10071-014-0796-2 PMID: 25107529

Článek IV.

Tvardíková K., Fuchs R. (2012): Tits recognize the potential dangers of predators and harmless birds in feeder experiments. Journal of Ethology 30:157-165.

J Ethol (2012) 30:157–165
DOI 10.1007/s10164-011-0310-0

ARTICLE

Tits recognize the potential dangers of predators and harmless birds in feeder experiments

Kateřina Tvardíková · Roman Fuchs

Received: 4 June 2011 / Accepted: 15 October 2011 / Published online: 6 November 2011

Abstract Accurate recognition of a predator is the necessary precondition for adequate antipredatory behaviour. We used feeder experiments to examine whether birds adopt the appropriate antipredatory response according to the level of threat posed by predators. The results support the idea that the tits made a decision on the threat level. The tits distinguished among equally sized obligatory predators (sparrowhawk, kestrel), an occasional predator (jay) and a harmless bird of similar size (pigeon) and a smaller harmless bird (thrush). The presence of both birds of prey was associated with a considerable reduction in the number of feeder visits when compared with the harmless birds. The number of visits to the feeder that had a dummy jay positioned on it did not significantly differ for harmless birds or for predators. Different sizes of harmless birds did not influence the tits' behaviour. The increasing risk lowered not only the number of visits to the feeder but also the success of the visit, pecking rate, and the direction of arrival to the feeder. Generally, birds assessed the risk during food searching, evaluated the situation, and adapted their behaviour accordingly.

Keywords Feeders · Predator recognition · Risk · Tits · Winter experiments

Introduction

The ability to avoid predators is a very important precondition for fitness in wild animals (Devereux et al. 2006). Antipredatory behaviour (e.g. escape or mobbing) is usually energetically exacting (Krams and Krama 2002). In addition to direct costs, antipredatory behaviour also prevents further activities, most specifically food searching. A repetitive daily trade-off between the need to search for food and yet avoid predators occurs throughout the animal's life (Devereux et al. 2006). Underestimating the danger posed by an animal can be fatal. On the other hand, the evaluation of a harmless animal as threatening can also be detrimental (Caro 2005). Accurate recognition is the first step in effective predator avoidance. Predator recognition demands not only distinguishing between predators and harmless animals but also between predatory levels of threat.

Studies on predator recognition that compare both dangerous and harmless animals have been made during the breeding period within the scope of mobbing trials by birds defending their nests. Small passerines have been studied in many experiments (tits *Parus* spp., e.g. Curio et al. 1983; Rytkönen and Soppela 1995; Reed Warblers *Acrocephalus* spp., e.g. Kleindorfer et al. 2005; Red-winged Blackbird *Agelaius phoeniceus*, Knight and Temple 1988; American Goldfinch *Carduelis tristis*, Knight and Temple 1986), because nest predation is the principal cause of passerine nesting mortality (Schmidt and Whelan 1999). These studies showed that parents respond differentially according to the threat posed by different predators (Caro 2005). The ability to recognise harmless and dangerous objects was proved in almost all the studies.

The recognition and evaluation of differentially dangerous predators is less studied. Often, predators of adults

K. Tvardíková · R. Fuchs
Faculty of Science, University of South Bohemia,
Ceske Budejovice, Czech Republic

K. Tvardíková (✉)
Institute of Entomology, Biology Centre AS CR, v. v. i.,
Ceske Budejovice, Czech Republic
e-mail: katerina.tvardikova@gmail.com

were compared with predators of broods (e.g. Buitron 1983; Jacobsen and Ugelvik 1992; Rytkönen and Soppela 1995). The comparison of more or less dangerous predators has been less frequent (Patterson et al. 1980; Buitron 1983; Curio et al. 1983; Jacobsen and Ugelvik 1992; Clemmons and Lambrechts 1992; Kleindorfer et al. 2005), and differences have been found in hunting capabilities and technique (aerial vs. land). Therefore, a different reaction does not necessarily express the recognition of a predator species. The reaction of birds to a predator of adults or broods will also be different. Birds' decision-making in active nest defence is quite complex. Threats to adults or broods, as well as the actual threat arising from the situation (e.g. the age of offspring or the distance of a predator from the nest), have to be taken into account (Kleindorfer et al. 2005). The results of these experiments often reveal ambiguity in the bird's abilities to recognize individual predator species.

Previous studies outside the breeding season were mainly focused on vocal signals given to conspecifics and/or to a predator. Templeton et al. (2005) found that calls of black-capped chickadees (*Poecile atricapilla*) were likely to contain information about the degree of threat (body size, wing-span) that a predator represented, but not precise discrimination between raptors and mammals. Siberian jays (*Perisoreus infaustus*) recognized and communicated predator category (owls, birds of prey, corvids), predator species (goshawk, sparrowhawk, hobby, hawk owl, etc.) and predator behaviour (perching, searching, attacking) to other group members (Griesser 2008, 2009). Similarly, Palleroni et al. (2005) showed that domestic fowl produced highly distinctive responses to three raptors of varying sizes while controlling for as many other differences between the raptors as possible. Chickens tended to show highly evasive responses to the largest raptor, and more aggressive responses to the smaller raptors. Predators of different sizes appeared in all these studies, and it is unclear whether tested birds were able to recognize individual predator species.

Winter experiments at a feeder offer another method to study risk assessment in passerines outside the breeding season. We can examine the simple interaction between the need for predator avoidance and that of feeding when exposing birds at a feeder to the presence of a predator.

The majority of studies that have attempted to manipulate the risk of predation on a feeder were conducted in aviaries, and they have often yielded inconclusive results (Gentle and Gosler 2001). They examined how bird mass changes in the presence of a model predator (Lilliendahl 1997, 1998, 2000; Pravosudov and Grubb 1998; Carrascal and Polo 1999). Others assessed the effect on corticosteron response (Cockrem and Silverin 2002) or foraging trade-off (Van der Veen 1999; Devereux et al. 2006; Lind et al. 2005). Only three studies altered the risk of predation in field experiments using a feeder. Gentle and Gosler (2001) and MacLeod and Gosler (2006) investigated the effect of predator presence on fat reserves in a manner similar to what was done in the aviary experiments. Desrochers et al. (2002) assessed whether exposure to mobbing calls or a stuffed predator elicited changes in risk perception on the feeders at various distances from the forest edge. The results of the afore-mentioned studies suggest that birds are able to react in a complex way (in field experiments using feeders) and can even change their physiology quite quickly.

The inconclusive results from aviary experiments could be caused by stress from handling or from being kept in an experimental cage. Because of the contradictory nature of the results from aviary experiments, we opted for field feeder experiments. We aimed to investigate whether birds select the correct antipredatory response according to the danger posed by predators. We tested reactions to aerial "predators" only (except for an artificial object), because it is very hard to compare the relative potential dangers of terrestrial and aerial predators. Moreover, as we used dummy predators, we assumed that any differences in perception would be similar for all bird species. We tested sparrowhawk, kestrel, jay, pigeon, thrush, and a lump of cotton wool (similar in size to a pigeon) as the potential predators. The two birds of prey (sparrowhawk, kestrel) are similar in size but differ from each other in feeding specialisation (Götmark 2002). The sparrowhawk is the most dangerous predator for small passerines (Rytkönen et al. 1998), while small mammals predominate in kestrels' diet (Kubler et al. 2005). A differential reaction to them should show that the tested birds recognized individual predator species and not just their size. The same applies to the jay and pigeon. The jay is an important predator of eggs or hatchlings (Shields 1984; Ehrlich and McLaughlin 1988; Reyer et al. 1998). A jay's ability to hurt other birds is very limited, but not impossible (Ehrlich and McLaughlin 1988) and a jay cannot be regarded as completely harmless. This should not be the case for the pigeon and thrush as they can only play the role of competitors. A pigeon could be perceived as more dangerous due to its bigger size. The last object was the lump of cotton wool, which should represent an unknown artificial object, to which birds have no prior experience.

The following hypotheses were tested: (1) the presence of predators (sparrowhawk, kestrel) reduces feeder use more than the presence of other "objects"; (2) the presence of the sparrowhawk reduces feeder use more than the presence of the kestrel; (3) the presence of the jay reduces feeder use more than the presence of the pigeon and thrush; (4) the presence of the pigeon reduces feeder use more than the presence of the thrush; (5) the presence of the thrush and cotton do not reduce feeder use; and (6) birds visiting feeders with predators are more vigilant and less successful than those visiting feeders with harmless bird.

Materials and methods

Study site and species

The experiment was undertaken during the winter of 2005/2006 in a marshy, broad-leaved woodland area near the village of Chodská Lhota (49°21′15″N, 30°47′25″W), West Bohemia, Czech Republic. The experiments were conducted during 13 weekends (experiments started on Saturday) in November (3, 10, 17, 24) January (1, 14, 21, 28), February (4, 11, 19, 26), and partly in March (12). The site is 640 m above sea level, and is one of the colder parts of Bohemia (it was a particularly harsh winter). The site was situated in a shrubby area along a stream, which served as a corridor for birds.

Four species of tit, great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), marsh tit (*Poecile palustris*) and willow tit (*Poecile montanus*), were used as experimental species, as they are the most common and abundant species in the area during the winter season. We also recorded a few arrivals of different bird species (e.g. chaffinch *Fringilla coelebs*, Blackbird *Turdus merula*), but were unable to analyse them statistically due to the scarcity of their arrivals.

Experimental design

The feeder was positioned in a small clearing, surrounded by mixed deciduous woodland and shrubs, where the shortest distance to cover was 4 m. The shrubs served as a relatively safe lookout point for the birds. The feeder was a large (75 × 75 cm—because of suppression of competition among attendant birds) desk lying on the ground with a raised edge to avoid the scattering of food. Between experiments, the feeder was covered by a roof and sunflower seeds were used as food. Sunflower seeds were attentively removed and replaced by grated walnuts just before the trial. Grated walnut was used because the extra effort required by the birds to feed forced them to remain longer at the feeder (Desrochers et al. 2002). Tits carry away sun-flower seeds and consume them under cover, whereas the grated walnuts have to be pecked at the feeder. Stuffed models of a sparrowhawk, kestrel, jay, pigeon, thrush, and a lump of cotton wool (similar size of a pigeon) were used as the tested "predators". All the dummies were new and made by the same dummy maker. They were placed on a 75-cm-high stake at the rear right corner (from the camera) of the feeder and always faced the feeder. Thus, birds arriving at the feeder from the left and front sides (from the camera) were coded as arriving head on to the dummy, and birds arriving from the right and rear sides were coded as arriving from behind it.

Each series of six trials with dummies was distributed within the two contiguous experimental days. The sequence of six dummies within each series was randomly arranged. Individual trials lasted 30 min and they were separated by 30-min-long breaks that were also videotaped. One of these breaks (including 30 min before the first experiment) was then randomly chosen and used as the control. There were 5 days between each series. Each experimental day started with a control trial and ended with a trial with a dummy.

Each experimental day started half an hour after daybreak. The experimental feeder was recorded the full length of the experiments. The camera was set up in a fixed position facing the experimental feeder and 15 m away. Snow cover and temperature were noted for each experimental day. There were 13 series conducted, resulting in 6 × 13 half-hours of trials with dummies ("objects") and 13 half-hours of control trials.

In total, 42,326 arrivals of tits were recorded, but those obviously included many pseudoreplications (repeated arrival of one individual). Therefore, only the first arrivals of ringed birds to each of the trials (both experimental and control) were used in the analysis.

The birds were mist-netted continuously during the winter, and the trapping effort was constant at about 50 birds per ringing day. Mist-nets were in use the day before each experiment (Friday) just around the feeder and 634 birds were ringed during the winter. Each trapped individual was both fitted with a standard metal leg-ring with a unique number and an individual combination of colour-ring was then fitted under the license (Czech Ringing Association, 1062). Each bird was thus uniquely identifiable on videotape. We revealed great alternation of birds on our feeder. Only 44.41 ± 1.1 (mean ± SD) % of birds ringed during one series stayed until the next series (7 days later) and, having appeared once during the series, the bird usually arrived 6.101 ± 1.01 times to the feeder but only during 4.1 ± 1.78 unique trials. Only 20.91 ± 4.8% birds stayed until the third series (14 days later) and 2.8 ± 1.1% of ringed birds appeared again in the fourth series (22 days later).

Statistical analysis

To avoid pseudoreplication, all the presented models and analyses were counted for the first visit of a ringed bird under unique experimental situation. Thus, the individual bird was included only once in each of six experimental trials and one random control. One bird could thus come maximally seven times into the analysis and no more than once under the same treatment. Therefore, 2,752 visits of 634 ringed birds were included in analyses.

The number of visits was entered into the GLM model (R 2.10.1, R project 2008). The following explanatory variables were used: dummy (6 dummies and 1 control), bird species (4 species), series (1–13), and 2-way interactions were included. Snow (cm) and temperature (°C) were added as a continuous variable in the model. The data had a Poisson distribution and link function log was used. The Tukey post hoc test in R (Hothorn et al. 2008) was performed in the multcomp package (function glht) of the R software, for the variable dummy.

Another GLM (function glm in basic library, gaussian distribution) model was constructed for the pecking rate (the number of pecks per second). The experimental situation (all dummies and control) at the feeder and series, tit species and 2-way interactions were used as explanatory variables. Temperature and snow cover were added as continuous variables in the model.

To examine the success of visits (successful = bird pecked at least once, unsuccessful = bird did not peck) and the direction of arrivals (head on to dummy, from the back), another two models (glm, R) were constructed in a similar manner as for pecking rate. The data had a binomial distribution and the logit link function was used. Tukey post hoc tests (multcomp package, glht function) were conducted to reveal differences between individual dummies for all dependent variables.

To examine temporal patterns, the number of arrivals during individual trials with dummies was analysed using ANOVA. The number of arrivals for 5-min-long intervals within individual trials was then compared (repeated measure ANOVA) to reveal any possible habituation to a motionless predator. These statistical calculations were made using STATISTICA 8 for Windows (StatSoft 2007).

Results

The number of visits in a trial were significantly influenced only by the type of presented dummy and by temperature–dummy interaction (Table 1). Comparison of the number of arrivals to individual dummies revealed significant differences between predators (sparrowhawk, kestrel) and all “harmless trials” (pigeon, thrush, cotton, control). There were no significant differences within these two groups. The jay was somewhere in between these groups, but insignificantly different from either (Fig. 1).

The success of individual visits to the feeder (successful = bird pecked at least once, unsuccessful = bird did not peck) was significantly influenced by the type of presented dummy, tit species, and type of dummy in interaction with snow layer or temperature (Table 1). Post hoc testing divided dummies into three groups (Fig. 2). There was no significant difference within predators (sparrowhawk, kestrel, $P = 0.76$) or within “harmless trials” (control, cotton, thrush and pigeon, $P > 0.08$) while there was a difference between these two groups ($P < 0.02$). The jay formed the third group differing significantly from all other trials. These results were similar for all tit species. The success of the great tit was significantly lower than success of the other tit species (Tukey post hoc test; Fig. 4).

The pecking rate (measured as number of pecks per second) was influenced by the dummy presented at the feeder and by dummy type in interaction with snow layer (Table 1). The post hoc test separated only the control from both predators (sparrowhawk: $P < 0.001$, $F = 4.53$; kestrel: $P = 0.008$, $F = 2.36$) and thrush from sparrowhawk ($P = 0.042$, $F = 3.01$). The birds visiting the feeder with a bird of prey, pecked more slowly (sparrowhawk 1.261 ± 0.052, kestrel 1.245 ± 0.063) than in the presence of the thrush (1.576 ± 0.068) and during the control (1.507 ± 0.082).

The direction of arrival to the feeder differed significantly for individual dummies and tit species (Table 1). The interactions snow with temperature, temperature with series and snow with series also had a significant influence. All tit species arrived when more dangerous dummies (sparrowhawk, kestrel, and jay) were present less often from the rear and more often head on (Fig. 3). The 50% (e.g. trial with pigeon) of arrivals head on to the feeder mean that tits did not care about the direction of arrival and arrived accidentally. Great tits arrived significantly more head on to the predator than the other bird species. On the other hand, blue tits approached the feeder more randomly than the other birds. There was no difference in the direction of arrival of willow and marsh tits (Tukey post hoc test; Fig. 4).

The birds did not get accustomed to dummies as there was no effect of the order of series during the winter (Table 1). Moreover, the number of arrivals during the individual trials did not change significantly either (repeated measures ANOVA for 5-min intervals, interval: dummy, $F_{6,30} = 0.42$, $P = 0.213$).

Discussion

The results support most of our hypotheses because tits made decisions on the basis of threat level. On the other hand, we did not confirm the ability of birds to distinguish between two differently dangerous predators of the same size. Both predators (sparrowhawk, kestrel) lowered not only the number of arrivals at the feeder but also pecking

Table 1 Factors affecting (*R*, generalized linear model) the number of arrivals (Poisson distribution, log link function), pecking rate (Gaussian distribution, Identity link function), success (binomial distribution, logit link function), and direction of arrival (binomial distribution, logit link function)

	df	Number of arrivals		Pecking rate		Success		Dirrection of arrival	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Dummy	6	23.17	**<0.001**	14.03	**<0.001**	64.03	**<0.001**	97.6	**<0.001**
Bird	3	0.27	0.847	0.05	0.921	11.73	**0.043**	58.76	**<0.001**
Snow	1	3.11	0.079	1.76	0.115	2.53	0.102	1.42	0.234
Temperature	1	3.08	0.062	0.19	0.656	0.38	0.642	1.54	0.233
Series	1	7.066	0.073	<0.01	0.981	0.58	0.44	1.85	0.241
Dummy: snow	6	0.595	0.733	6.88	**<0.001**	4.51	**<0.001**	0.56	0.881
Dummy: temperature	6	3.474	**0.003**	1.89	0.83	26.5	**<0.001**	1.49	0.124
Snow: temperature	1	0.003	0.957	2.34	0.22	0.11	0.737	11.7	**<0.001**
Dummy: bird	18	0.472	0.966	0.05	0.87	1.08	0.09	1.29	0.200
Bird: snow	3	0.145	0.932	<0.01	0.918	1.06	0.345	1.38	0.249
Bird: temperature	3	0.062	0.979	0.06	0.78	2.56	0.077	1.16	0.310
Dummy: series	6	0.999	0.427	1.01	0.42	0.54	0.090	0.566	0.891
Snow: series	1	0.383	0.537	2.74	0.071	0.64	0.422	7.4	0.011
Temperature: series	1	0.467	0.496	0.01	0.942	0.04	0.841	53.96	**<0.001**
Birds: series	3	0.041	0.988	0.01	0.897	3.76	0.068	0.63	0.53

Significant values are marked in bold

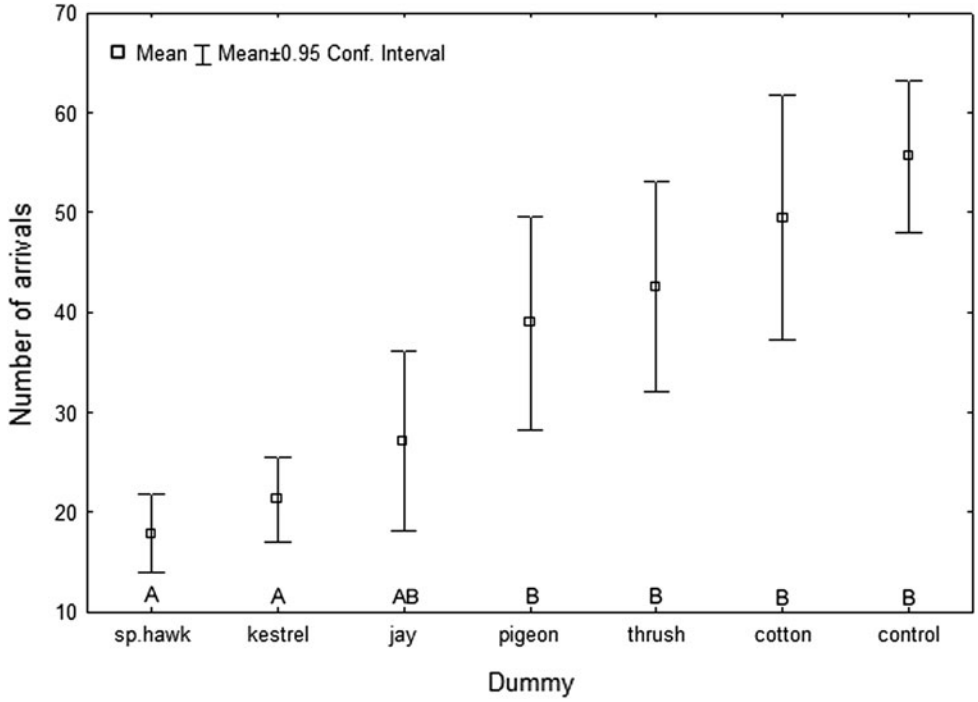


Fig. 1 The number of arrivals to a feeder with presented dummy or during a control trial (all tit species together); *A*, *B* groups without significant difference ($P > 0.08$) within them, and significantly different from each other ($P < 0.5$)

rate, success of realized visits, and even the direction of arrival to the feeder. In the presence of a predator, the tits that risked arrival left the feeder site after a longer time, with lower energy gain (low pecking rate), and very often without consumption at all (without success). The success of birds shows that the bird at least considered taking the risk of bending down in the presence of a potentially dangerous object. The speed of pecking shows how long a bird is willing to stay with his head down, without the possibility to control for the predator's behaviour. Birds apparently used the period of stay without consumption to assess the risk of the dummy. This result seems to be

Fig. 2 Total success of visits on the feeder in the presence of individual dummies; *A*, *B*, *C* groups without significant difference ($P > 0.08$) within groups, and different from each other ($P < 0.5$)

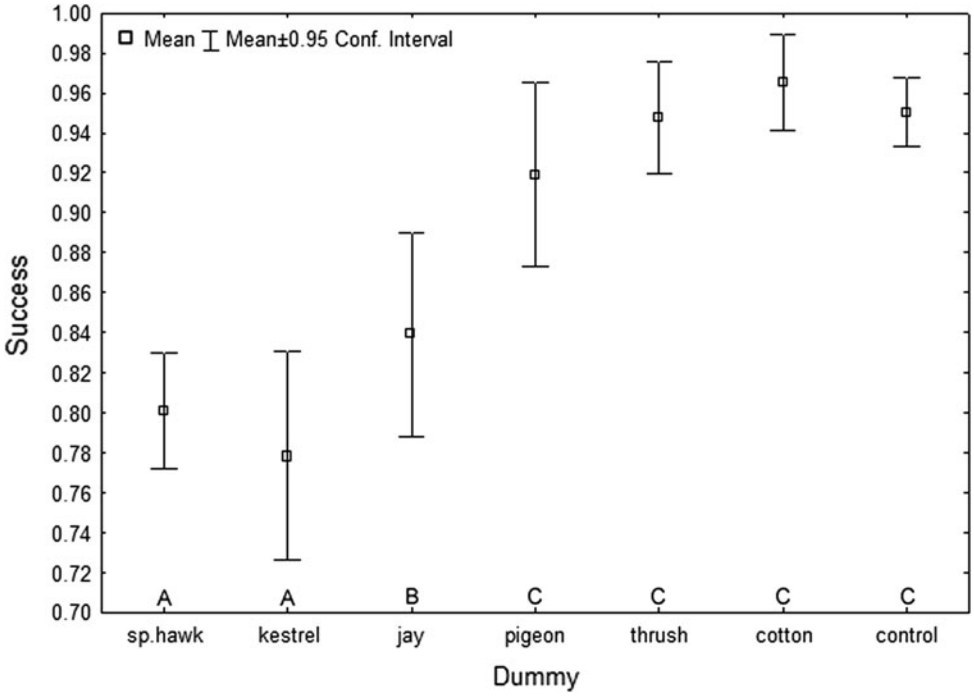
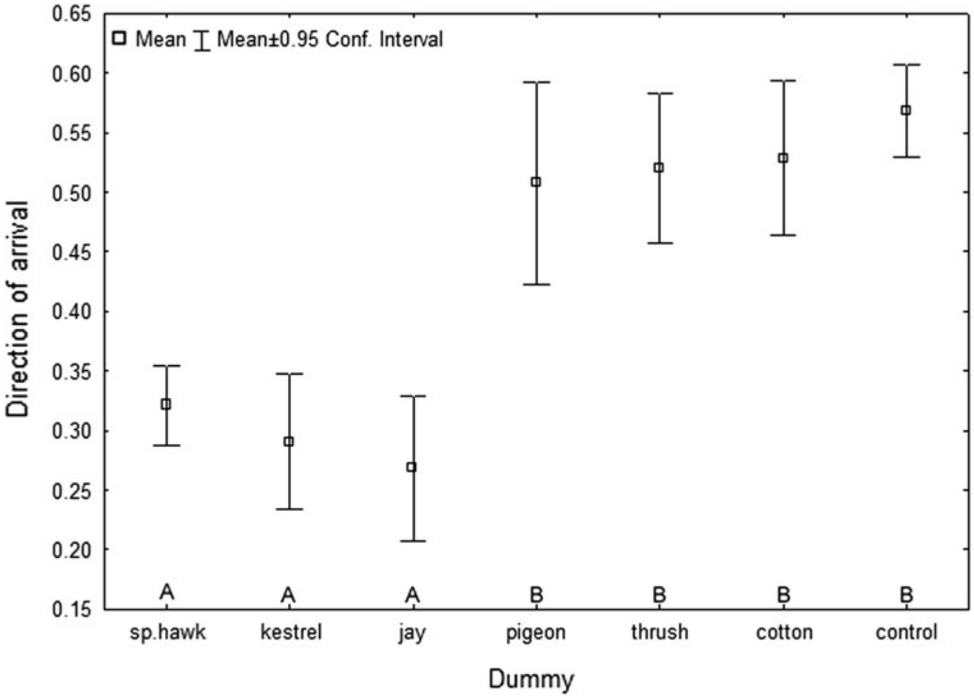


Fig. 3 The direction of arrival to feeder (0 head on arrival, 1 arrival from backside, 0.5 birds arrived randomly); *A*, *B* groups without significant difference ($P > 0.06$) within groups, and groups different from each other ($P < 0.5$)



contra-intuitive. We expected that a risk-taking bird would take advantage of being alone at a feeder, and would feed as quickly and as much as possible. The results suggest overall that the period of stay at the feeder without consumption might be used for predator identification and controlling. We have to take into account that only a few birds visited the feeder with a predator present and performed such unexpected behaviour. These birds were not only young individuals, and this behaviour can be most likely explained as inexperience because most of these birds elicited delayed alarm calls. A similar delayed response to a predator was found by Cresswell et al. (2009), who worked on the use of freezing behaviour for risk assessment in chaffinches (*Fringilla coelebs*). He explains delayed response in chaffinches as the functions of an effective economic risk assessment period.

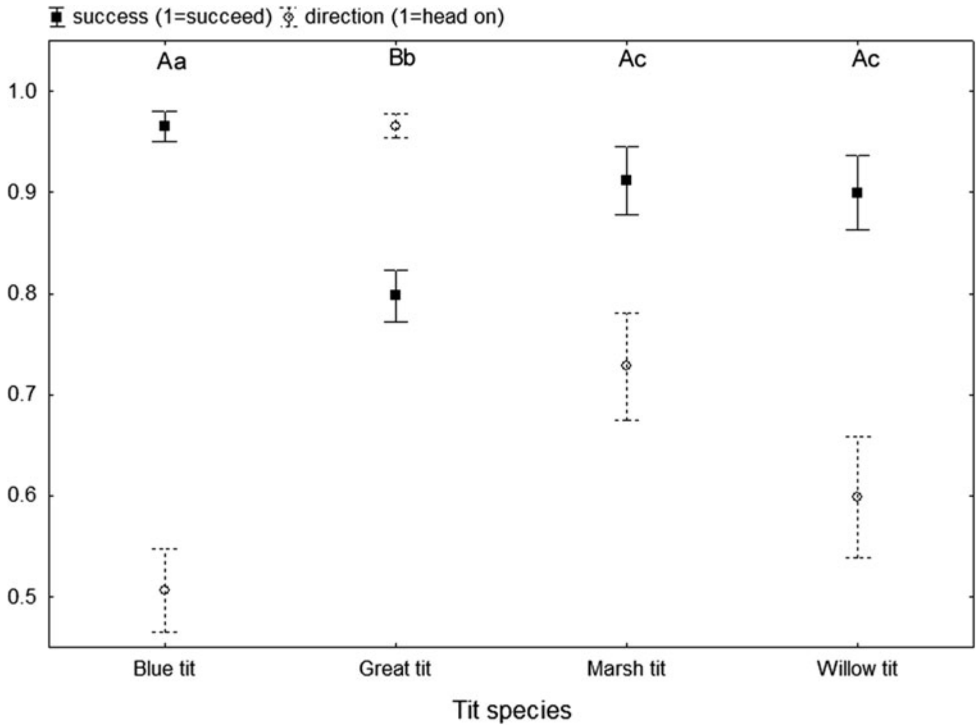


Fig. 4 Success of visits on the feeder and direction of arrival to feeder of individual tit species with the results of Tukey post hoc test marked in capital letters for success, and in lowercase letters for the direction of arrival. *A*, *B* and *a*, *b*, *c* groups without significant difference ($P > 0.05$) within groups. Success: 1 bird pecked at least once, 0, bird did not peck. Direction of arrival: 1, birds arrived head on to the dummy; 0, birds arrived from the backside; 0.5, birds arrived randomly

Finally, the number of arrivals from behind the predator and jay dummies decreased and birds approached head on more often. This can be due to the effort to control for a predator's behaviour during an arrival. Dummies "were looking" at the feeder and birds approaching from the rear had to pass over them. Similar behaviour has not been described until now, but Kaby and Lind (2003) discovered that blue tits reacted to sparrowhawks earlier when arriving from the side rather than from the rear. Generally, birds appear to assess the risk during food searching, evaluate the situation, and adapt their behaviour accordingly.

Tits seem to evaluate the sparrowhawk and kestrel as being equally dangerous, because both lowered the number of arrivals equally. This holds even though the sparrowhawk is a specialized predator of small passerines (Rytkönen et al. 1998; Götmark 2002) and should represent a bigger threat. There could be two causes: tits were not able to distinguish between either predators or they really evaluated them as the same threat level. Tits could evaluate the kestrel as more dangerous in winter than in summer, because of an increasing proportion of small birds in their food (Kubler et al. 2005). Our assumption was made for a natural predator foraging situation, however, and not when the predator is literally sitting near the feeder. From that distance, both raptors could be similarly lethal if prey were to approach them. Comparing our work with the available literature, we noted an overall higher number of arrivals with both predators than could be expected. This could be due to the conditions of our experimental setting that was reducing the perceived risk of all dummies (approving mainly on the dangerous ones). The feeder was surrounded by shrubs on three sides, where the tits could hide, within 4 m from the feeder. However, this hypothesis is not supported by Desrochers et al. (2002) who studied changes in risk perception at feeders separated from tree cover by a strip of open area with widths of 0.6 and 10 m. When a stuffed merlin was present sitting near the feeder, chickadees only rarely visited the feeder, regardless of the distance to cover. Nevertheless, Desrocher's experiment differed in two aspects. He used 25 feeders and only 1 of them was experimental in each trial. Moreover, the trials lasted for only 5 min per day.

Tits were not afraid of either the thrush or pigeon dummies. No matter how large they were, neither of them lowered the number of visits to the feeder. Wariness was not increased even by the unknown object (lump of cotton). The evaluation of the jay was ambiguous. The jay did not differ in the number of arrivals from other harmless dummies or from predators. Moreover, its presence lowered the success of birds in a manner significantly different from both harmless and dangerous dummies. It can be summarised that tits can distinguish obligatory predators (sparrowhawk, kestrel), potentially dangerous corvids (jay) and the harmless birds (pigeon, thrush). The size of a harmless bird did not influence the tits' behaviour.

When we discuss the number of arrivals to the feeder, we also have to point out the potential problems of our experimental design. Since we used only one feeder in the experiment, it may be difficult to consider our data as independent because the response recorded during the experiment may reflect a particular flock that frequently visited the feeder. We would have to set more feeders over a wide area of the field site to collect independent data from different flocks. This was not feasible in our case and therefore we decided to set the experimental feeder in a well-visited place, where the birds migrated, and we were able to record hundreds of individuals. However, multiple individuals visited the feeder in the same trial and we have to consider that the individuals in the same trials do not have to be independent (i.e. some individuals might respond to predator models, while the others might respond to warning signals given by the other individuals). We believe that such behaviour should be recognizable in the changes during the trials. Birds would come less and less with more warning signals, but we did not find any changes in the number of arrivals during trials when we analysed 5-min-long intervals.

Existing studies investigating differences in risk assessment between various predators have been conducted mainly during the breeding season, and only a few studies compared various aerial predators. A stronger reaction to a more dangerous predator was observed in most of the studies (falcons vs. hawks vs. eagles vs. great horned owl *Buteo virginianus*, Buitron 1983; sparrowhawk vs. pygmy owl *Glaucidium passerinum* vs. tawny owl *Strix aluco*, Curio et al. 1983; sparrowhawk vs. pygmy owl, Rytkönen and Soppela 1995; Forsman et al. 1998). Griesser (2009) compared jay reactions to three hawk and three owl species (goshawk *Accipiter gentilis*, sparrowhawk *Accipiter nisus*, hobby *Falco subbuteus*, Ural owl *Strix uralensi*, hawk owl *Surnia ulula*, pygmy owl *Glaucidium passerinum*) of varying danger, and the jay's ability to communicate the threats. He proved that mobbing calls can simultaneously encode information about both predator category and the risk posed by a predator. Similar results were obtained by Palleroni et al. (2005) who found that chickens are able to distinguish between variously sized trained raptors. Templeton et al. (2005) proved that calls of black-capped chickadees varied with the size of predator. Edelaar and Wright (2006) observed that arabian babblers (*Turdoides squamiceps*) distinguished between many birds representing low and high predation risk. These studies were based mainly on the differences between raptors and owls or between raptors of different size, thus they could not be compared with our study.

Corvids are often subjects in experiments studying nest defence. The studied species usually strike with at least the same intensity at the corvids as at birds of prey or owls (Gottfried 1979; Patterson et al. 1980; Buitron 1983; Knight and Temple 1986; Ghalambor and Martin 2002; but see Arnold 2000). The weak response to a jay in our case shows that birds recognize its threat level for adults (lower) and nestlings or eggs (higher). The tits may recognize a jay as a facultative predator of small passerines (Ehrlich and McLaughlin 1988). On the other hand, the jay may be dangerous from a competition standpoint, such as the ability of the jay to attack another adult bird, although that bird would not want to get too close to it. So, the response to the jay can be likely based more on proximity, perceived competition, and the willingness to get close than on recognition and the risk of predation.

The four studied species responded very similarly to all dummies. However, we could see some differences in the success, and the direction of arrival to feeder, in blue and great tits. Blue tits showed more bravery to more dangerous species and were more successful once sitting on feeder. On the other hand, great tits spent a longer time assessing the situation. Great tits arrived more often head on to the feeder, and were less successful in the presence of more dangerous dummies. Great tits are dominant in winter flocks and they do not have to risk being in the presence of potential danger. Smaller tit species are also faster and/or agile and they can afford to approach danger (Ekman 1989).

Our results show that birds are willing to increase risk (higher number of arrivals, quicker pecking rate, and higher success of individual visits) during harsh climatic conditions. Similar trends have been documented in many studies (Brittingham and Temple 1988; Walther and Gosler 2001; Carrascal and Alonso 2006). However, existing studies were carried out without the presence of a predator dummy.

Acknowledgments We are grateful to the anonymous reviewers for their truly helpful comments that have driven us to review once again. I am also grateful to Philip Butterill and Legi Sam for their comments, and support during my work on manuscript. The study was financially supported by grants of the Academy of Sciences of the Czech Republic (IAA601410803), and the Ministry of Education, Youth, and Sports (MSM6007665801).

References

Arnold KE (2000) Group mobbing behavior and nest defence in a cooperatively breeding Australian bird. Ethology 106(5): 385–393

Brittingham MC, Temple SA (1988) Impactsof supplemental feeding on survival rates ofblack-capped chickadees. Ecology 69:581–589

Buitron D (1983) Variability in the responses of Black-billed Magpies to natural predators. Behaviour 87(3–4):209–235. doi:10.1163/156853983X00435

Caro TM (2005) Antipredator defenses in birds and mammals. The University of Chicago Press, London

Carrascal LM, Alonso CL (2006) Habitat use under latent predation risk. A case study with wintering forest birds. Oikos 112:51–62

Carrascal ML, Polo V (1999) Coal tit, *Parus ater*, lose weight in response to chases by predators. Anim Behav 58:281–285

Clemmons JR, Lambrechts MM (1992) The waving display and other nest site antipredator behavior of the black-capped chickadee. Wilson Bull 104(4):749–756

Cockrem JF, Silverin B (2002) Sight of a predator can stimulate a corticosterone response in the great tit (*Parus major*). Gen Comp Endocrinol 125(2):248–255. doi:10.1006/gcen.2001.7749

Cresswell W, Butler S, Whittingham MJ, Quinn JL (2009) Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. Behaviour 146: 795–813

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it turned to predator risk? Oecologia 60:83–88

Desrochers A, Belisle M, Bourque J (2002) Do mobbing calls affect the perception of predation risk by forest birds? Anim Behav 64:709–714. doi:10.1006/anbe.2002.4013

Devereux CL, Whittingham MJ, Fernández-Juricic E, Vickery JA, Krebs JR (2006) Predator detection and avoidance by starlings under differing scenarios of predation risk. Behav Ecol 17(2): 303–309. doi:10.1093/beheco/arj032

Edelaar P, Wright J (2006) Potential prey make excellent ornithologists: adaptive, flexible responses towards avian predation threat by Arabian babblers *Turdoides squamiceps* living at a migratory hotspot. Ibis 148:664–671. doi:10.1111/j.1474-919X.2006.00567.x

Ehrlich PR, McLaughlin JF (1988) Scrub jay predation on starling and swallows-attack and interspecific defense. Condor 90(2): 503–505

Ekman J (1989) Ecology of non-breeding social system of Parus. Wilson Bull 101:263–288

Forsman JT, Mönkkönen M, Inkeröinen J, Reunanen P (1998) Aggregate dispersion of birds after encountering a predator: experience evidence. J Avian Biol 29:44–48

Gentle LK, Gosler AG (2001) Fat reserves and perceived predation risk in the great tit, *Parus major*. Proc R Soc Lond B 268(1466):487–491. doi:10.1098/rspb.2000.1405

Ghalambor CK, Martin TE (2002) Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behav Ecol 13(1):101–108

Götmark F (2002) Predation by sparrowhawks favours early breeding and small broods in great tits. Oecologia 130(1):25–32. doi: 10.1007/s004420100769

Gottfried BM (1979) Anti-predator aggression in bird nesting in old field habitats-experimental analysis. Condor 81:251–257

Griesser M (2008) Referential calls signal predator behavior in a group-living bird species. Curr Biol 18:69–73. doi:10.1016/j.cub.2007.11.069

Griesser M (2009) Mobbing calls signal predator category in a kin group-living bird species. Proc R Soc Lond B 276:2887–2892. doi:10.1098/rspb.2009.0551

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50(3):346–363

Jacobsen OW, Ugelvik M (1992) Antipredator behavior of breeding Eurasian wigeon. J Field Ornithol 63(3):324–330

Kaby U, Lind J (2003) What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? Behav Ecol Sociobiol 54(6):534–538. doi:10.1007/s00265-003-0665-5

Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. Anim Behav 69:307–313. doi:10.1016/j.anbehav.2004.06.003

Knight RL, Temple SA (1986) Nest defense in the American goldfinch. Anim Behav 34:887–897. doi:10.1016/S0003-3472(86)80075-6

Knight RL, Temple SA (1988) Nest-defense behavior in the red-winged blackbird. Condor 90:193–200

Krams I, Krama T (2002) Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches. *Fringilla coelebs*. Proc R Soc Lond B 269(1507):2345–2350. doi:10.1098/rspb.2002.2155

Kubler S, Kupko S, Zeller U (2005) The kestrel (*Falco tinnunculus* L.) in Berlin: investigation of breeding biology and feeding ecology. J Ornithol 146(3):271–278. doi:10.1007/s10336-005-0089-2

Lilliendahl K (1997) The effect of predator presence on body mass in captive greenfinches. Anim Behav 53:75–81. doi:10.1006/anbe.1996.0279

Lilliendahl K (1998) Yellowhammers get fatter in the presence of a predator. Anim Behav 55:1335–1340. doi:10.1006/anbe.1996.0279

Lilliendahl K (2000) Daily accumulation of body reserves under increased predation risk in captive greenfinches *Carduelis chloris*. Ibis 142(4):587–595

Lind J, Jongren F, Nilsson J et al (2005) Information, predation risk and foraging decisions during mobbing in great tits *Parus major*. Ornis Fenn 82(3):89–96

MacLeod R, Gosler AG (2006) Capture and mass change: perceived predation risk or interrupted foraging? Anim Behav 71:1081–1087. doi:10.1016/j.anbehav.2005.07.022

Palleroni A, Hauser M, Marler P (2005) Do responses of galliform birds vary adaptively with predator size? Anim Cogn 8:200–210

Patterson TL, Petrinovich L, James DK (1980) Reproductive value and appropriateness of response to predators by white-crowned sparrows. Behav Ecol Sociobiol 7(3):227–231

Pravosudov VV, Grubb TC (1998) Management of fat reserves in tufted titmice *Baelophus bicolor* in relation to risk of predation. Anim Behav 56:49–54. doi:10.1006/anbe.1998.0739

R DEVELOPMENT CORE TEAM (2008) r: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org

Reyer HU, Fischer W, Steck P et al (1998) Sex-specific nest defense in house sparrows (*Passer domesticus*) varies with badge size of males. Behav Ecol Sociobiol 42(2):93–99

Rytkönen S, Soppela M (1995) Vicinity of sparrowhawk nest affects willow tit nest defense. Condor 97:1074–1078

Rytkönen S, Kuokkanen P, Hukkanen M et al (1998) Prey selection by Sparrowhawks *Accipiter nisus* and characteristics of vulnerable prey. Ornis Fenn 75(2):77–87

Schmidt KA, Whelan CJ (1999) Nest placement and mortality: is nest predation a random event in space and time? Condor 101: 916–920

Shields WM (1984) Barn swallow mobbing: self-defense, collateral kin defense, groupdefense, or parental care? Anim Behav 32: 132–148

StatSoft (2007) STATISTICA, version 8.0. http://www.statsoft.com

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

van der Veen IT (1999) Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). Behav Ecol 10(5):545–551. doi:10.1007/BF00299368

Walther BA, Gosler AG (2001) The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: Parus). Oecologia 129:312–320

Článek V.

Tvardíková K., Fuchs R. (2011): Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behavioral Ecology and Sociobiology 65:727-733.

Behav Ecol Sociobiol (2011) 65:727–733
DOI 10.1007/s00265-010-1075-0

ORIGINAL PAPER

Do birds behave according to dynamic risk assessment theory? A feeder experiment

Kateřina Tvardíková · Roman Fuchs

Received: 6 June 2010 / Revised: 25 August 2010 / Accepted: 4 October 2010 / Published online: 16 November 2010

Abstract Pair-wise preference experiments were used to reveal predator discrimination by four tit species wintering in the Czech Republic. The reactions of the tits to a more dangerous predator (sparrowhawk) and a less dangerous (kestrel) one were compared. The number of visits to a feeder with a predator present expressed the perceived dangerousness of the predator. The tits' behaviour towards the feeders was in agreement with predictions, according to dynamic risk assessment theory. The presence of any predator at the feeder lowered the number of visits to the feeder. Similarly, the tits were judged to have evaluated the sparrowhawk as being more dangerous than the kestrel, as its presence lowered the number of arrivals more than did the kestrel. The duration of stay and number of pecks of individual birds were also used as measures of predator dangerousness. The results not only confirm that tits behave according to dynamic risk assessment theory, but also show the exceptional suitability of preference experiments for the research of predator differentiation and evaluation.

Keywords Common kestrel · Eurasian sparrowhawk · Feeders · Pair-wise experiments · Predator discrimination · Preference experiments · Paridae

Communicated by I. Hartley

K. Tvardíková (✉) · R. Fuchs
Department of Zoology, Faculty of Biological Science,
University of South Bohemia,
Branišovská 31,
370 05 České Budějovice, Czech Republic
e-mail: katerinatvardikova@seznam.cz

Introduction

In animals, food intake is generally connected with the risk of predation. A repeated daily trade-off is made between the need to search for food and that to avoid predators; this takes place throughout an animal's entire life (Devereux et al. 2006). The animals chose to use the risky feeding site only if the potential additional energy gains outweighed the fitness costs of the additional predation risk; otherwise, it would be better off using a safer feeding site (Abrahams and Dill 1989). Therefore, each animal has to continuously make decisions as to which behaviour has the better net ‘pay-off’.

The trade-off between the risk of predation and the energetic gain leads to habitat choices. Each habitat has an associated rate of gain, as well as danger of predation (Houston et al. 1993). However, the choice of habitat could be based not on those qualities alone, but also on the actual state of the animal (Houston et al. 1993) and the time of day, or even time of year (MacLeod et al. 2005). Often, the intake rate that a forager achieves in a habitat also depends on the number of conspecifics also feeding in that habitat. Where there are many competitors, intake rates may decrease, either from interference or exploitation competition (Moody et al. 1996). In such a situation, an animal may do better by moving to a feeding site where there are fewer competitors, even if the overall food quality is lower. This issue has been extensively investigated in what is known as ideal free distribution (Fretwell and Lucas 1970; see Milinski and Parker 1991 for a review). Conversely, a higher number of conspecifics may result in lower levels of vigilance of individuals and, thus, increase the rate of energetic gain for each of them (Houston et al. 1993). Moreover, higher numbers of conspecifics can also decrease the risk of predation through the effects of dilution and confusion (Quinn and Cresswell 2005 and references therein). The assumption of dynamic risk assessment is that individuals that continuously assess these trade-offs and dynamically modify their behaviour accordingly will have a fitness advantage (Kleindorfer et al. 2005).

The proximity of a predator does not determine the rate of predation risk in itself. This is principally because of the different feeding specialisations and hunting techniques of individual predator species (Curio et al. 1983). In birds, the ability to discriminate between differentially dangerous predator species has primarily been studied with nest defences within the breeding season (e.g. Patterson et al. 1980; Buitron 1983; Kleindorfer et al. 2005). Until now, predator discrimination in birds has not been studied with respect to the trade-offs between potential food gain and the risks of predation.

The trade-offs between the risk of predation and energetic gain can be studied in preferential experiments where feeding sites which are associated with different danger levels are offered. Abrahams and Dill (1989) measured the influence of the predation risk on patch choice by guppies (*Poecilia reticulata*) using combinations of three risk levels and three diet levels. Similar winter field experiments on a feeder should also perform well with birds. Feeder experiments have been used to assess the willingness of birds to cross an exposed space (Hinsley et al. 1995; Desrochers et al. 2002; Turcotte and Desrochers 2003), or how the birds manipulate their body masses (MacLeod et al. 2005), both under an experimentally manipulated predation risk. More recently, a similar experiment (Jones et al. 2009) was used to assess this trade-off, with regards to the different danger levels of the birds' predators.

We tested the following predictions: (1) The birds will behave according to risk assessment theory and, when confronted with simultaneous risks (differentially dangerous predator species), they will choose the least dangerous. (2) The food intake rate will decrease in those feeders with higher abundances of birds, and visits to a more risky feeder will be compensated with higher food intake by individual birds.

Methods

Experimental site and species

The experiment was undertaken during the winter of 2006/2007 at the edge of broad-leaved tree growth near the village of Chodská Lhota (49°21′15″, 30°47′25″), West Bohemia, Czech Republic. Even though the site is 640 m above sea level and is located in a relatively cold part of Bohemia, this particular winter (mostly without snow cover) was not harsh. Four species of tits were studied: the great tit (*Parus major*), the blue tit (*Parus caeruleus*), and the “marsh” tit, which predominate at the feeders. The ‘marsh’ tit was represented by both the marsh tit (*Parus palustris*) and willow tit (*Parus montanus*). As these two species are indistinguishable on videotape, they were lumped together as one species.

Experimental design

Two feeders were situated in a field, 7 m from the edge of tree growth. The feeders were 20 m apart and the space between them was free of trees. Shrubs and trees at the edge of tree growth served as an observation place and as a shelter for the birds. The feeders were square boards (45 by 45 cm) lying upon the ground, with raised edges (1.5 cm) to avoid scattering of the food. Between experiments, the feeders were covered with a roof. Sunflower seeds were used as food only for the attraction of the birds. The feeders were filled 4 weeks before the first experimental series. Sunflower seeds were carefully removed and replaced with grated walnuts just before the start of trials. The tits were not able to carry the grated walnuts away, to consume them under cover, as they had with the sun-flower seeds. Therefore, they had to remain at the feeder for a longer period of time if they wanted to achieve sufficient food intake. Food gain is thus the direct proportion of undergone risk.

Stuffed sparrowhawk and kestrel dummies were used as the test predators. They were placed on a 75-cm-high stake at the outer (from edge of forest) right corner of the feeder, and always faced into the centre of the feeder. Individual trials lasted 30 min.

The following experimental treatments (combinations of dummies) were tested: kestrel vs sparrowhawk, kestrel vs feeder without predator, kestrel vs kestrel, sparrowhawk vs feeder without predator and sparrowhawk vs sparrowhawk. Two feeders without predator served as the control (reference) treatment. This amounted to six different treatments in one series. The sequence of treatments within each series was arranged randomly. The placing of the dummy (on the left or the right feeder) for each treatment was randomly arranged, as well.

Each series was carried out in a single day. Usually, there was a 5- or 6-day break between each series. Each experimental series started 0.5–1 h after daybreak. Feeders were continuously taped during the duration of the experiments. Cameras were set up in a fixed position 8 m away facing the feeders. The snow cover and temperature were noted for each experimental day. Ten series were conducted and amounted to 60 half-hour trials.

As part of this study, birds were trapped using mist-nets to reveal the rate of pseudo replications. Mist-nets were used the day before each experimental series, and the trapping efforts were constant during the study (about 30 birds were ringed per day). Under licence (Czech Bird Ring Association, 1062), each trapped bird was fitted with both a standard metal leg-ring with a unique number plus a unique combination of colour rings. Each bird was thus uniquely identifiable on the videotape.

Altogether, 265 birds were ringed during the winter. It was found that 54.53±4.95% of ringed birds stayed on to be in the next series (approximately 1 week after ringing), and 40.39±1.49% stayed until the third series (approximately 14 days later). Less than 1.95±2.7% of ringed birds dwelled in the locality longer than 1 month. Individual birds usually visited the feeder in 1.46±0.6 trials (at most in four trials) during one series. Once having appeared during the trial, a bird arrived at the feeder an average of 3.23± 0.97 times.

Statistical analysis

Firstly, the number of visits of individual tit species during the trials was analysed. Before the main analysis, the numbers of visits to the left and right feeders within the control (reference) trial were compared and found to be non-significant (Mann–Whitney *U* test: $U=47$, $N1=N2=10$, $P=0.819$), and thus, the arithmetic means were counted for each series. The numbers of arrivals to the experimental feeders (to the left, as well as to the right) in each experimental trial (with a dummy on at least one feeder) were divided by the number of visits during the reference trial, and all the created ratios (relative change of the number of visits) were included in the analysis as a dependent variable.

The following experimental variables were used: the dummy at an experimental feeder (from which the number of arrivals were included in the analysis), the situation at the alternative feeder (dummy or feeder without predator), the sequence number of the series during the winter (1–10), tit species (interaction of dummy vs species), temperature (°C) and snow cover (cm). The temperature was measured at the beginning and at the end of experiment, and the average was rounded off. Snow cover was measured next to the feeder on a pole planted in the ground. We acknowledged the problem of statistical independence, as the left and right feeders were simultaneously in any one trial. Therefore, in order to examine which of the experimental variables had an effect on the relative change of the number of visits to each experimental feeder, generalised linear mixed models (GLMM, function aov in library lme4) in R 2.9.0.(R DEVELOPMENT CORE TEAM 2008) were modelled, and the random effect was set up for both feeders within one trial. GLMM was modelled for data with a Poisson distribution, using the link function identity. The results mentioned in the text are the results of step-wise selection. All interactions were also included in the model. Only meaningful interactions, i.e. interaction between experimental dummy and situation at alternative feeder (the only significant one), and interaction between tit species and experimental dummy (insignificant, but important for interpretation of results), were mentioned in the results. The Tukey post hoc test (function glht in library multcomp, R 2.9.0.) was done to reveal the differences between combinations of dummy and alternative dummy.

To determine the possibility of habitualisation to motionless predators, the number of visits was analysed in 5-min-long intervals (within a half-hour trial). The number of visits during the experimental trials did not significantly change (repeated measures ANOVA, dummy: section: $F=0.414$, $P=0.938$).

Another GLM (function glm in basic library, Poisson distribution, R 2.9.0.) model was constructed for the number of pecks, and for the duration of stay of individual birds visiting the feeder during the different experimental situations: (1) feeder with a predator; (2) feeder without predator, when a predator is present at the alternate feeder and (3) feeder without a predator, while the alternate feeder is also without a predator. Results from all feeders with the sparrowhawk or kestrel were clumped together as a feeder with a predator because only a few birds visited the feeders during their presence. The three above mentioned situations at the feeders were used as the explanatory variables together with the sequence of series during the winter, tit species, temperature and snow cover. The Tukey post hoc test (glht function in library multcomp, R 2.9.0.) was performed in order to reveal the differences between the individual situations at the feeders.

Finally, we compared (ANOVA, Statistica 8) whether the number of pecks of individual birds differed in those situations where a bird was at a feeder alone, as opposed to the situation where at least one other bird is present.

Results

Over the winter, 5,292 individual visits were recorded at the feeders. The dummy at an experimental feeder, the situation at the alternative feeder (dummy or feeder without predator) and the temperature were predictors of relative changes in the number of visits. The interaction between the experimental dummy and the situation at the alternative feeder was also significant. The snow layer, the series sequence and the interaction between the dummy and the tit species had no significant effect (Table 1). Low temperatures lessened the decrease in the number of visits to the feeder with a predator (Fig. 1).

Table 1 The effects of the predictors on the relative change of the number arrivals to the feeder (step-wise selection, GLMM, only particular interactions mentioned—see “Methods” section)

Effect	Df	*F*	*P*
Dummy	2	414.056	<0.001
Situation on alternative feeder	1	17.865	<0.001
Temperature	1	9.360	0.020
Snow	1	0.830	0.365
Species	2	0.316	0.598
Series	1	0.210	0.648
Dummy: species	10	0.561	0.543
Dummy: Altern. feeder	4	10.016	<0.001

Table 2 Differences between the relative changes of the number arrivals to kestrel and to sparrowhawk in trials with different treatment on the alternative feeder (noted in parentheses)

		Sparrowhawk		
		(sp)	(0)	(ke)
Kestrel	(0)	0.989	0.987	0.978
		0.952	*0.001*	*0.001*
	(sp)	<0.001	<0.001	<0.001
		−7.439	*−7.267*	*−7.267*
	(ke)	<0.001	<0.001	<0.001
		−7.384	*−6.981*	*−6.981*

The Tukey post hoc test results show *P* (above) and *t* (below, italic) values

ke kestrel, *sp* sparrowhawk, 0 empty feeder

The kestrel dummies decreased the relative number of visits less than the sparrowhawk dummies did; however, this was only in those treatments in which a kestrel was combined with a sparrowhawk or kestrel on the alternative feeder. The decrease in the number of visits did not differ between the kestrel and sparrowhawk in those treatments in which a predator was combined with the alternative feeder without a predator (Table 2, Fig. 2).

A kestrel decreased the number of visits less if it was combined with a predator than if it was combined with an alternative feeder without a predator. The relative change in the number of visits did not differ in any treatment with a sparrowhawk (Table 3, Fig. 2).

The duration of stay of individual birds at the feeders was only influenced by snow cover and temperature (Table 4). The duration of stay did not differ under any of the experimental situations: (1) feeder with a predator; (2) feeder without a predator, while a predator was present at the alternate feeder and (3) feeder without predator, while the alternative feeder is also without a predator. On the other hand, the birds pecked much less in the presence of a predator (N=1460, 3.36±7.868), when compared to its absence (N=3832, 7.56±11.75, Table 4). A Tukey post hoc test revealed that the number of pecks at a feeder with a predator significantly differed from the other experimental situations (a feeder with a predator vs a feeder without a predator, while the alternative feeder is also without a predator: St.Er.=0.38, Z=−5.251, P<0.001; feeder with a predator vs feeder without a predator, while a predator is present at the alternate feeder: St.Er.=0.37, Z=−5.418, P<0.001). The differences between the two experimental situations without a predator were not significant (St.Er.= 0.06, Z=0.882, P=0.624). Of the climatic variables, only snow influenced the number of pecks (Table 4).

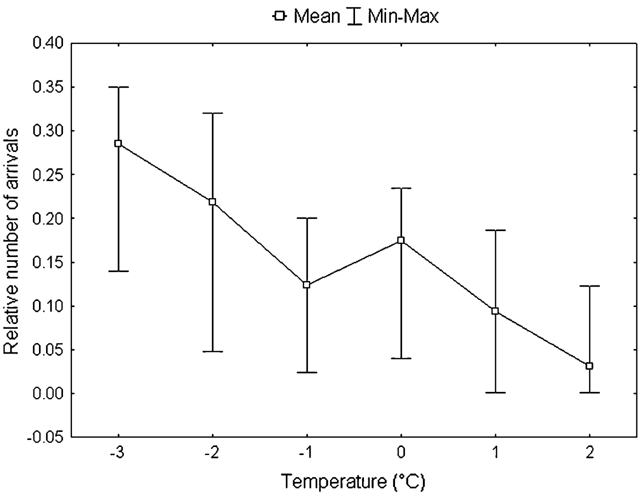


Fig. 1 Effect temperature on the number of arrivals to the feeder—for experimental trials with predator

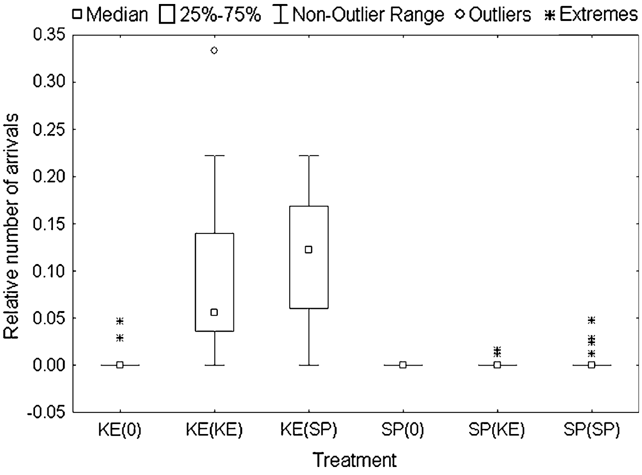


Fig. 2 Relative changes on the number of arrivals (the number of arrivals to feeder with dummy/the number of arrivals to feeder during the reference control) to kestrel and sparrowhawk in trials with different treatment on alternative feeder (noted in parenthesis). Treatments on both feeders: *ke* kestrel, *sp* sparrowhawk, *0* empty feeder

Table 3 The differences between the relative changes of the number of arrivals to kestrels, or to sparrowhawks, in trials with different treatment on alternative feeder (noted in parentheses)

Compared trials	*t*	*P*
ke(sp) × ke(0)	7.267	<0.001
ke(sp) × ke(ke)	1.141	0.888
ke(ke) × ke(0)	6.981	<0.001
sp(sp) × sp(0)	0.952	0.989
sp(sp) × sp(ke)	0.952	0.989
sp(ke) × sp(0)	<−0.001	0.987

Tukey post hoc test results show *P* and *t* values

ke kestrel, *sp* sparrowhawk, *0* empty feeder

At a feeder with a predator present, birds always pecked much more (Chi^2=683.17, $P<0.001$) in the presence of at least one other bird (Mean ± St.Er., 5.7±11.77) than when they were alone (1.9±3.3). Although less significant (Chi^2=56.3, $P=0.046$), the same difference was found at a feeder without a predator (alone: 4.3±11.12, accompanied: 6.22±13.826).

Discussion

The behaviours of tits at the feeders were in agreement with the predictions of dynamic risk assessment theory (Montgomerie and Weatherhead 1988). The presence of any predator at a feeder lowered the number of arrivals to that feeder. Correspondingly, the tits evaluated a sparrowhawk as more dangerous than a kestrel, as the presence of a sparrowhawk lowered the number of arrivals more than did a kestrel. In the presence of a sparrowhawk, the gain from food only sporadically overrides the risk of predation while as many as 30% of the birds (compared with reference trials) decided to visit the feeder with a kestrel present. This difference is in agreement with current knowledge about sparrowhawk and kestrel feeding ecology. Small mammals predominate in the kestrel's diet (Kübler et al. 2005). On the other hand, the sparrowhawk is a specialised predator of small passerines (Rytkönen et al. 1998; Götmark 2002), and thus should represent a bigger threat than the kestrel.

Moreover, the willingness to risk a visit to the feeder with a kestrel was lowered by the possibility of using an alternative safe feeder. When the alternative feeder was without a predator, tits kept completely away from the kestrel, much like they did in the presence of the sparrowhawk. When there was a predator (no matter of which species) on the alternative feeder, some tits fed at the feeder with the kestrel, while the number of arrivals to the feeder with a sparrowhawk was still negligible. This result suggests that the tits' decisions (to visit or not to visit a feeder) not only depend on the general dangerousness of the predator present, but also on the available alternative solutions.

Our results not only confirm that tits behave according to dynamic risk assessment theory; it also demonstrates the exceptional suitability of field preferential experiments on feeders for research of predator recognition and evaluation. The preference experiment allowed us to distinguish whether the higher willingness to risk visits to the feeder with a kestrel was caused by its "non-recognition" as a predator or by its evaluation as being less dangerous than a sparrowhawk. If the first situation was true, the number of arrivals during treatments in which the alternative feeder was without a predator would not have differed from treatments in which the kestrel was present there.

The ability of birds to differentiate between various dangerous raptors has only been discussed in a limited number of studies. Experiments have mostly been conducted during the breeding season on birds defending their nests. Rytkönen and Soppela (1995) found that responses towards the pygmy owl (*Glaucidium passerinum*) were generally more intense than those towards the sparrowhawk. Similarly, Curio et al. (1983) revealed that the great tit not only differentiated between different orders of raptors (bird of prey, owl), but also among different genera of owls.

Table 4 The effects of the predictors on the duration of stay at feeder and number of pecks (step-wise selection, GLMM, quasi-Poisson distribution, only particular interaction mentioned—see "Methods" section)

Effect	Duration of stay				Number of pecks		
	Df	Dev	Res. Dev	*P*	Dev	Res. Dev	*P*
Situation on feeder	2	135	34,064	0.065	102	28,245	<0.001
Temperature	1	181	33,884	0.007	1	28,163	0.400
Snow	1	411	33,473	0.001	131	28,350	<0.001
Species	2	27	30,205	0.869	2	28,150	0.501
Series	1	45	32,016	0.127	46	28,112	0.432
Species: situation at feeder	4	35	31,439	0.789	54	28,011	0.061

They found that the pygmy owl (*G. passerinum*, specialised on birds) was responded to more than the tawny owl (S*trix aluco*, a predator of rodents). In Buitron's (1983) study, the black-billed magpie (*Pica pica*) reacted more strongly to the falcon (*Falco mexicanus* and *Falco columbarius*, predators of birds) than to the hawk (*Buteo jamaicensis*, *Circus cyaneus* and *Accipiter cooperi*, predators of small rodents). The decision (if any, and how intensively) to defend the nest is influenced by the dangerousness of the predator for adults and offspring (this can differ tremendously), past investment in nesting and the chance of renesting in the current breeding season (for review, see Caro 2005). Therefore, our feeder experiments represent unambiguous evidence that birds categorise predators according to the perceived danger to themselves. This evidence corresponds with the findings of Templeton et al. (2005), who showed that intensity of mobbing calls is related to the size and threat of a potential predator.

In the situation with many conspecifics, an animal may do better by moving to a patch where there are fewer competitors, even if the overall risk of this patch is higher, but might be compensated with a higher food intake for any individual bird (Moody et al. 1996). We were not able to confirm this theory, as our birds did not stay longer in patches with fewer competitors, and even pecked fewer times in the presence of a predator. The lower number of pecks during the same length of stay shows that the birds increased their vigilance. Presumably, this is caused by the lower number of birds at a feeder at that time (the total number of birds visiting a feeder with a predator did not reach over 25% of the birds visiting a feeder during control trials). The decrease in both the collective probability of detecting attack (group size effect) and numerical dilution of risk (dilution effect) with a decreasing group size can cause an increase in the individual levels of vigilance, as well as a decrease in the time devoted to feeding (see McNamara and Houston 1992; Cresswell 1994; Bednekoff and Lima 1998). This is supported by our findings that all birds pecked more times in the cases when some conspecific was present at the same feeder, even in the situation without a predator at the feeder. This could indicate that a bird felt safer when accompanied by others. Conditions always agreeing with an ideal free distribution at our feeder would be the simplest explanation of the unchanged duration of stay for birds at the feeder. However, the decreased interference competition being compensated by a decreased dilution effect cannot be ruled out.

We cannot confirm the differences in the behaviour of individual bird species. The significance of explanatory variable “species” indicates that different numbers of individual species visited the feeder. Only the interaction between species and an explanatory variable (e.g. dummy) would indicate that a bird species behaved differently from another. This was not true in any of our analyses. Individual tit species have different abilities in their competition for food (Dhondt and Eyckerman 1980). The Blue Tit is limited by the Great Tit but the smallest and least forcefulness is the Marsh Tit. The tits with lower competitive abilities should be more willing to visit feeders with a predator present. Our failure to support this hypothesis could again be caused by the ideal free distribution of birds at our feeder, without regard to the experimental situation.

Maintenance of a constant high body temperature becomes increasingly difficult in colder conditions, especially for small birds (e.g. Caraco et al. 1990). Thus, many birds should be expected to exploit less profitable (including more dangerous) sources of food. We demonstrated that lower temperatures did cause a much higher number of arrivals (greater willingness to risk) at the feeder. A decrease of the temperature from 2 to −3°C increased the mean proportion of birds visiting the feeder with a predator from 5 to nearly 30% (in comparison with the control trial). This result is in concordance with the findings of previous studies (Walther and Gosler 2001; Carrascal and Alonso 2006; Desrochers et al. 2002).

Acknowledgement The study was supported by grants of the Academy of Sciences of the Czech Republic (IAA601410803), and the Ministry of Education, Youth, and Sports (MSM6007665801).

References

Abrahams MV, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. Ecology 4(70):999–1007

Bednekoff PA, Lima SL (1998) Re-examining in numbers: interaction between risk dilution and collective detection depend upon predator targeting behaviour. Proc Roy Soc Lon B 265:2021–2026

Buitron D (1983) Variability in the responses of Black-billed Magpies to natural predators. Behaviour 87(3–4):209–235. doi:10.1163/156853983X00435 (27)

Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GM, Zwicker SM (1990) Risk-sensitivity: ambient temperature affects foraging choice. Anim Behav 39(2):338–345

Caro TM (2005) Antipredator defenses in birds and mammals. The University of Chicago Press, London, 591 p

Carrascal LM, Alonso CL (2006) Habitat use under latent predation risk. A case study with wintering forest birds. Oikos 112:51–62

Cresswell W (1994) Flocking is an effective anti-predation strategy in Redshanks, *Tringa totanus*. Anim Behav 47:433–442

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it turned to predator risk? Oecologia 60:83–88

Desrochers A, Belisle M, Bourque J (2002) Do mobbing calls affect the perception of predation risk by forest birds? Anim Behav 64:709–714. doi:10.1006/anbe.2002.4013

Devereux CL, Whittingham MJ, Fernández-Juricic E, Vickery JA, Krebs JR (2006) Predator detection and avoidance by starlings under differing scenarios of predation risk. Behav Ecol 17 (2):303–309. doi:10.1093/beheco/arj032

Dhondt AA, Eyckerman R (1980) Competition between Great Tit and the Blue Tit outside the breeding season in field experiments. Ecology 61:1291–1296

Fretwell SD, Lucas HL (1970) On territorial behaviours and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36

Götmark F (2002) Predation by sparrowhawks favours early breeding and small broods in great tits. Oecologia 130(1):25–32. doi:10.1007/s004420100769

Hinsley SA, Bellamy PE, Moss D (1995) Sparrowhawk Accipiter nisus predation and feeding site selection by tits. Ibis 137 (3):418–420

Houston AI, McNamara JM, Hutchinson JMC (1993) General results concerning the trade-off between gaining energy and avoid predation. Phil Trans R Soc Lon B 341(1298):375–397

Jones KA, Krebs JR, Whittingham MJ (2009) Heavier birds react faster to predators: individual differences in the detection of stalking and ambush predators. Behav Ecol Sociobiol 63 (9):1319–1329. doi:10.1007/s00265-009-0778-6

Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. Anim Behav 69:307–313. doi:10.1016/j.anbehav.2004.06

Kübler S, Kupko S, Zeller U (2005) The kestrel (*Falco tinnunculus* L.) in Berlin: investigation of breeding biology and feeding ecology. J Ornithol 146(3):271–278. doi:10.1007/s10336-005-0089-2

MacLeod R, Gosler AG, Cresswell W (2005) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. J Anim Ecol 74(5):956–964. doi:10.1111/j.1365-2656.2005.00993.x

McNamara JM, Houston AI (1992) Risk-sensitive foraging-a review of the theory. Bull Math Biol 54:355–378

Milinski M, Parker GA (1991) Competition for resources. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell Scientific Publications, Oxford, pp 137–168

Montgomerie RD, Weatherhead PJ (1988) Risk and rewards of nest defense by parent birds. Q Rev Biol 63(2):167–187

Moody AL, Houston AI, McNamara JM (1996) Ideal free distributions under predation risk. Behav Ecol Sociobiol 38 (2):131–143

Patterson TL, Petrinovich L, James DK (1980) Reproductive value and appropriateness of response to predators by white-crowned sparrows. Behav Ecol Sociobiol 7(3):227–231

Quinn JL, Cresswell W (2005) Escape response delays in wintering redshrank, Tringa totanus, flocks: perceptual limits and economic decisions. Anim Behav 69:1285–1292

R DEVELOPMENT CORE TEAM (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Templeton CS, Greene E, Davis K (2005) Allometry of alarm calls: Black-Capped Chickadees encode information about predator size. Science 308(5730):1934–1937. doi:10.1126/science.308.5730.1853a

Turcotte Y, Desrochers A (2003) Landscape-dependent response to predation risk by forest birds. Oikos 100:614–618. doi:10.1034/j.1600-0706.2003.12234.x

Rytkönen S, Soppela M (1995) Vicinity of sparrowhawk nest affects willow tit nest defense. Condor 97:1074–1078

Rytkönen S, Kuokkanen P, Hukkanen M et al (1998) Prey selection by Sparrowhawks Accipiter nisus and characteristics of vulnerable prey. Ornis Fen 75(2):77–87

Walther BA, Gosler AB (2001) The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: Parus). Oecologia 129(2):312–320

Článek VI.

Beránková J., Veselý P., Sýkorová J., Fuchs R. (2014): The role of key features in predator recognition by untrained birds. Animal Cognition 17:963-971.

Anim Cogn
DOI 10.1007/s10071-014-0728-1

ORIGINAL PAPER

The role of key features in predator recognition by untrained birds

Jana Beránková · Petr Veselý · Jana Sýkorová · Roman Fuchs

Received: 23 September 2013 / Revised: 13 January 2014 / Accepted: 14 January 2014

Abstract The most important role in the recognition and categorization of predators (as well as other animals) is usually attributed to so-called key features. Under laboratory conditions, we tested the role of yellow eyes (specific for the genus *Accipiter* in European raptors) and hooked beak (common for all European birds of prey) in the recognition of the sparrowhawk (*Accipiter nisus*) by untrained great tits (*Parus major*) caught in the wild. Using wooden dummies, we interchanged either one of these potential key features or the body of the sparrowhawk (predator) and domestic pigeon (harmless bird). The tested tits showed three types of behaviour in the presence of the dummies: fear, interest without fear, and lack of interest. Eye interchange lowered fear of the sparrowhawk, but did not cause fear of the pigeon. Beak interchange did not lower fear of the sparrowhawk. Eye interchange caused increased interest in both species. Thus, a specific sparrowhawk feature is necessary for correct sparrowhawk dummy recognition but a general raptor feature is not. On the other hand, a specific sparrowhawk feature on a pigeon dummy is not enough to prompt sparrowhawk recognition. Thus, key features play an important, but not exclusive, role in predator recognition. An increased interest in some of the modified dummies implies that the tits have a general concept of a sparrowhawk. The individual variability in behaviour of tits is discussed.

Keywords Key features · Recognition · Categorization · Concept · Untrained birds

---

J. Beránková (✉) · P. Veselý · J. Sýkorová · R. Fuchs
Faculty of Science, University of South Bohemia,
Branišovská 31a, 37005 Ceske Budejovice, Czech Republic
e-mail: jaja.berankova@gmail.com

Introduction

Almost any aspect of animal decision-making (from foraging behaviour to mate choice) can be influenced by the risk of predation (Lima and Dill 1990). Only fast and accurate predator recognition gives prey a chance to choose the right anti-predator behaviour and escape tactic (Curio 1976).

If all types of predator pose the same threat and require the same response, then there is no need to distinguish among them (Kullberg and Lind 2002). For example, the mouth size and distance between eyes are sufficient for predator recognition in piscivorous fish, and no further cues are needed (Karplus and Algom 1981; Karplus et al. 1982). However, when different types of predator represent different levels or kinds of threat, then selection of the appropriate response requires their more specific recognition and categorization (McLean and Rhodes 1991). It is obvious that birds are able to distinguish between predators of different taxa (Curio et al. 1983; Suzuki 2012; Strnad et al. 2012) or size (Klump and Curio 1983; Palleroni et al. 2005), but the mechanisms that facilitate recognition are poorly understood.

The most important role in the recognition and categorization of predators (as well as other animals) is usually attributed to so-called key features. The origin of this idea dates to 1935 when Konrad Lorenz defined the term "releaser" (Auslöser) as an acoustic or visual stimulus causing a specific reaction (Lorenz 1937). Later on, different terms, such as "sign stimuli", were used (Tinbergen 1948), but the central idea remained the same. The term "key feature" comes from feature theory (Bruner et al. 1956; Marr and Nishihara 1978; Smith and Medin 1981). According to this theory, objects are assigned to categories on the basis of the features of which they are composed (Pearce 2008).

The role of key features in predator recognition has been only rarely tested. The first studies focused on the "short neck" in the silhouettes of birds of prey. It was found that even a cardboard dummy that has a short neck prompts an escape response independently of the colour or shape of the wings and tail (Krätzig 1940; Lorenz 1940; Tinbergen 1948). The first more complex study was carried out by Curio (1975) who tested the reaction of the pied flycatcher (*Ficedula hypoleuca*) to the modified dummies of two similar-sized predators, the pygmy owl (*Glaucidium passerinum*), and the male red-backed shrike (*Lanius collurio*). Several further studies aimed at the 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), or sexual partners (Burley and Coopersmith 1987; Pincemy et al. 2009) followed. They confirmed the importance of eyes (Scaife 1976; Watve et al. 2002; Trnka et al. 2012), beak (Burley and Coopersmith 1987; Gill et al. 1997), and coloration patterns (Davies and Welbergen 2008; Pincemy et al. 2009; Welbergen and Davies 2011) for recognition of tested stimuli.

Key feature theory (Marr and Nishihara 1978) has also been repeatedly tested under laboratory condition by training birds (most often the domestic pigeon) to respond to drawings or photographs with key features present/absent (Kirkpatrick-Steger et al. 1998; Huber 2001; Matsukawa et al. 2004) or to objects composed of several previously learnt stimuli (Cerella 1980; Aust and Huber 2001; Werner et al. 2004). The results imply that pigeons are able to use local features for categorization, but their importance depends largely on the stimuli used. Moreover, most of the tested stimuli were unrelated to the real life of birds. Animal reactions to relevant and irrelevant stimuli may be different, and therefore, the categorization mechanism may also be different (Pashler 2002).

The reactions of untrained birds to natural stimuli have only occasionally been tested under laboratory conditions. Patton et al. (2010) examined the reaction of male pigeons to an altered picture of a female using their tendency to perform courtship behaviour in the presence of a relevant sexual partner. He proved that the beak and eyes are important features for mate recognition because pigeons showed no reaction to a pigeon head without these features.

In birds in general, some of the potential key features are species specific, while others characterize whole taxonomical and/or ecological groups of species. One example is the yellow eyes and hooked beak in birds of prey in Central Europe. Conspicuous yellow eyes are specific for the genus *Accipiter*, while a hooked beak characterizes all members of Falconiformes (and Strigiformes as well).

We tested the role of these features in the recognition of the sparrowhawk (*Accipiter nisus*). The replacement of key features on predator dummies applied in all the studies mentioned above tests whether those features are necessary, but not whether they are in themselves sufficient for proper recognition. Therefore, in our study, we interchanged either eye or beak of a sparrowhawk (predator) and a domestic pigeon (harmless bird). However, the sparrowhawk possesses potential key features on the body as well (especially the coloration pattern or claws). Therefore, we interchanged also the whole body of sparrowhawk and pigeon.

The great tit (*Parus major*) was chosen as a model species as we know that tits are able to recognize pigeons and sparrowhawks from our previous field study (Tvardíková and Fuchs 2012). The amount of stress in this experiment was measured by the number of arrivals at the feeder with the presented dummy. Our current experiments were carried out in the laboratory which facilitated more detailed behavioural analysis and discrimination among stress response and other relevant reactions (e.g. stimulus exploration).

We tested five hypotheses: (1) the presence of the sparrowhawk eyes on the sparrowhawk dummy is necessary for the recognition of the dummy as a sparrowhawk (the sparrowhawk dummy without sparrowhawk eyes will be treated as less dangerous than the unmodified sparrowhawk dummy). (2) The presence of the sparrowhawk eyes on the pigeon dummy is sufficient for its recognition as a sparrowhawk (the pigeon dummy with sparrowhawk eyes will not be treated as less dangerous than the unmodified sparrowhawk dummy). (3) The presence of the raptor beak on the sparrowhawk dummy is not necessary for the recognition of the dummy as a sparrowhawk (the sparrowhawk dummy without raptor beak will not be treated as less dangerous than the unmodified sparrowhawk dummy). (4) The presence of the raptor beak on the pigeon dummy is sufficient for its recognition as a raptor (the pigeon dummy with raptor beak will be treated as more dangerous than the unmodified pigeon dummy). (5) Change of the body does not influence the recognition of pigeon and sparrowhawk (the sparrowhawk dummy with pigeon body will not be treated as less dangerous than the unmodified sparrowhawk, and the pigeon dummy with sparrowhawk body will not be treated as more dangerous than the unmodified pigeon).

Materials and methods

Subjects

The great tit (*Parus major*) was chosen as a model species. Great tits are very adaptable to laboratory conditions (e.g. Dingemanse 2002). Moreover, no neophobic reaction that could negatively influence their behaviour in the presence of an unfamiliar stimulus has been confirmed in them (Cole et al. 2011).

Birds were trapped in mist-nets in the suburban areas of České Budějovice (Czech Republic) during the winter seasons of the years 2008–2011. Tits were ringed after capturing to avoid testing individuals repeatedly. After that, the birds were held in cages and provided with water and sunflower seeds ad libitum. Each bird was tested only once. Altogether we used 160 individuals for all the experiments (20 birds to each presented dummy).

Experimental stimuli

A sparrowhawk dummy was used as a predator because it is a specialized predator of small birds in Europe (Zawadzka and Zawadzki 2001; Bujoczek and Ciach 2009; Chamberlain et al. 2009). Wild great tits strictly avoid the sparrowhawk and are able to recognize and distinguish it from other predator species (Tvardíková and Fuchs 2011). The domestic pigeon dummy was used as a harmless species because its size is comparable to the sparrowhawk. Great tits living in suburban areas encounter it commonly, and they do not express any fear in the presence of a pigeon dummy (Tvardíková and Fuchs 2012).

We assumed that if there is no difference in reaction to the chimera (a dummy with changed key feature) and to the unmodified sparrowhawk, the tits recognize the dummy as a sparrowhawk. If they are afraid of the chimera less than the unmodified sparrowhawk, but more than the unmodified pigeon, it may be concluded that they recognize the dummy as a raptor (but not sparrowhawk). If the stress reaction does not differ from the reaction to the unmodified pigeon dummy, it may be concluded that tits do not recognize the dummy as any raptor.

Both dummies consisted of carved wood with detachable and interchangeable parts (beak, eyes, and the whole body including the trunk, folded wings, tail, and legs). In preliminary studies, we found that there is no difference in the reaction to a wooden and a stuffed sparrowhawk dummy (Poláková et al in prep.). In our study, we used 8 types of dummies: unmodified sparrowhawk (HHH), sparrowhawk with pigeon eyes (PHH), sparrowhawk with pigeon beak (HPH), sparrowhawk with pigeon body (HHP), unmodified pigeon (PPP), pigeon with sparrowhawk eyes (HPP), pigeon with sparrowhawk beak (PHP), and pigeon with sparrowhawk body (PPH). For coding explanation, see Table 1.

Table 1 Abbreviations of dummy types

Eye	Beak	Body	Code
Hawk	Hawk	Hawk	HHH
Pigeon	Hawk	Hawk	PHH
Hawk	Pigeon	Hawk	HPH
Hawk	Hawk	Pigeon	HHP
Pigeon	Pigeon	Pigeon	PPP
Hawk	Pigeon	Pigeon	HPP
Pigeon	Hawk	Pigeon	PHP
Pigeon	Pigeon	Hawk	PPH

The eye, beak, and body features are represented by the first, second, and third alphabets

Experimental design

Before the experiment, the birds were deprived of food for 1.5 h. Afterwards they were released into an experimental cage (2 × 1 × 0.5 m). The cage was equipped with corn bedding, perches, a nesting box, and a dish with sunflower seeds in the front part. The dummy was placed in front of the cage above the dish with food. The experiment started after the removal of a wooden barrier between the tested bird and the dummy. The behaviour of the birds during their exposure to the dummies was recorded on video for 10 min.

The video was analysed in Observer XT 6.1 (Noldus Information Technology 1990–2006) by a single observer. The following behaviours were quantified: total occurrence of raising feathers on head (cap), knee bending (knee), warning calls (warn), approach of the dummy to less than 1 m away (approach), movement from one perch to another (move), pecking the equipment in the cage (peck), total duration of scanning the dummy from less than 1 m away (scan), surveying the corn bedding for food (bedding), feeding on the provided sunflower seeds (feeding), sitting still (sit). The inter-rater reliability was estimated by analysing all recorded experiments by another rater. The correlations between the two sets of behavioural measures were calculated using Correlation matrices in STATISTICA 9.1 (StatSoft Inc. 2009). The results show significant correlations ($p < 0.05$) in most of the observed behaviours (warn, $r = 0.99$; knee, $r = 0.61$; cap, $r = 0.51$; move, $r = 0.90$; peck, $r = 0.57$; feeding, $r = 0.93$; bedding, $r = 0.98$; sit, $r = 0.71$).

The behavioural elements mentioned above have been already used in various behavioural studies on birds (e.g. Kullberg and Lind 2002; Stuber and Bartell 2013). Studies on tits' personality established that individual birds are consistent in such behavioural traits as exploratory behaviour, risk taking, fearfulness, and reactivity (see Groothuis and Carere 2005 for review).

Statistical analysis

Tit behaviour (all the activities mentioned above) was analysed using the multivariate technique—the principal component analysis (PCA) in Canoco 4.5 (ter Braak and Šmilauer 1998) to find out whether there was a consistent reaction to the dummies. Thus, the dummies were used as supplementary environmental data in PCA. PCA scores of the first and second axis were used as synthetic dependent variables in ANOVA in STATISTICA 9.1 (StatSoft Inc. 2009) to test the effect of the dummies on the tits' behaviour. Differences among the individual dummies were consequently compared using the Tukey's HSD test. We also used redundancy analysis (RDA) in Canoco 4.5 with the dummies as environmental data to compare behaviour of individual tits toward tested dummies. Data for PCA and RDA analysis were logarithmically adjusted and centred.

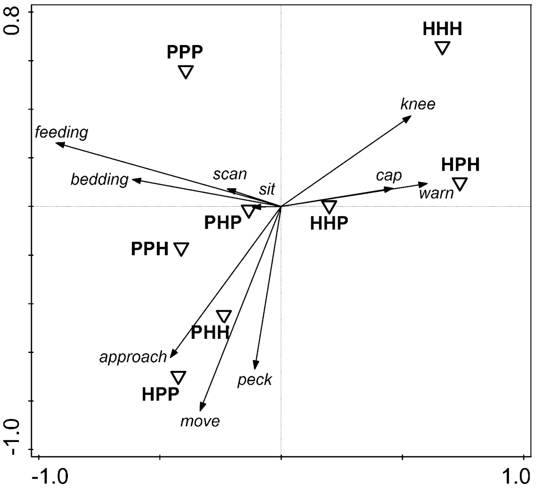


Fig. 1 Behaviour of tested tits in the presence of individual dummies visualized on the first and second axis of PCA. For explanations of behavioural types, see "Materials and methods". For explaining the abbreviations of dummy types, see Table 1

Results

Principal component analysis shows that there are consistent reactions to presented dummies (Fig. 1). The first PCA axis explains 39.4 % of variability and separates stress behaviour (knee bending, warning calls, raised feathers on the head) from other behavioural types (exploration or feeding). The second PCA axis explains 17.7 % of variability and divides exploration of the dummy (approaching and scanning the dummy) or displacement activity (moving and pecking of the cage equipment) from other behaviours (stress or feeding).

The particular dummy presented significantly influences the tested birds' PCA scores on the first axis (ANOVA, $F = 5.430$, $p < 0.001$) and the second axis (ANOVA, $F = 4.901$, $p < 0.001$). The following p values refer to post hoc Tukey's HSD test. The tits showed more stress behaviour (first PCA axis) in the presence of the dummy HHH and HPH than in the presence of PHH ($p = 0.040$, $p = 0.018$) HPP ($p = 0.004$, $p = 0.002$), PPH ($p = 0.005$, 0.002), and PPP ($p = 0.007$, 0.003). The dummies HHP and PHP differ from neither group (Fig. 2). Effects of the key features manipulation are summarized in Table 2.

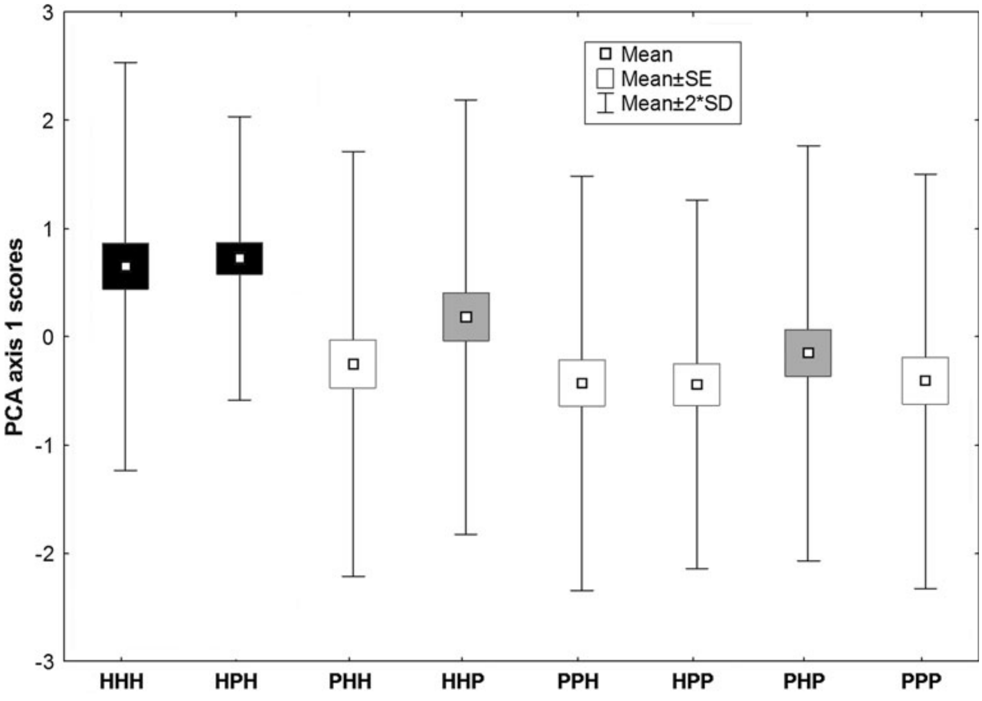


Fig. 2 The effect of the presence of individual dummies on the behaviour of tested tits (first PCA axis scores). *Positive values* indicate the stress behaviour (feather cap, knee bending, and warn calls). For explaining the abbreviations of dummy types, see Table 1. *Black* and *white boxes* differ significantly from each other. *Grey boxes* do not differ from any other

Table 2 Comparison of responses of great tits to various presented dummies on the first PCA axis

Dummies in comparison		Post hoc Tukey's HSD test, *p* value
Effect of the eye		
PHH	HHH	**0.040**
HPP	PPP	1.000
Effect of the beak		
HPH	HHH	1.000
PHP	PPP	0.987
Effect of the body		
HHP	HHH	0.746
PPH	PPP	1.000

Significant differences in bold. For explaining the abbreviations of dummy types, see Table 1

More intense exploration (second PCA axis) was observed in the presence of dummies with interchanged eyes (PHH, HPP) than unmodified dummies HHH ($p = 0.004$, $p < 0.001$) and PPP ($p = 0.014$, $p < 0.001$). Other dummies (PPH, HHP, PHP, and HPH) differ from neither group (Fig. 3).

Redundancy analysis also showed that there are significant differences in the tits' behaviour in the presence of individual dummies (Monte Carlo permutation test, $F = 4.886$, $p = 0.002$). The first RDA axis explains 11.0 %; the second axis explains 3.8 % of variability. The marginal effects of all the dummies besides HHP are significant (Table 3). The size of the effect was the largest for HHH and HPH. However, projection of scores of individual tits on RDA axes (Fig. 4) shows that there is great inter-individual variability in behaviour toward most of the dummies. The behaviour of the individual birds was rather consistent during the experiment. The most of the birds are located further from the intersection of the RDA axes (in the positive as well as negative values). It means that behavioural elements correlated with either the first or the second axis prevailed in their behaviour. There was only a minority of the birds with balanced representation of antagonistic types of behaviour during the experiment. These birds are located near the intersection of the RDA axes.

Discussion

The hypotheses that the presence of the sparrowhawk eyes is necessary and also sufficient for the recognition the dummy as a sparrowhawk were confirmed only partially. Pigeon eyes on the sparrowhawk dummy (PHH) make the dummy less dangerous than the unmodified sparrowhawk dummy (HHH). However, the sparrowhawk eyes on the pigeon dummy (HPP) do not make the dummy as dangerous as the HHH. It means that the mere yellow eyes are necessary but not sufficient for sparrowhawk recognition and another cue is therefore needed for the correct recognition. This is not surprising because yellow eyes are a unique for the genus *Accipiter* within the birds of prey in Central Europe but they occur also in other harmless bird

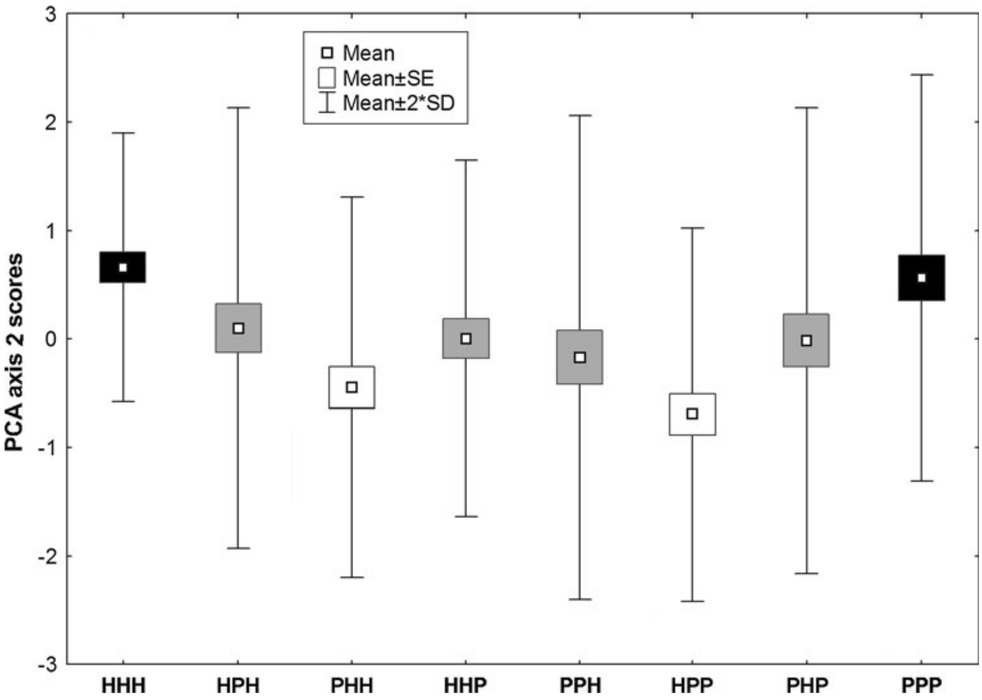


Fig. 3 The effect of the presence of individual dummies on the behaviour of tested tits (second PCA axis scores). *Negative values* indicate interest in the dummy (scanning and approaching it). For explaining the abbreviations of dummy types, see Table 1. *Black* and *white boxes* differ significantly from each other. *Grey boxes* do not differ from any other

Table 3 Marginal effects of presence of individual dummies on tested tits behaviour (RDA)

Dummy type	Explained variability (%)	Pseudo-*F*	*p* value
HPH	4.4	7.2	0.002
HHH	4.3	7.1	0.002
PPP	2.9	4.8	0.002
HPP	2.8	4.5	0.006
PHH	2.2	3.5	0.006
PPH	1.9	3.1	0.028
PHP	1.6	2.6	0.022
HHP	0.9	1.5	0.202

For explaining the abbreviations of dummy types, see Table 1

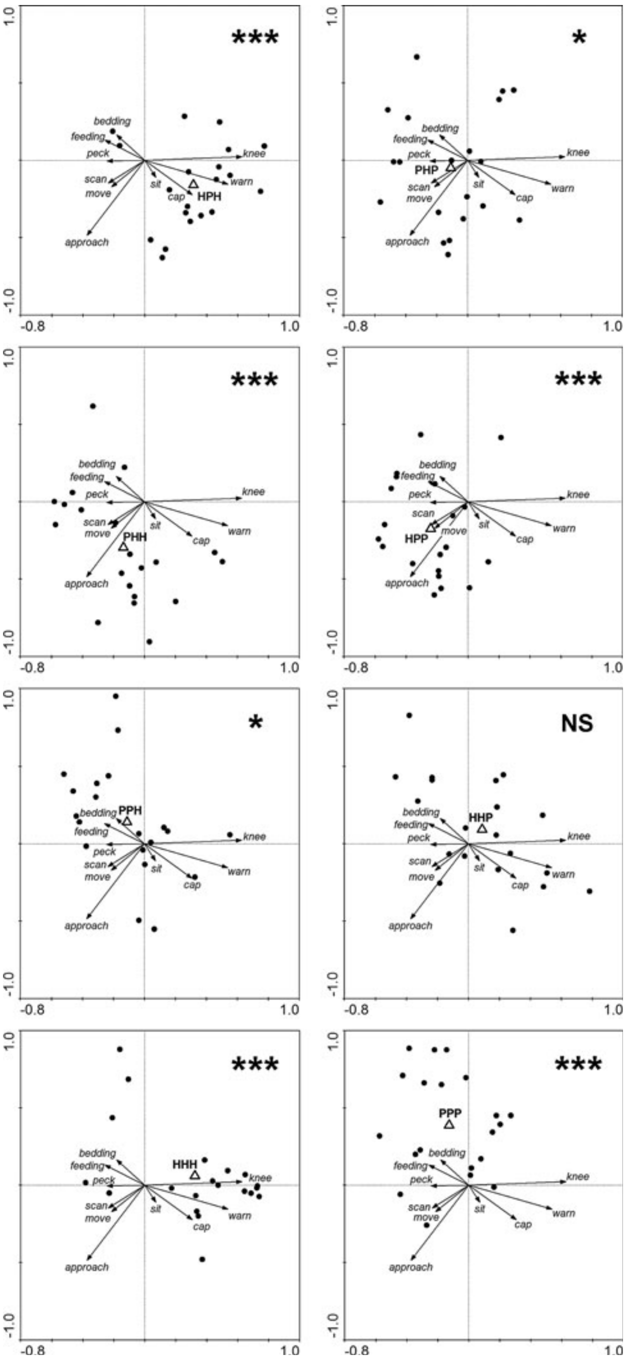


Fig. 4 Scores of individual tits on the first and second RDA axis in the presence of individual dummies. For explanations of behavioural types, see "Materials and methods". For explaining the abbreviations of dummy types, see Table 1. *Triple asterisk* indicates the dummies with very significant effect on behaviour of tits ($p < 0.01$). *Asterisk* indicates the dummies with significant effect on behaviour of tits ($p < 0.05$). *NS* indicates the dummy with no significant effect on the behaviour of tits ($p > 0.05$)

species (e.g. tufted duck *Aythya fuligula*, common cuckoo *Cuculus canorus,* or barred warbler *Sylvia nisoria*).

The hypotheses that the presence of the raptor beak is not necessary for the dummy recognition as a sparrowhawk but sufficient for recognition as a raptor in general were confirmed in part. The pigeon beak on sparrowhawk dummy (HPH) does not lower the fear of the dummy significantly as compared to the HHH. It means that the wrong beak does not influence the recognition when the appropriate sparrowhawk eye and body are present. The pigeon dummy with raptor beak (PHP) is not treated as more dangerous than the unmodified pigeon dummy (PPP) but also not less dangerous than HHH. It means that PHP is not conclusively treated as harmless or as dangerous. It seems that individual birds are not uniform in the reaction to it but at least a portion of the tits recognized the dummy as a raptor due to the hooked beak although the other features belonged to the pigeon (see below). Raptor recognition based on a single feature would be useful in the categorization of unfamiliar bird species, and a hooked beak is appropriate for this purpose because this feature is unique for birds of prey in Central Europe, where parrots do not occur.

In accordance with the hypothesis that change of the body does not influence the recognition, the sparrowhawk with pigeon body (HHP) is not treated as less dangerous than HHH, and the pigeon with sparrowhawk body (PPH) is not more dangerous than the PPP. However, the HHP is also not treated as more dangerous than PPP. It implies that some of the cues usable for recognition of sparrowhawk are present on its body.

Based on these results, we may rule out the theory that any of the typical predator features (general—hooked beak, or species specific—yellow eye) acts as a universal key feature for predator recognition in untrained birds as proposed by the classical ethological school (Tinbergen 1948). Moreover, the behaviour reflected by the second PCA axis implies that tits have a complex image of how the pigeon and sparrowhawk should appear. Tits showed interest in the modified dummies, and it seems that they are aware of any strangeness in the chimeras. Tits were the most interested in the dummies with interchanged eyes (PHH and

HPP). Thus, it seems that tits use both key features and more complex concepts for predator recognition and categorization. Local key features allow the fast and simple recognition and categorization of familiar species which is necessary for effective anti-predatory behaviour. On the other hand, complex concepts may be used for the discrimination of unfamiliar species that must be further examined.

The importance of local key features for recognition and categorization in untrained birds has been tested rather rarely. Several studies show that the absence or replacement of appropriate eyes (Scaife 1976; Trnka et al. 2012) or beak (Gill et al. 1997; Patton et al. 2010) results in a decrease in the ability to recognize a predator (Scaife 1976), nest parasite (Gill et al. 1997; Trnka et al. 2012), or sexual partner (Patton et al. 2010). Only (Patton et al. 2010) compared the effect of eye and beak removal. In contrast to our results, he found that the beak is more important than the eye for recognition. Male pigeons showed more courtship behaviour to the image of female pigeon without eyes than to the one without a beak. The author hypothesizes that the beak provides useful information about the quality of a sexual partner such as efficacy of feeding and parasite control (Patton et al. 2010). The reason why the eye was a more important feature in our study could be that it allows the recognition of a specific (and extremely dangerous) predator species while the beak allows only the recognition of raptors in general. Therefore, it seems that the importance of key features is context dependent.

Scaife (1976), Davies and Welbergen (2008), and Trnka et al. (2012) compared the effect of the absence of key features on the dummy of a harmful species and their presence on harmless birds. Scaife (1976) found that a European kestrel with covered eyes caused less stress reaction in chickens than a kestrel with conspicuous yellow eyes (inappropriate for European kestrel) visible, whereas the presence of yellow eyes on a harmless kiwi increased the stress reaction significantly. In our study, a similar effect of mere yellow eyes on the pigeon dummy was not significant. The reason could be that Scaife (1976) tested a captive, naïve chicken whose ability to recognize a predator could differ from our experienced wild great tits (Kullberg and Lind 2002, see below). Davies and Welbergen (2008) tested the importance of hawk-like underparts for cuckoo and sparrowhawk recognition. They found that the absence of this coloration pattern in a cuckoo lowers fear of the dummy and the presence of it in a dove increases fear of that dummy in tits on winter feeders. On the other hand, the absence of barring did not lower the ability of the tested tits to recognize the dummy as a sparrowhawk. It seems that the manipulation with underpart barring in this study influenced the dummies' recognition more than the body manipulation in our experiments. The explanation could be in the different experimental design. The tits in the experiment at winter feeder (Davies and Welbergen 2008) observed the presented dummies from a further distance, while in our experiments, they could see them at close range. Extensive and contrast barring should be visible and recognizable from further distance than the detailed features like eyes or beak. Trnka et al. (2012) found that the reaction of great reed warblers was not aggressive to an unmodified dove and to the dove with cuckoo body. Thus, contrary to the experiments of Davies and Welbergen (2008), the mere barred underparts did not cause aversion to the dummy. The reaction to the dummy of the cuckoo with a dove body did not differ from the reaction to the unmodified cuckoo. These results are in better agreement with ours than the results of Davies and Welbergen (2008). The explanation may be that the great reed warblers were physically attacking the dummies and so they could assess all the potential key features from proximity.

Categorization processes have also been intensively studied in pigeons under laboratory condition using operational conditioning. Discrimination between the chimeras of cats and dogs (Ghosh et al. 2004) or mammals and birds (Cook et al. 2013) has been tested. Contrary to our results, the chimeras' discrimination was based rather on the body than on the head. The main difference between their and our experiments is that pigeons were presented two-dimensional images which may not be relevant to them (see Weisman and Spetch 2010 for review). We may hypothesize that our tits were searching for key features on the head part, because they were aware of the stimulus being an animal. Pigeons confronted with non-relevant stimuli search for the features usable for categorization on the greatest part of the stimulus, which is the body.

Our results can be compared with the experiments aimed at human face recognition as well. Matsukawa et al. (2004) examined the effect of deletion of individual elements of line drawings. Deletion of eyes and eyebrows considerably suppressed responding, while the deletion of the other parts (nose and mouth, ears, and head contours) did not. It is in accordance with our results about the importance of the eyes. However, the pigeons' discriminative performance was substantially impaired by fragmentation. It suggests that the pigeons use both global and local features for discrimination. Jitsumori and Yoshihara (1997) trained pigeons to discriminate between happy and angry human faces. The pigeons directed their pecks predominantly to the mouth or eyes, eventually the area between them, which implies that these features were important for face recognition. The pigeons were subsequently tested with stimuli manipulated by substitution or removal of facial features. The importance of particular features differed considerably among the birds but generally, the pigeons did not perform as single-feature detectors because no feature was dominant over the others and discrimination was based on an additive integration of individual features. Both studies imply that the pigeon is able to adjust the discrimination depending on the particular perceptual context and it is possible that untrained tits can also adapt the choice of the cues for recognition to the situation they are just facing.

As previously mentioned, the reaction to the dummies was not unequivocal. There was a fluid gradient of the tits' responses both in stress (first PCA axis) and interest (second PCA axis) to particular tested dummies, more significant in the case of the interest in chimeras. These results may have been caused either by inconsistency in the behaviour of individual tits or by differences in behaviour among the individual tits. The results of RDA with the depicted reactions of individual tits show that their behaviour is rather consistent during the experiment but there is a great variability among individuals. The tits were mostly scared in the presence of the sparrowhawk and mostly calm (feeding) in the presence of the pigeon, while in the presence of some chimeras, a portion of the tits were scared while others were calm (Fig. 4). It seems that individual tits evaluate the cues provided by the chimeras in different ways.

The reason for individual differences in behaviour toward the chimeras may be the different experience or personality of the tested birds. We are not able to gauge these differences because we have no prior knowledge of the experience or personality of the tested tits before they are caught in the wild. Great tits are one of the first birds whose personality has been tested and shown. There are consistent behavioural differences among individual tits, which are usually referred as "fast" or "slow" (e.g. Verbeek et al 1994; Dingemanse 2002). Quinn et al. (2012) tested and showed that personality influences the resolution of trade-off between foraging and anti-predatory behaviour. Slow females and juveniles were less responsive to increasing predation risk than fast females and juveniles. Another possibility could be that the individual birds differ in their cognitive style which could influence their ability or propensity to see the stimuli as not real (Carere and Locurto 2011; Sih and Del Giudice 2012).

The importance of experience in predator recognition has also been tested. A comparison between naïve 30-day-old great tit fledglings and wild-caught 4-month old tits showed that the naïve tits were not able to discriminate the predator from a harmless species but the wild-caught tits were (Kullberg and Lind 2002). Studies with birds from areas without the presence of predator also confirm the importance of experience. Birds from areas without predators are not able to recognize a predator, but one-event learning is enough for proper later recognition (Maloney and McLean 1995; McLean et al. 1999). Our tits come from Central and Eastern Europe (Cepák et al. 2008), and so, all of them have had the opportunity to encounter resident sparrowhawks (Cramp et al. 1994). However, a significant portion of the birds are yearlings (Cepák et al. 2008) in which we can assume lesser experience with predators than in older individuals.

Acknowledgments We thank B. A. Christopher Mark Steer for the language improvement. We thank the Grant agency of the University of South Bohemia (159/2013/P) for financial support.

Ethical standard Experiments carried out in this research comply with the current laws of the Czech Republic. Authors are licensed for catching and ringing birds (Bird Ringing Centre Prague No. 1004 and 1159), for animal experimentation (Czech Animal Welfare Commission No. 489/01) and for conducting laboratory experiments with titmice (Ministry of Education, Youth and Sports, licence no. 8809/2011-30). Faculty of Science of the University of South Bohemia has accredited breeding of titmice (Ministry of Agriculture, Licence No. 9103/2009-17210).

Conflict of interest The authors declare that they have no conflict of interest.

References

Aust U, Huber L (2009) Representational insight in pigeons: comparing subjects with and without real-life experience. Anim Cogn 13:207–218

Bruner JS, Goodnow JJ, Austin GA (1956) A study of thinking. Wiley, New York

Bujoczek M, Ciach M (2009) Seasonal changes in the avian diet of breeding sparrow hawks *Accipiter nisus*: how to fulfil the offspring's food demands? Zool Stud 48:215–222

Burley N, Coopersmith C (1987) Bill color preferences of zebra finches. Ethology 76:133–151

Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. Curr Zool 57:491–498

Cepák J, Klvaňa P, Škopek J, Schröpfer L, Jelínek M, Hořák D, Formánek J, Zárybnický J (2008) Atlas migrace ptáků České republiky a Slovenska. Aventinum, Praha (in Czech with English summaries)

Cerella J (1980) The pigeon's analysis of pictures. Pattern Recogn 12:1–6

Chamberlain DE, Glue DE, Toms MP (2009) Sparrowhawk *Accipiter nisus* presence and winter bird abundance. J Ornithol 150:247–254

Cole EF, Cram DL, Quinn JL (2011) Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81:491–498

Cook RG, Wright AA, Drachman EE (2013) Categorization of birds, mammals, and chimeras by pigeons. Behav Process 93:98–110

Cramp S, Perrins CM, Brooks DJ et al (1994) Handbook of the birds of Europe the Middle East and North Africa. Oxford University Press, Oxford, New York

Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim Behav 23:1–115

Curio E (1976) The ethology of predation. Springer, Berlin

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? Oecologia 60:83–88

Davies NB, Welbergen JA (2008) Cuckoo–hawk mimicry? An experimental test. Proc R Soc B 275:1817–1822

Dingemanse N (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim Behav 64:929–938

Ghosh N, Lea SE, Noury M (2004) Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. J Exp Anal Behav 82:125

Gill SA, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. Anim Behav 53:1287–1293

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav R 29:137–150

Huber L (2001) Visual categorization in pigeons. In: Cook RG (ed) Avian visual cognition. http://www.pigeon.psy.tufts.edu/avc/huber/. Accessed 24 Feb 2013

Jitsumori M, Yoshihara M (1997) Categorical discrimination of human facial expressions by pigeons: a test of the linear feature model. Q J Exp Psychol-B 50:253–268

Karplus I, Algom D (1981) Visual cues for predator face recognition by reef fishes. Z Tierpsychol 55:343–364

Karplus I, Goren M, Algom D (1982) A preliminary experimental analysis of predator face recognition by *Chromis caeruleus* (Pisces, Pomacentridae). Z Tierpsychol 58:53–65

Kirkpatrick-Steger K, Wasserman EA, Biederman I (1998) Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. J Exp Psychol Anim Behav Process 24:34–46

Klump GM, Curio E (1983) Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. Bird Behav 4:78–81

Krätzig H (1940) Untersuchungen zur Lebensweise des Moorschneehuhns (Lagopus l. lagopus L.) während der Jugendentwicklung. J Ornithol 88:139–165

Kullberg C, Lind J (2002) An experimental study of predator recognition in great tit fledglings. Ethology 108:429–441

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lorenz K (1937) The companion in the bird's world. Auk 54:245–273

Lorenz K (1940) Vergleichende Verhaltensforschung. Verh deutsch Zool Gesellsch 1939:69–102

Maloney RF, McLean IG (1995) Historical and experimental learned predator recognition in free-living New-Zealand robins. Anim Behav 50:1193–1201

Marr D, Nishihara HK (1978) Representation and recognition of the spatial organization of three dimensional shapes. Proc R Soc Lond B 200:269–294

Matsukawa A, Inoue S, Jitsumori M (2004) Pigeon's recognition of cartoons: effects of fragmentation, scrambling, and deletion of elements. Behavi Process 65:25–34

McLean IG, Rhodes G (1991) Enemy recognition and response in birds. Current Ornithol 8(173–211):1

McLean IG, Hölzer C, Studholme JS (1999) Teaching predator-recognition to a naive bird: implications for management. Biol Cons 87:123–130

Palleroni A, Hauser M, Marler P (2005) Do responses of galliform birds vary adaptively with predator size? Anim Cogn 8:200–210

Pashler H (2002) Stevens' handbook of experimental psychology I: sensation and perception. Wiley, New York

Patton TB, Szafranski G, Shimizu T (2010) Male pigeons react differentially to altered facial features of female pigeons. Behaviour 147:757–773

Pearce JM (2008) Animal learning and cognition: an introduction. Psychology Press, New York

Pincemy G, Dobson FS, Jouventin P (2009) Experiments on colour ornaments and mate choice in king penguins. Anim Behav 78:1247–1253

Quinn JL, Cole EF, Bates J, Payne RW, Cresswell W (2012) Personality predicts individual responsiveness to the risks of starvation and predation. Proc R Soc B 279:1919–1926

Scaife M (1976) The response to eye-like shapes by birds. I. The effect of context: a predator and a strange bird. Anim Behav 24:195–199

Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc B 367:2762–2772

Smith EE, Medin DL (1981) Categories and concepts. Harvard University Press, Cambridge

StatSoft Inc (2009) STATISTICA, version 9.1. http://www.statsoft.com

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 Fenn 89:206–215

Stuber EF, Bartell PA (2013) Seasonal differences in behaviour patterns of the migratory white-throated sparrow. J Ethol 31:151–158

Suzuki TN (2012) Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. Anim Behav 84:53–57

ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco for windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY

Tinbergen N (1948) Social releasers and the experimental method required for their study. Wilson Bull 60:6–51

Trnka A, Prokop P, Grim T (2012) Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? PLoS ONE 7:e37445

Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav Ecol Sociobiol 65:727–733

Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. J Ethol 30:157–165

Verbeek M, Drent PJ, Wiepkema P (1994) Consistent individual differences in early exploratory behaviour of male great tits. Anim Behav 48:1113–1121

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. Anim Cogn 5:253–259

Weisman R, Spetch M (2010) Determining when birds perceive correspondence between pictures and objects: a critique. Comp Cogn Behav Rev 5:117–131

Welbergen JA, Davies NB (2011) A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav Ecol 22:574–579

Werner CW, Tiemann I, Cnotka J, Rehkämper G (2004) Do chickens (Gallus gallus f. domestica) decompose visual figures? Anim Cogn 8:129–140

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 Ornithol 36:25–31

Článek VII.

Beránková J., Veselý P., Fuchs R. (2015): The role of body size in predator recognition by untrained birds. Behavioural Processes 120:128-134.

Behavioural Processes 120 (2015) 128–134

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

The role of body size in predator recognition by untrained birds

Jana Beránková, Petr Veselý*, Roman Fuchs

Faculty of Science, University of South Bohemia, Branišovská 31a, 37005 České Budějovice, Czech Republic

ARTICLE INFO

Article history:
Received 2 July 2015
Received in revised form
24 September 2015
Accepted 28 September 2015
Available online 9 October 2015

Keywords:
Predator
Body size
Colouration
Recognition
Categorization
Untrained birds

ABSTRACT

It is supposed that body size serves as an important cue in the recognition of relevant stimuli in nature. As predators of varying body size pose differing levels of threat, their potential prey should be able to discriminate between them. We tested the reaction of great tits (*Parus major*) to the dummies of their common predator (the European sparrowhawk—*Accipiter nisus*) in natural and reduced body sizes under laboratory conditions. All of the tested dummies possessed local raptor-specific features (hooked beak, claws with talons, and conspicuous eyes), but differed in global species-specific features: body size (large – the size of a sparrowhawk, small – the size of a great tit) and colouration (sparrowhawk, great tit, robin, and pigeon). The sparrowhawk-coloured dummies evoked fear regardless of their size while both great tit- and pigeon-coloured dummies evoked no fear reaction. The body size was used as the cue only for the discrimination of the robin-coloured dummies. The differences in reactions to the dummies with robin colouration (species unimportant to the great tits) could be explained as that the tits are able to recognize these birds in nature, but not so undoubtedly as the predator or the conspecific.

1. Introduction

Object recognition and categorization play an important role in animal life as it allows for an effective, fast, and appropriate reaction to objects (Shettleworth, 1993, 2010). Animals in the wild possess the ability to recognize objects that are in some way relevant to them (Shettleworth, 2010). Such objects usually represent food, sexual partners, or predators (Strnad et al., 2012; Veselý and Fuchs, 2009; Veselý et al., 2013). The animals can use either local or global features for precise object recognition (Jitsumori and Delius, 2001).

The largest portion of our knowledge on the usage of these two types of features comes from experiments with captive animals that were trained to discriminate modified pictures of conspecifics (e.g. Marsh and MacDonald, 2008), humans (e.g. Aust and Huber, 2002), or other objects (e.g. Kirkpatrick-Steger et al., 1998; Goto et al., 2004; Matsukawa et al., 2004). Partial local features typical for natural stimuli (e.g. eyes, head, or hands of animals or humans) were shown to play an important role in natural stimuli recognition, whereas more conspicuous, global features (such as overall body shape) were important for artificial stimuli recognition. However, it seems that animals are able to use both local and global features and switch between them when needed (Fremouw et al., 1998; Fremouw et al., 2002).

Some experiments were also conducted with untrained animals, either in natural (e.g. Curio, 1975; Gill et al., 1997; Thorogood and Davies, 2012; Trnka et al., 2012), or laboratory conditions (e.g. Karplus and Algom, 1981; Patton et al., 2010; Beránková et al., 2014).

These studies found that local features like the colour of eyes, shape of beak and mouth, or conspicuous components in colouration are essential for the proper recognition of a predator (e.g. Curio, 1975; Karplus and Algom, 1981; Gill et al., 1997; Beránková et al., 2014), nest parasite (e.g Thorogood and Davies, 2012; Trnka et al., 2012) or conspecific (e.g. Patton et al., 2010). Moreover, some studies imply that birds are able to use a combination of features in object recognition (e.g. Trnka and Prokop, 2012; Beránková et al., 2014). If the local features are not available for recognition, birds can do without them and use only global features. An example is the recognition of raptor silhouettes (e.g. Evans et al., 1993).

Another possible global feature used in predator recognition is body size. Predators of different body size should be discriminated between because they can pose different levels of threat to the potential prey in invertebrates (e.g. Binz et al., 2014) as well as vertebrates (e.g. Swaisgood et al., 1999). Body size is especially important in birds of prey because they are quite similar in overall appearance as well as body shape, but their size provides a reliable indicator of the level of threat they pose to the potential prey. A small raptor is more dangerous for small prey, while a large raptor is a greater threat to large prey.

---

* Corresponding author. Fax: +420 385310366.
E-mail address: petr-vesely@seznam.cz (P. Veselý).

http://dx.doi.org/10.1016/j.beproc.2015.09.015
0376-6357/

It has been repeatedly showed that various bird species can distinguish between raptors differing in size. Domestic hens (*Gallus gallus f. domestica*) react differently to the variously sized trained live raptors (Palleroni et al., 2005). Wild Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and captive black-capped chickadees (*Poecile atricapilla*) react differently to stuffed raptors of various sizes via differing the intensity of their warning calls (Soard and Ritchison, 2009; Courter and Ritchison, 2010; Templeton et al., 2005). Chickens (*Gallus gallus f. domestica*) as well as blue tits (*Cyanistes caeruleus*) can even recognize differences in the size of flying silhouettes (Evans et al., 1993; Klump and Curio, 1983).

All of the stimuli used in the studies mentioned above were either real or created to simulate real raptors. These results show that birds are able to distinguish between raptors differing in size, but they do not answer the question of whether size is an important feature in the recognition of particular raptor species. In other words, if the particular raptor species can be recognized in its "proper" as well as its "wrong" size.

The fact that birds are able to use size as a cue in object recognition was supported by experiments testing trained animals. It was shown that European starlings (*Sturnus vulgaris*) can perceive a difference of as little as 5% in size asymmetry (Swaddle and Johnson, 2007). Pigeons (*Columba livia f. domestica*) are also able to notice a size change in the stimuli. On the other hand, this change does not disrupt the birds' ability of discriminate regarding the sameness or differentness of the multi-item array (Castro and Wasserman, 2010). Pigeons are also able to generalize their object discrimination of smaller and larger versions of objects familiar to them through training, but their performance drops as the size increases or decreases relatively to the trained size (Peissig et al., 2006).

We decided to test how untrained birds (great tits) generalize the most dangerous predator of small passerines in Europe (the European sparrowhawk, *Accipiter nisus*) using a smaller dummy of the species, which they have no experience of. The sparrowhawk is characterized not only by raptor specific features (eye, beak and claws) but by a species specific features (size, overall colouration) as well. Raptor specific features are typical local features. On the other hand, overall colouration pattern composed of the set of the partial local features (e.g. barred under-part, greyish back) can be considered as a global feature (Aust and Huber, 2001) the same way as the size. Therefore, we used dummies with the colouration of three harmless birds: a pigeon (comparable in body size to the sparrowhawk), robin (comparable in body size to the great tit) and great tit (conspecific colouration) as well as the dummies with sparrowhawk colouration. The dummies possessing the above-mentioned colourations were made in the sizes of a sparrowhawk as well as in the size of a great tit. Behaviour of the tits without the presence of any dummy was used as a control condition.

Null hypothesis of our experiments states that recognition is based on the raptor specific features and all of the dummies would induce fear (the same amount) in the tits. Falsification of this hypothesis means that recognition is based also on the coloration and/or size. Then we can predict that: (1) only larger dummies would induce fear in the tits—the recognition is based on the presence of raptor-specific features on the dummy of the size of a sparrowhawk, (2) only the dummies with the sparrowhawk colouration would induce fear in the tits—the recognition is based on the presence of raptor-specific features and sparrowhawk colouration, (3) only the unmodified, realistic sparrowhawk dummy would induce fear—the recognition is based on the presence of raptor-specific features and body size as well as the colouration of the sparrowhawk, (4) all but the dummies with conspecific (great tit) colouration would induce fear—the recognition is based only on the presence of raptor-specific features, but the conspicuous conspecific colouration cancels out their effect.

1.1. Terminological comment

We often use a term "recognition" that unfortunately has no unambiguous meaning. It is the term connected to the memory in psychological research and refers to the successful recalling of the previously learnt stimuli. However, recognition can also refer to classifying objects or other animals appropriately on the first encounter by means of some distinctive feature (Shettelworth, 2010). This meaning is common in behavioural ecology and we use it for purposes of our study. The reason is that experiments with untrained animals do not allow testing the recognition based on previous learning. The ability to recognize presented stimuli in behavioural studies is evaluated on the basis of appropriate reaction to the biologically meaningful stimulus (Krebs and Davies, 2009).

2. Methods

2.1. Subjects

The great tit was chosen as a model species. Great tits are very adaptable to laboratory conditions (e.g. Dingemanse et al., 2002). Moreover, no neophobic reaction that could negatively influence their behaviour in the presence of an unfamiliar stimulus has been found in this species (Cole et al., 2011).

The birds were trapped in mist-nets in the suburban areas of České Budějovice (Czech Republic) during the winter seasons of the years 2011–2012 using the same procedure as in Beránková et al. (2014). Experiments conducted during the winter season ensure that yearlings are already able to recognize the sparrowhawk properly (Kullberg and Lind, 2002). Each bird was tested only once. One hundred eighty individuals were used for all the experiments (20 tits for each dummy, with eight dummies presented and 20 control tits). Sex ratio in our experiments was balanced and had no significant effect on great tits reactions to the presented dummies ($p = 0.677$).

Authors have complied with APA ethical standards. Experiments carried out in this research comply with the current laws of the Czech Republic.

2.2. Experimental stimuli

The European sparrowhawk is the main predator of small passerines in Europe (Zawadzka and Zawadzki, 2001; Bujoczek and Ciach, 2009; Chamberlain et al., 2009). It has already been established that wild great tits are able to recognize a sparrowhawk and distinguish it from less dangerous raptor species (Tvardíková and Fuchs, 2011).

Plush dummies were made of hollow textile fibres on a wire skeleton. The plush surface was painted with acrylic colours to imitate the bird's feathers. The beak and claws were made from modelling clay; the eyes were made of glass. The efficiency of such dummies in experiments with passerines has already been demonstrated by Němec et al. (2015). In our study, we used four different colour modifications of the sparrowhawk (Fig. 1). As well as for the unmodified, realistic sparrowhawk colouration (indexed as H), we used the colourations of a pigeon (P) and a robin (R) as they are harmless birds approximately of the same body sizes of a sparrowhawk and a great tit respectively. The last colouration used was that of a conspecific great tit (T). One set of dummies was larger (indexed as L—LH, LP, LR, LT)—the size of a female sparrowhawk (body length 35 cm), and the second set was smaller (indexed as S—SH, SP, SR, ST)—the size of a great tit (body length 15 cm). All of the dummies we made to imitate a sparrowhawk resting on a perch. There is no raptor with a body size similar to that of the

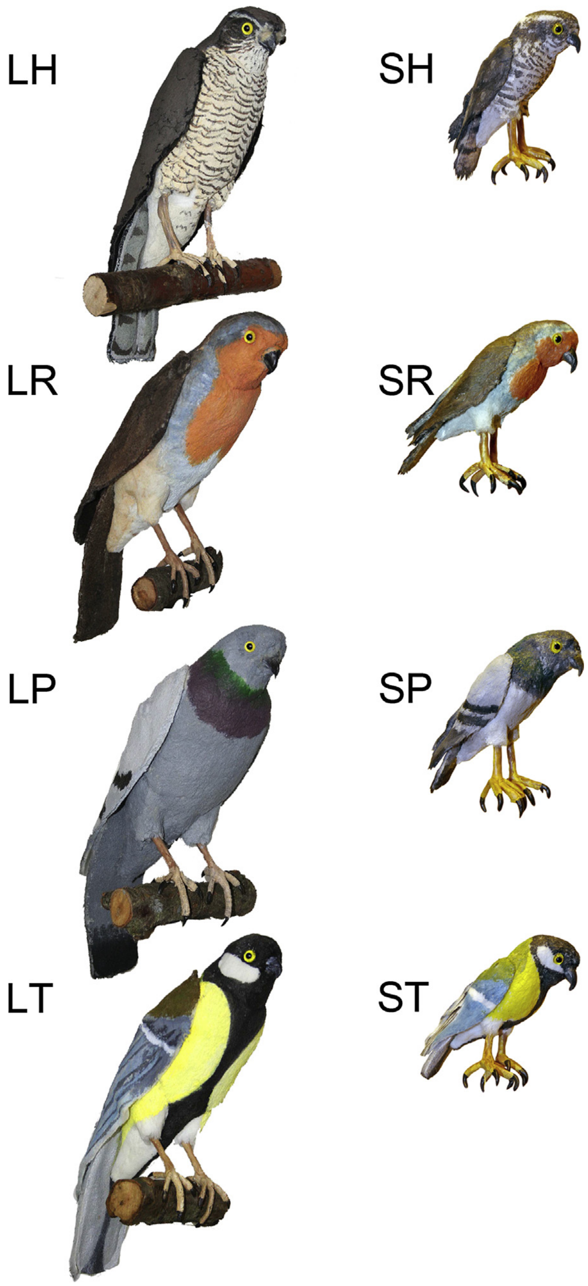


Fig. 1. Presented dummies. LH—large hawk, SH—small hawk, LR—large robin, SR—small robin, LP—large pigeon, SP—small pigeon, LT—large tit, ST—small tit.

great tit in Europe; thus, the smaller sparrowhawk dummies could not be familiar to great tits.

2.3. Experimental design

Before the experiment started, the birds had been deprived of food for 1.5 h to gain motivation. Afterwards, they were released into an experimental cage (2 × 1 × 0.5 m). The cage was equipped with corn bedding, perches, a nesting box and a dish with sunflower seeds in the front part. The dummy was positioned in front of the experimental cage so that it was facing toward the subject. In the case of the control sessions, only an empty perch was presented in front of the cage. The experiment started after the removal of a wooden barrier between the tested bird and the rest of the cage, including the dummy. The behaviour of the birds during their exposure to the dummies was recorded on video for 10 min.

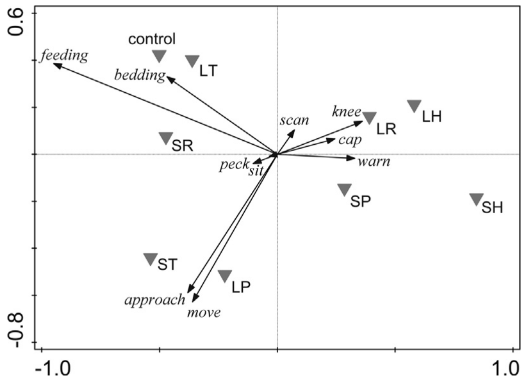


Fig. 2. Position of particular dummies on the first and second canonical axis of the principal component analysis created on the basis of particular behavioural responses of the birds performed towards these dummies. The first axis explains 44.6% of variability; the second axis explains 27.0% of variability. Control = no dummy, ST—small tit, SR—small robin, LT—large tit, LP—large pigeon, SP—small pigeon, LR—large robin, LH—large hawk, SH—small hawk.

The video was analysed in Observer XT 6.1 (Noldus Information Technology, 1990–2006). The total occurrence of the following behaviours was recorded: raising feathers on head (cap), knee bending (knee), warning calls (warn), approaching the dummy up to a distance of less than 1 m (approach), movement from one perch to another (move), scanning the dummy from a distance of less than 1 m (scan). The total duration of the following behaviours was recorded: surveying the corn bedding for food (bedding), feeding on the provided sunflower seeds (feeding), sitting still (sit), and pecking the equipment in the cage (peck). The inter-rater reliability was estimated by analysing experiments by two raters (J.B. and P.V.). The correlations between the two sets of behavioural measures were calculated using correlation matrices (package Hmisc) in R 2.12.2 (R Development Core Team, 2011). The results show significant correlations ($p < 0.01$) in all of the observed behaviours (cap, $r = 0.73$; knee, $r = 0.83$; warn, $r = 0.99$; approach, $r = 0.80$; move, $r = 0.95$; scan, $r = 0.32$; bedding, $r = 0.92$; feeding, $r = 0.99$; sit, $r = 0.87$; peck, $r = 0.79$).

2.4. Statistical analysis

The tit behaviour (including all of the activities mentioned above) was analysed using the multivariate technique—the principal component analysis (PCA) using Canoco 5 software (ter Braak and Šmilauer, 1998) to find out if there was a consistent reaction to the dummies. The dummies were used as supplementary environmental data in PCA. PCA scores on the first and second axis were of a Gaussian distribution and were subsequently used as synthetic dependent variables in ANOVA using STATISTICA 9.1 software (StatSoft Inc., 2009) to test the effect of particular parameters of the tested dummies (the size, colour, and their interaction) on the tits' behaviour. The differences among the individual dummies were consequently compared using the Tukey HSD post hoc test (again in STATISTICA 9.1 software). We also ran a redundancy analysis (RDA) in Canoco 5 software with the dummies as environmental data to compare the behaviour of individual tits towards the tested dummies. The data for PCA and RDA analysis were logarithmically adjusted and centred.

3. Results

Principal component analysis (PCA) shows that there are consistent reactions to the presented dummies (Fig. 2). The first PCA axis explains 44.6% of the variability of the birds' behaviour and separates the stress behaviour (knee-bending, warning calls,

Table 1
Differences in the reaction to individual dummies on the base of scores on the first canonical axis of the principle component analysis (PCA), Tukey HSD test, *p*-values. Significant *p* values indicated in bold.

Dummy	LH	LT	LR	LP	SH	ST	SR	SP
LH		–	–	–	–	–	–	–
LT	**0.023**		–	–	–	–	–	–
LR	0.999	0.157		–	–	–	–	–
LP	0.099	1.000	0.417		–	–	–	–
SH	0.991	**<0.001**	0.797	**0.005**		–	–	–
ST	**0.002**	0.999	**0.027**	0.971	**<0.001**		–	–
SR	**0.006**	1.000	0.055	0.994	**<0.001**	1.000		–
SP	0.981	0.344	1.000	0.679	0.550	0.082	0.150	
Control	**0.004**	1.000	**0.040**	0.987	**<0.001**	1.000	1.000	0.117

LH—large hawk, LT—large tit, LR—large robin, LP—large pigeon; SH—small hawk, ST—small tit, SR—small robin, SP—small pigeon, control = no dummy.

raised feathers on the head) from other behavioural types (cage exploration or feeding). The second PCA axis explains 27.0% of the variability. Negative values on this axis correlate with an increased movement of the tits in the cage (flying and approaching the dummy). The type of dummy influences the position of the tested birds on the first PCA axis (one-way ANOVA, $F_{8,171} = 7.047$, $p < 0.001$). The tits showed higher amounts of stress-induced behaviour (positive values on the first PCA axis) in the presence of both sparrowhawk dummies (LH and SH) and the large dummy with robin colouration (LR) than during the control trial. The behaviour of tits in the presence of the great tit dummies (LT, ST), pigeon dummies (LP and SP) and the small dummy with robin colouration (SR) did not differ from behaviour during the control trial. (Tukey HSD test, Table 1, Fig. 3). The type of dummy influenced the position of the tits on the second PCA axis as well (one-way ANOVA, $F_{8,171} = 2.459$, $p = 0.015$). However, none of the pot-hoc tests testing the differences among individual dummies was significant.

RDA confirmed that there were significant differences in the tits' behaviour in the presence of most of the individual dummies (Monte Carlo permutation test, $F = 4.616$, $p = 0.002$; Fig. 4). The first RDA axis explains 12.9%; the second axis explains 3.0% of the variability of the birds' behaviour. The marginal effects of all the dummies besides SP and LR are significant (Table 2). The RDA scores for most of the individual tits for the first as well as second canonical axes are far from the zero value in the case of all the dummies. This means that there was always a consistent response by individual birds to them. In most of the dummies, this response was predominantly stress, unconcern, or interest. Nevertheless, in the case of SP and LR, particular birds occur evenly on opposite positions on both axes. This means that some birds considered these dummies to be dangerous, other observed them and behaved as if there was no relevant stimulus.

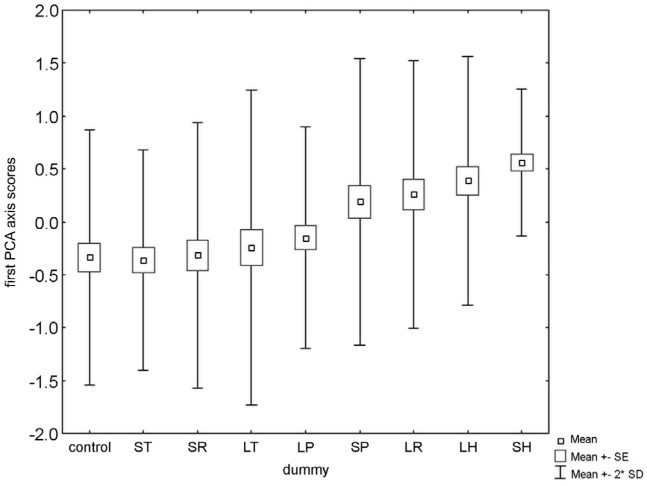


Fig. 3. Position of the birds confronted with particular dummies on the first canonical axis of the principal component analysis (PCA scores). Positive values reflect the stress behaviour; negative values reflect the interest in dummies or comfort behaviour. Control = no dummy, ST—small tit, SR—small robin, LT—large tit, LP—large pigeon, SP—small pigeon, LR—large robin, LH—large hawk, SH—small hawk.

Table 2
Marginal effects of individual dummies in redundancy analysis (RDA).

Dummy	Explains%	*F*-values	*p*-Values
SH	5.2	9.8	**0.002**
Control	3.1	5.7	**0.002**
LH	2.7	5.0	**0.004**
ST	2.4	4.4	**0.004**
SR	1.6	3.0	**0.026**
LT	1.4	2.6	**0.048**
LP	1.4	2.6	**0.05**
LP	1.0	1.9	0.116
SP	0.9	1.7	0.116

4. Discussion

None of our predictions was fully supported by our results. The reason is that the great tits probably combined local raptor-specific features (hooked beak, claws with talons, conspicuous eye with prominent eyebrow) and species-specific global features (colouration and size) in the process of predator recognition. Their actual importance probably depends on the whole context of the other stimulus properties, especially their relevance to the tested tits. The presence of key features by itself is not enough for tits to recognize the dummy as a sparrowhawk, or raptor. Neither the great tit dummies (LT and ST), pigeon dummies (LP and SP), nor the small dummy with robin colouration (SR) were considered dangerous, regardless of the presence of conspicuous raptor features. On the other hand, a combination of raptor features and appropriate colouration was certainly enough, but not necessary, for the tested birds to recognize a predator in the presented dummy because besides both sparrowhawk dummies (LH and SH), the large dummy with robin colouration (LR) was considered dangerous as well.

Also, according to our results, size does not play a simple role in raptor recognition. Two of the large dummies (LH and LR) were treated as dangerous while the other large dummies (LT and LP) were treated as harmless. Most of the small dummies were treated as harmless. However, the reaction to the small sparrowhawk dummy (SH) was as strong as to the unmodified sparrowhawk (LH) regardless of its improper size. It is supposed that the typical colouration pattern overwhelmed the effect of the improper body size in this case. Similarly, sparrowhawk-like colouration increases fear of the grey form of the cuckoo (*Cuculus canorus*) (Welbergen and Davies, 2011) or modified dove dummy (Trnka et al., 2012). In concordance with our fourth prediction, conspecific (great tit) colouration in the dummies (LT and ST) really does eliminate fear of those dummies. However, pigeon (LP and SP) and partially also robin colouration (SR) eliminates fear as well.

Unlike the other studies testing the role of predator size in recognition, we found no difference in the reaction to the small and large sparrowhawk dummies unmodified in colour. The reason could be that the colouration of both of our dummies was identical whereas the other studies used stuffed (Soard and Ritchison, 2009; Courter and Ritchison, 2010; Templeton et al., 2005) or living (Palleroni et al., 2005) birds of prey (raptors and owls) of different species. Pronounced differences in colouration—e.g. sharp-shinned hawk (*Accipiter striatus*) vs. red-tailed hawk (*Buteo jamaicensis*) in Soard and Ritchison (2009) or northern pygmy-owl (*Glaucidium gnoma*) vs. short-eared owl (*Asio flammeus*) in Templeton et al. (2005) might

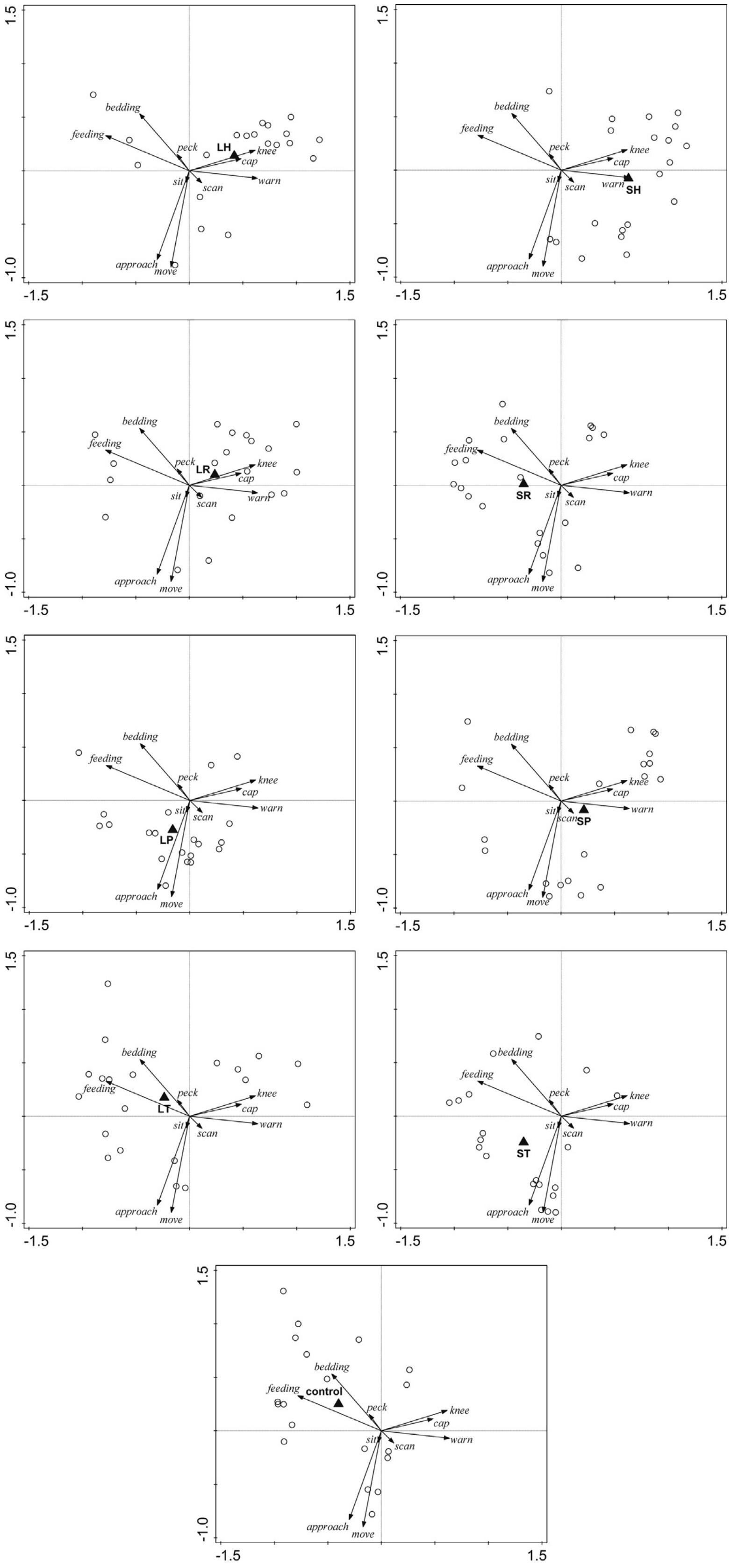


Fig. 4. Position of particular birds on the first and second canonical axis of the redundancy analysis (RDA) created on the basis of behavioural responses of the birds performed towards particular dummies. The first axis explains 12.9% of variability; the second axis explains 3.0% of variability. LH—large hawk, SH—small hawk, LR—large robin, SR—small robin, LP—large pigeon, SP—small pigeon, LT—large tit, ST—small tit, control = no dummy. Significant *p* values indicated in bold.

serve as a cue for the discrimination of species varying in body size. The use of colouration in raptor recognition was confirmed by different responses towards equally sized raptors—sharp-shinned hawk vs. American kestrel (*Falco sparverius*) in Soard and Ritchison (2009) or prairie falcon (*Falco mexicanus*) vs. peregrine falcon (*Falco peregrinus*) in Templeton et al. (2005). All of the studies mentioned above used real raptors or owls. Tested birds therefore may have some experience of them, and they also pose some, varying, level of threat to them. For example, in the study of Courter and Ritchison (2010), tufted titmice are less threatened by the larger red-tailed hawk (hunting mostly squirrels and gophers, Fitch et al., 1946) than by the smaller sharp-shinned hawk (preferring small passerines, Mueller and Berger, 1970).

Similarly, birds were able to react differently to variously sized raptor silhouettes (Evans et al., 1993; Klump and Curio, 1983). The amount of fear induced by the silhouettes increases with size in both of the studies. The reason is that the size of the silhouette provides more information about the height of the flying raptor above the ground than the actual body size, and thus, warns about the danger presented by the raptor at that moment (Evans et al., 1993).

A raptor with a body size comparable to that of our SH does not occur in Europe and thus tits had no pre-formed ability to differentiate between SH and LH. Therefore, we tested only the importance of size as a feature for raptor recognition and we showed that size plays no role when appropriate key features and colouration is present.

Experiments with artificial stimuli under laboratory conditions showed that the birds are able to perceive negligible differences in the stimulus size (e.g. Swaddle and Johnson, 2007). On the other hand, they are able to treat the stimuli differing in size as equal, when they are trained to do so (Castro and Wasserman, 2010; Peissig et al., 2006). It means that under some conditions they are able to use other determining features and ignore the stimulus size.

The inappropriate size of the dummies seems to play no role in discrimination in the case of the dummies carrying great tit colouration, similarly as in the dummies carrying sparrowhawk colouration. The conspecific colouration is such a strong cue that even the presence of raptor-specific features cannot make the dummy dangerous for great tits. It is understandable that conspecific colouration is such a strong cue because all of the individuals must know it thoroughly to recognize an appropriate mate, competitor, etc.

In a concordance with our first prediction that the larger dummies would cause more fear than the smaller dummies, the dummy size influenced only the reaction to the dummies carrying robin colouration. Unlike the sparrowhawk and conspecifics, the robin is definitely a less important bird species for great tits because it is neither a predator nor a competitor for them. Therefore, we can assume that great tits have no motivation to learn how to recognize them. However, both dummies were treated as harmless in the case of pigeon colouration and the pigeon is as unimportant as the robin for great tits at the same time. Of course, the difference between the pigeon and the robin relies on the fact that the improper size is the smaller one in the case of the pigeon, and the larger one in the case of the robin.

Therefore, differences in the reactions to the dummies with pigeon and robin colouration may be explained by tits being able to recognize these birds in nature but not so undoubtedly as predator or conspecifics. A large pigeon and a small robin would then be recognized as familiar harmless birds regardless of raptor-specific features. A small pigeon may be perceived as an unfamiliar bird species, but because of his size probably a harmless one. To the contrary, a large robin may be perceived as unfamiliar and a potentially dangerous bird species because of its large size and the presence of raptor features. Such a conclusion may seem to be rather speculative, but it is supported by the overall reaction to the small dummy with the pigeon colouration and the large dummy with robin colouration. In the presence of both of these dummies, the significant part of the tested birds reacted conversely to the rest (see later). This fact indicates that these dummies carry conflicting features for great tits.

It is certain that wild living great tits repeatedly meet both pigeons and robins. Despite the fact that they are not biologically relevant to them, the ability to recognize them could probably help tits to quickly discriminate between novel and potentially relevant stimuli, e.g. an unfamiliar predator. Our results actually suggest that the birds are able to discriminate between more objects in the nature than might be expected based on their basic need to feed, avoid predation, and successfully reproduce. Indeed, experiments based on operant conditioning showed that trained pigeons under laboratory conditions are able to learn to discriminate between as many as 320 particular photographs of non-relevant stimuli and remember them for at least two years (Vaughan and Greene, 1984).

Our results could seem too complicated at the first sight but we can assume one general conclusion. There is a lot of studies showing the ability of untrained birds to distinguish among various predator species, but only a little is known about the process of predator recognition. Strong emphasis was put on the role of the key features in predator recognition since the time of experiments conducted by founders of classical ethology (Lorenz, 1937; Tinbergen, 1948). However, the laboratory experiments with trained birds imply that object recognition is a complex process based on more than a few local features (Huber, 2001).

Our study using untrained birds and altered naturally relevant stimuli under controlled laboratory conditions demonstrate that even the untrained bird spontaneously use rather a complex approach to the recognition and do not rely on a simple presence or absence of partial key features.

The results of the redundancy analysis showed that the behaviour of the individual tits was rather consistent during the experiment which further shows absence of habituation. However, there was a great variability among the tested individuals. Especially in the case of SP and LR dummies, various attitudes were adopted by various birds. It means that a portion of the birds used rather the harmless features in recognizing the ambiguous dummies while the other portion of the birds used rather the predator-specific features. Similarly to our previous study (Beránková et al., 2014) we can see that reaction to the ambiguous stimuli varies highly according to the individual, probably because of either different experience or personality.

Acknowledgements

We thank Silvie Lišková and Christopher Mark Steer for the language improvement. We thank the Grant agency of the University of South Bohemia (159/2013/P) for financial support.

References

Aust, U., Huber, L., 2002. Target-defining features in a people-present/people-absent discrimination task by pigeons. Learn. Behav. 30, 165–176.

Beránková, J., Veselý, P., Sýkorová, J., Fuchs, R., 2014. The role of key features in predator recognition by untrained birds. Anim. Cogn. 17, 963–971, http://dx.doi.org/10.1007/s10071-014-0728-1.

Binz, H., Bucher, R., Entling, M.H., Menzel, F., 2014. Knowing the risk: crickets distinguish between spider predators of different size and commonness. Ethology 120, 99–110, http://dx.doi.org/10.1111/eth.12183.

Bujoczek, M., Ciach, M., 2009. Seasonal changes in the avian diet of breeding sparrowhawks *Accipiter nisus*: how to fulfil the offspring's food demands? Zool. Study 48, 215–222.

Castro, L., Wasserman, E.A., 2010. Effects of stimulus size and spatial organization on pigeons' conditional same–different discrimination. Behav. Process. 83, 162–171, http://dx.doi.org/10.1016/j.beproc.2009.10.007.

Chamberlain, D.E., Glue, D.E., Toms, M.P., 2009. Sparrowhawk *Accipiter nisus* presence and winter bird abundance. J. Ornithol. 150, 247–254, http://dx.doi.org/10.1007/s10336-008-0344-4.

Cole, E.F., Cram, D.L., Quinn, J.L., 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. 81, 491–498.

Courter, J.R., Ritchison, G., 2010. Alarm calls of tufted titmice convey information about predator size and threat. Behav. Ecol. 21, 936–942, http://dx.doi.org/10.1093/beheco/arq086.

Curio, E., 1975. The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim. Behav. 23, 1–115.

Dingemanse, N., Both, C., Drent, P.J., Van Oers, K., van Noordwijk, A.J., 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim. Behav. 64, 929–938, http://dx.doi.org/10.1006/anbe.2002.2006.

Evans, C., Macedonia, J., Marler, P., 1993. Effects of apparent size and speed on the response of chickens, Gallus–Gallus, to computer-generated simulations of aerial predators. Anim. Behav. 46, 1–11, http://dx.doi.org/10.1006/anbe.1993.1156.

Fitch, H.S., Swenson, F., Tillotson, D.F., 1946. Behavior and food habits of the red-tailed Hawk. Condor 48, 205–237.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 1998. Priming of attention to local or global levels of visual analysis. J. Exp. Psychol. Anim. Learn. Cogn. 24, 278–290.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 2002. Dynamic shifts of pigeon local/global attention. Anim. Cogn. 5, 233–243, http://dx.doi.org/10.1007/s10071-002-0152-9.

Gill, S.A., Neudorf, D.L., Sealy, S.G., 1997. Host responses to cowbirds near the nest: cues for recognition. Anim. Behav. 53, 1287–1293.

Goto, K., Wills, A.J., Lea, S.E.G., 2004. Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. Anim. Cogn. 7, 109–113, http://dx.doi.org/10.1007/s10071-003-0193-8.

Huber, L., 2001. Visual categorization in pigeons. In: R.G. Cook (Ed.), Avian visual cognition [on-line]. Available: <www.pigeon.psy.tufts.edu/avc/huber/>.

Jitsumori, M., Delius, J.D., 2001. Object recognition and object categorization in animals. In: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer, Berlin, pp. 269–293.

Karplus, I., Algom, D., 1981. Visual cues for predator face recognition by reef fishes. Z. Tierpsychol. 55, 343–364, http://dx.doi.org/10.1111/j.1439-0310.1981.tb01277.x.

Kirkpatrick-Steger, K., Wasserman, E.A., Biederman, I., 1998. Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. J. Exp. Psychol. Anim. Learn. Cogn. 24, 34–46.

Klump, G.M., Curio, E., 1983. Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. Bird Behav. 4, 78–81.

Krebs, J.R., Davies, N.B., 2009. Behavioural Ecology: An Evolutionary Approach. Blackwell Publishing, Oxford.

Kullberg, C., Lind, J., 2002. An experimental study of predator recognition in great tit fledglings. Ethology 108, 429–441.

Lorenz, K., 1937. The companion in the bird's world. Auk 54, 245–273.

Marsh, H.L., MacDonald, S.E., 2008. The use of perceptual features in categorization by orangutans (*Pongo abelli*). Anim. Cogn. 11, 569–585, http://dx.doi.org/10.1007/s10071-008-0148-1.

Matsukawa, A., Inoue, S., Jitsumori, M., 2004. Pigeon's recognition of cartoons: effects of fragmentation, scrambling, and deletion of elements. Behav. Process. 65, 25–34, http://dx.doi.org/10.1016/s0376-6357(03)00147-5.

Mueller, H.C., Berger, D.D., 1970. Prey preferences in the sharp-shinned hawk: the roles of sex, experience, and motivation. Auk 87, 452–457.

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. Anim. Cogn. 18, 259–268.

Palleroni, A., Hauser, M., Marler, P., 2005. Do responses of galliform birds vary adaptively with predator size? Anim. Cogn. 8, 200–210, http://dx.doi.org/10.1007/s10071-004-0250-y.

Patton, T.B., Szafranski, G., Shimizu, T., 2010. Male pigeons react differentially to altered facial features of female pigeons. Behaviour 147, 757–773, http://dx.doi.org/10.1163/000579510X491090.

Peissig, J.J., Kirkpatrick, K., Young, M.E., Wasserman, E.E., Biederman, I., 2006. Effects of varying stimulus size on object recognition in pigeons. J. Exp. Psychol.: Anim. Learn. Cogn. 32, 419–430, http://dx.doi.org/10.1037/0097-7403.32.4.419.

R Development Core Team, 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Shettleworth, S.J., 1993. Where is the comparison in comparative cognition? Alternative research programs. Psychol. Sci. 4, 179–184, http://dx.doi.org/10.1111/j.1467-9280.1993.tb00484.x.

Shettleworth, S.J., 2010. Cognition, Evolution, and Behavior, 2nd ed. Oxford University Press, New York.

Soard, C.M., Ritchison, G., 2009. Chick-a-dee calls of Carolina chickadees convey information about degree of threat posed by avian predators. Anim. Behav. 78, 1447–1453.

StatSoft Inc. (2009) STATISTICA, version 9.1. <www.statsoft.com>.

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.

Swaddle, J.P., Johnson, C.W., 2007. European starlings are capable of discriminating subtle size asymmetries in paired stimuli. J. Exp. Anal. Behav. 87, 39–49, http://dx.doi.org/10.1901/jeab.2007.103-05.

Swaisgood, R.R., Owings, D.H., Rowe, M.P., 1999. Conflict and assessment in a predator–prey system: ground squirrels versus rattlesnakes. Anim. Behav. 57, 1033–1044, http://dx.doi.org/10.1006/anbe.1998.1069.

Templeton, C.N., Greene, E., Davis, K., 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308, 1934–1937, http://dx.doi.org/10.1126/science.1108841.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY.

Thorogood, R., Davies, N.B., 2012. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. Science 337, 578–580, http://dx.doi.org/10.1126/science.1220759.

Tinbergen, N., 1948. Social releasers and the experimental method required for their study. Wilson Bull. 60, 6–51.

Trnka, A., Prokop, P., 2012. The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. Anim. Behav. 83, 263–268, http://dx.doi.org/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.

Tvardíková, K., Fuchs, R., 2011. Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav. Ecol. Sociobiol. 65, 727–733, http://dx.doi.org/10.1007/s00265-010-1075-0.

Vaughan, W., Greene, S.L., 1984. Pigeon visual memory capacity. J. Exp. Psychol.: Anim. Learn. Cogn. 10, 256–271, http://dx.doi.org/10.1037/0097-7403.10.2.256.

Veselý, P., Fuchs, R., 2009. Newly emerged Batesian mimicry protects only unfamiliar prey. Evol. Ecol. 23, 919–929.

Veselý, P., Luhanová, D., Prášková, M., Fuchs, R., 2013. Generalization of mimics imperfect in colour patterns: the point of view of wild avian predators. Ethology 119, 138–145.

Welbergen, J.A., Davies, N.B., 2011. A parasite in Wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav. Ecol. 22, 574–579.

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 Ornithol. 36, 25–31.

Článek VIII.

Veselý P., Buršíková M., Fuchs R. (2016): Birds at the Winter Feeder do not Recognize an Artificially Coloured Predator. Ethology 122: 1-8

ethology international journal of behavioural biology

Ethology

RESEARCH PAPER

Birds at the Winter Feeder do not Recognize an Artificially Coloured Predator

Petr Veselý, Markéta Buršíková & Roman Fuchs

Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

Correspondence
Petr Veselý, Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, 37005 České Budějovice, Czech Republic.
E-mail: petr-vesely@seznam.cz

Received: March 4, 2016
Initial acceptance: May 20, 2016
Final acceptance: September 11, 2016
(M. Herberstein)

doi: 10.1111/eth.12565

Keywords: predator, salient features, coloration, titmice, sparrowhawk, Paridae

Abstract

It is supposed that coloration may affect the recognition of predators by prey species; nevertheless, the significance of the coloration and its particular components in the recognition process remains unknown. We presented dummies of the European sparrowhawk (*Accipiter nisus*) with changed body coloration, but with all other typical features preserved (body size and shape, beak, eyes, legs), to great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) visiting a winter feeder. A pigeon (*Columba livia f. domestica*) dummy was used as a harmless control. Neither tit species showed passive avoidance in the presence of a dummy with an artificial, violet-white chequered coloration. They obviously did not consider such an object to be a predator despite the presence of the raptor beak, eyes and talons. Sparrowhawk dummies with the coloration completely changed (altered with those of a harmless European robin) or with the typical colour feature removed (barred pattern on the underparts) were considered to be as dangerous as the unmodified sparrowhawk. We discuss the possibility that the effect of salient raptor-like features such as beak shape, eye coloration, and leg and talons shape overwhelmed the effect of body coloration in these cases. Birds visiting the feeder probably were able to generalize the vigilance towards the sparrowhawk to other realistically coloured dummies, but not to the non-natural dummy.

Introduction

Various predators substantially differ in the level of peril they represent to prey (Caro 2005). These differences are obvious seen not only between foraging guilds – for example, aerial vs. terrestrial predators (McLean & Rhodes 1991; Hogstad 2005) or predators of nest content vs. predators of adult birds (Amat & Masero 2004; Hogstad 2005), but also within these groups (Tvardíková & Fuchs 2011; Strnad et al. 2012). The prey species should be able to assess the peril represented by particular predator species, in order not to be predated, but also not to spend energy on an inappropriate antipredatory behaviour (Caro 2005).

Accurate recognition of predators provides the context for the expression of appropriate antipredator behaviour. The ability of birds to recognize various predator species differing only in details (equal body size and shape, but different coloration) is surprisingly poorly studied; there is some evidence for this ability in mammals (e.g. Arnold et al. 2008 or Stankowich & Coss 2007). Several studies (Ash 1970; Tvardíková & Fuchs 2011; Strnad et al. 2012; Trnka & Grim 2013; Trnka et al. 2015) showed small passerines to be able to respond variously to the European kestrel (*Falco tinnunculus*) and European sparrowhawk (*Accipiter nisus*), which represent differing levels of threat, but vary only slightly in details of coloration.

Classical ethological studies have suggested the role of salient features in predator recognition. The first studies focused on the 'short neck' in the silhouettes of birds of prey (Lorenz 1939; Krätzig 1940). Conspicuous eyes, a curved beak, and long, curved talons are listed among the features essential for the recognition of a perching raptor (Scaife 1976; Watve et al. 2002; Trnka et al. 2012). Nevertheless, such salient features cannot be used in discrimination between particular raptor species, as they are common in most of them.

Coloration was suggested as the most probable feature, which can be used for the recognition of the kestrel and sparrowhawk (see previous paragraph), because all other features (size, body shape) are very similar in the two species. Nevertheless, coloration is a complex feature and relatively little is known about which components of this trait are actually utilized for recognition.

An experimental study by Curio (1975) proved that if the coloration of a predator (red-backed shrike – *Lanius collurio*) is partly changed (different colour of the back), the prey (pied flycatcher – *Ficedula albicollis*) is still able to recognize it as a predator. On the contrary, if a characteristic part of coloration (the band over the shrike's eyes) is absent, the ability to recognize the predator is notably reduced. More recently, Davies & Welbergen (2008) and Welbergen & Davies (2011) proved that the barred pattern on the belly of the European sparrowhawk is essential for sparrowhawk recognition. When this pattern is imitated by a cuckoo (*Cuculus canorus*), the cuckoo gains protection against mobbing by small passerines. These results suggest that some birds recognize their predators via specific visual patterns within the larger background coloration of their bodies. On the other hand, if the coloration of a raptor's body is completely different, the ability to recognize the predator is significantly lowered as well, despite the presence of the specific coloration trait (Curio 1975). Similar results were obtained in a study (Beránková et al. 2015), where textile sparrowhawk dummies were presented to great tits (*Parus major*). Tits showed lower fear towards the sparrowhawk coloured as pigeon (*Columba livia f. domestica*) or great tit than towards an unmodified sparrowhawk. Generally, it is hard to make a clear conclusion about what change of the coloration results in the inability of appropriate recognition.

In the present study, we decided to test the ability of titmice (great and blue tits – *Cyanistes caeruleus*) at the winter feeder to recognize dummies carrying all the features typical of their most common predator – the European sparrowhawk (curved beak, yellow eyes, long legs with curved talons), but differing in body coloration. The birds at the feeder seem to give the clearest and easily measurable response describing their ability to treat presented object as a predator. Multiple studies (e.g. Hill 1986; Davies & Welbergen 2008; Tvardíková & Fuchs 2010, 2011, 2012) have shown that in the presence of an object perceived as a danger, the birds cease to visit the feeder. The other parameter affecting feeder attendance is the weather, which must be checked and included in the analyses if necessary.

Tvardíková & Fuchs (2011) showed that tits avoided visiting the feeder significantly more when there was a stuffed sparrowhawk than when there was a stuffed kestrel. This gives us the opportunity to distinguish between the response to the sparrowhawk (the most dangerous) and to a general raptor (probably less dangerous). If the feeder attendance in connection with the colour modifications of the sparrowhawk does not differ from the feeder attendance in the presence of the unmodified sparrowhawk, we may consider that it was successfully recognized as a sparrowhawk (not as a raptor in general).

There were three experimental treatments using predator colour modifications with different degrees of visual complexity. The least complex modification omitted the cluster of repetitively horizontal bars on the dummy's underparts. According to some studies (Welbergen & Davies 2011), this trait is seen to be essential for recognition; nevertheless, other studies (e.g. Curio 1975; Trnka et al. 2012) show that such a change in coloration does not prevent successful recognition. A more complex modification completely changed the whole dummy coloration, yielding a pattern of coloration similar to that of a harmless small passerine bird, the European robin (*Erithacus rubecula*) familiar to the tested tits. Laboratory experiments of Beránková et al. (2015) showed that great tits recognize the very same dummy as a predator; while when coloured as another harmless bird, a pigeon, they treat it as a non-predator. The most complex modification completely changed dummy coloration by using a novel pattern of violet-white chequers that, despite the presence of eyes and a beak, might camouflage the overall shape of the sparrowhawk. Curio (1975) showed that a complete change of coloration to some non-natural (green shrike) prevents successful recognition of a predator and such a dummy may even be treated as a novel artificial object. We chose the violet-white chequered pattern as it cannot be familiar to tested birds from the natural environment, and, we supposed, such an artificial coloration might overwhelm the presence of eye, beak and talons, and prevent successful recognition.

We tested the following hypotheses:

1. A realistic-appearing sparrowhawk dummy will be recognized by subject birds as a dangerous predator and thus an attractive experimental setting, a bird feeder, will be avoided by bird subjects.
2. The dummy without the conspicuous barred pattern will not be recognized as a sparrowhawk predator, resulting in a feeder attendance by birds that is lower than the attendance when the sparrowhawk is present.

3 The robin-coloured dummy will not be recognized as a sparrowhawk predator, causing similar feeder attendance compared to the pigeon dummy but lower than the unmodified sparrowhawk dummy.

4 The chequered dummy will not be recognized as a sparrowhawk predator, also causing similar feeder attendance compared to the pigeon dummy but lower than the unmodified sparrowhawk dummy.

Material and Methods

Experimental Site and Tested Birds

The experiments were conducted during the winter of 2011/2012 and the experimental feeder was situated on the north-western edge of the town of České Budějovice (GPS: 48°59′37.583″N, 14°26′28.273″E; 393 m above sea level) in an oak–aspen (*Quercus sp., Populus tremula*) forest with willow (*Salix*) undergrowth, near a pond and a forest footpath. Despite a broad array of bird species visiting the feeder location, great tits and blue tits were used as experimental subjects, as their numbers at the feeder were constantly high during the whole winter. Other species (marsh tit – *Poecile palustris*, willow tit – *P. montanus* and nuthatch – *Sitta europaea*) visited the feeder only occasionally and their visits did not affect the responses of blue and great tits. These latter two species are common in the Czech Republic and they usually dominate the bird assemblage at winter feeders (Tvardíková & Fuchs 2010, 2011, 2012).

Predator and Dummies

We selected the European sparrowhawk for our predator-recognition study because it is one of the most common predators of small birds in central Europe (Bujoczek & Ciach 2009). For our predator presentations, we altered the coloration of the sparrowhawk by creating textile dummies which were the same size, same shape of body and possessed the same yellow eyes, claws and curved beak as present in a real female sparrowhawk. All the dummies were made from wire frame and cotton wool wadding covered with plush. The surface was painted using acrylic colours, so that the appearance of the surface was not fluffy as it is when simply covered with typical plush, but more compact and more similar to the texture of feathers. The eyes were made of glass and the legs of modelling clay. Němec et al. (2015) showed that birds defending their nest respond similarly to these textile dummies as to the stuffed ones and the ability of tits to recognize a sparrowhawk in the textile dummies has been proven in laboratory conditions (Beránková et al. 2015). As mentioned above, we examined the provocative effects of the following forms of sparrowhawk coloration: (1) the unmodified coloration of a female sparrowhawk, (2) the coloration of a female sparrowhawk with the barred pattern on the belly and breast removed, (3) the coloration of European robin and (4) a violet-white chequered pattern (Fig. 1). A plush dummy of a domestic pigeon in real size with the eyes, beak and legs of a domestic pigeon, a completely harmless bird, was used as a control.

Experimental Design

The feeder was a square, wooden, 50 × 50 cm board placed on the ground 1.5 m from the nearest shrub cover which could serve birds as both shelter and a surveillance position. This arrangement forced the birds to fly into an open space to get food from the feeder. The seeds of the sunflower (*Helianthus* sp.) were used as an attraction for the birds and provided *ad libitum* during the whole winter. The seeds were also supplied to the feeder immediately before the experiment. The tested dummies were placed on a 50 cm high wooden pole, 75 cm from the feeder, always in the same place and position facing the centre of the feeder. The digital video camera (Panasonic HC V-510) for recording the whole experiment was

Fig. 1: Presented textile dummies of sparrowhawk. From the left: unmodified female sparrowhawk, sparrowhawk with belly pattern removed, robin-coloured sparrowhawk, chequer-coloured sparrowhawk and unmodified pigeon. Colour figure can be viewed at wileyonlinelibrary.com

situated 8 m from the feeder and was covered by the shrubs. The human observer (MB) was at least 20 m from the feeder to prevent any disturbances.

The experiments were conducted from 18 Nov. 2011 to 24 Mar. 2012 always in the morning hours, beginning 1 h after sunrise and under good weather conditions. Altogether, there were 21 experiments, each testing all five dummies. One experiment consisted of five trials within 2 d because of time demands and to avoid any bird habituation. The total time of experimentation in each day did not exceed 3 h. Every trial consisted of two parts – an empty control without the dummy and the actual presentation of the dummy. Each of these two parts lasted 15 min and they were separated by only a few seconds delay as the dummy was introduced. The empty control was used to observe the numbers of birds present at the feeder in each particular morning. Particular trials within 1 d were separated by a 30-min pause allowing birds to calm down and feed on the provided seeds. The dummy was brought to the feeder covered by a dark blanket to prevent birds making a connection between the human intruder and the presented dummy. The dummies were presented in randomized order. The bird assemblage remained unknown to a large extent, but according to random captures and ringing of birds, we can conclude that the assemblage changed during the course of the winter, as there was very little proportion of marked birds present (30 great and 17 blue tits were captured, while only 2 great and 3 blue tits were recaptured). Therefore, we presumed that the effect of habituation/learning in the experimental procedure to be marginal. A previous study, where targeted captures of birds at the feeder were conducted (Tvardíková & Fuchs 2010), showed very strong turnover and thus very little effect of habituation and learning.

Recorded Parameters and Statistical Analyses

In each trial with dummy, we recorded air temperature (continuous predictor), the presence of snow cover (binomial categorical predictor), the dummy type (categorical predictor) and the order of the particular dummy within the series (categorical predictor). The number of visits at the feeder was used as the response variable. This measure roughly corresponds to the number of individuals visiting the feeder; nevertheless, a single individual, particularly bold or habituated to the dummy, could have potentially returned repeatedly to the feeder, increasing the apparent number of visits, which causes overdispersion. Therefore, we formed a single generalized mixed effect model (GLMM) with a negative binomial distribution. We tested the effect of the interaction of the predictors *bird species* (blue or great tit) and *type of dummy* present at the feeder. The categorical predictor dummy type included six values: hawk, belly, robin, chequer, pigeon and empty control. Given the specific design (which causes the measures relative to the absence of the dummy to be always paired with another treatment), a random effect 'trial number' was included. Other predictors included in the model were *presence of snow*, *air temperature* and *order of presented dummy* within the series (first fifth) on the number of visits at the feeder. Planned contrasts were used to compare particular levels of categorical variables. To test the first hypothesis, comparisons hawk × empty and hawk × pigeon were computed. Comparisons hawk × belly, hawk × robin and hawk × chequer were computed to test the second, third and fourth hypothesis, respectively. The P level of significance for these analyses was lowered from 0.05 to 0.01, as the data for the hawk dummy were used five times in planned contrasts.

All computations were carried out in the R for windows software (R 3.2.1, R developmental core team).

Results

The interaction of factors tit species, the type of dummy present at the feeder (GLMM, $df = 11$, $F = 6.21$, $p \ll 0.001$) and the absence or presence of snow (GLMM, $df = 1$, $F = 41.36$, $p \ll 0.001$) significantly affected the number of visits to the feeder. Other factors had no significant effect (air temperature: GLMM, $df = 1$, $F = 0.01$, $p = 0.977$; order of presentation: GLMM, $df = 4$, $F = 0.29$, $p = 0.137$).

In the case of great tits, the number of visits to the unmodified sparrowhawk was significantly lower than the number of visits to the pigeon dummy (planned contrasts; $t = 3.856$, $p = 0.001$; Fig. 2) as well as the empty control (planned contrasts; $t = 5.110$, $p \ll 0.001$; Fig. 2). The number of visits to the unmodified sparrowhawk was also lower than the number of visits to the chequered sparrowhawk (planned contrasts; $t = 3.112$, $p = 0.008$; Fig. 2), but did not differ from the number of visits to the plain-bellied sparrowhawk (planned contrasts; $t = 0.499$, $p = 0.538$; Fig. 2) or robin-coloured sparrowhawk (planned contrasts; $t = 0.678$, $p = 0.711$; Fig. 2).

In the case of blue tits, the number of visits to the unmodified sparrowhawk was significantly lower than the number of visits to the pigeon dummy (planned contrasts; $t = 3.101$, $p = 0.010$; Fig. 3) as well as the empty control (planned contrasts;

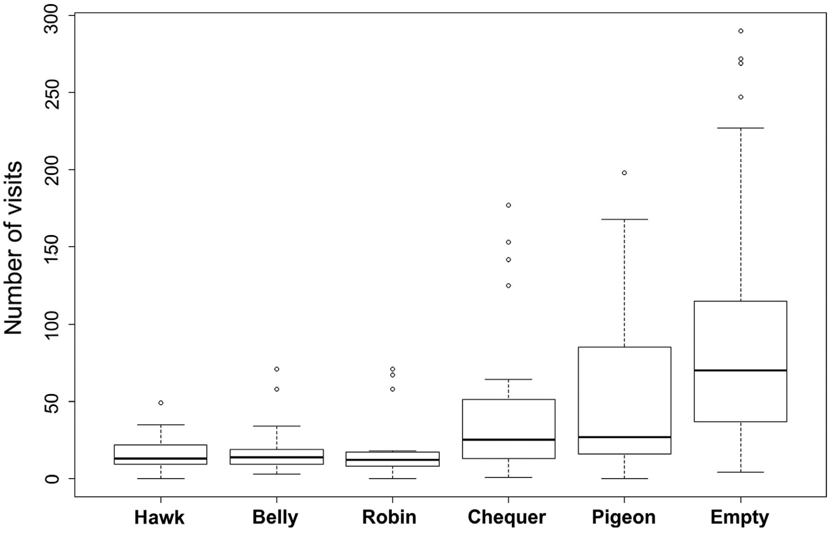


Fig. 2: The effect of the type of the dummy presented on the number of visits of great tits at the feeder in the presence of particular dummies. Hawk – unmodified female of the European sparrowhawk (*Accipiter nisus*); belly – sparrowhawk deprived of the coloration of underparts; robin – sparrowhawk coloured as the European robin (*Erithacus rubecula*); chequer – sparrowhawk with artificial violet-white chequer coloration; pigeon – unmodified feral pigeon (*Columba livia f. domestica*); empty – no dummy was present. Number of the sets of trials in each group is 21; in the case of the empty control, the N is 105.

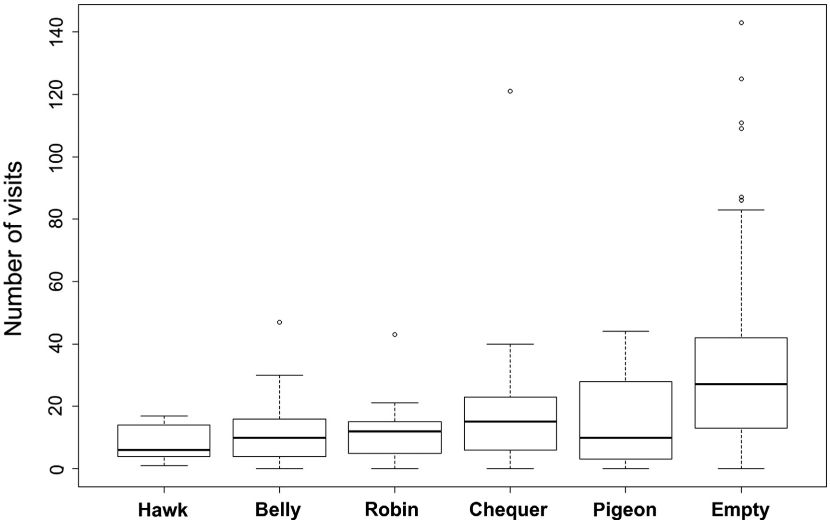


Fig. 3: The effect of the type of the dummy presented on the number of visits of blue tits at the feeder in the presence of particular dummies. Hawk – unmodified female of the European sparrowhawk (*Accipiter nisus*); belly – sparrowhawk deprived of the coloration of underparts; robin – sparrowhawk coloured as the European robin (*Erithacus rubecula*); chequer – sparrowhawk with artificial violet-white chequer coloration; pigeon – unmodified feral pigeon (*Columba livia f. domestica*); empty – no dummy was present. Number of the sets of trials in each group is 21; in the case of the empty control, the N is 105.

$t = 4.215$, $p < 0.001$; Fig. 3). The number of visits to the unmodified sparrowhawk was also lower than the number of visits to the chequered sparrowhawk (planned contrasts; $t = 3.111$, $p = 0.008$; Fig. 2), but did not differ from the number of visits to the plain-bellied sparrowhawk (planned contrasts; $t = 2.191$, $p = 0.138$; Fig. 2) or robin-coloured sparrowhawk (planned contrasts; $t = 2.611$, $p = 0.071$; Fig. 2).

Both tit species more commonly visited the feeder when there was snow cover (planned contrasts, $t = 8.259$, $p \ll 0.001$).

Discussion

The tits visited the feeder less when there was an unmodified sparrowhawk present. This result agrees with our previous study showing great tits in laboratory conditions responding to the textile dummy of the unmodified sparrowhawk with stress behaviour. The responses of great tits to both dummies for which the comparison can be made (unmodified sparrowhawk and sparrowhawk coloured like a robin) were similar in the laboratory and winter feeder conditions. This suggests that the low attendance of the feeder might be a result of fear.

Great tits showed similar passive avoidance in the presence of almost all of the modified sparrowhawks as in the presence of the unmodified sparrowhawk, the chequered sparrowhawk being the exception, which confirms our third hypothesis. Blue tits showed no less passive avoidance in the presence of almost all the modified sparrowhawks than in the presence of the unmodified sparrowhawk. The chequered sparrowhawk was again the exception.

Great tits had a generally lower feeder attendance than the blue tits in relation to most of the presented dummies (with the exception of the sparrowhawk with the violet-white chequered pattern). The reason for this behaviour may be explained in multiple ways, which all may be compatible. (1) Blue tits showed less neophobia towards modified dummies, which is unlikely, because blue tits are generally shown to be rather more neophobic than great tits (Veselý et al. 2006, 2013; Exnerová et al. 2007; Prokopová et al. 2010). (2) Blue tits are not able to identify the sparrowhawk in the robin and belly dummies, while, at the same time, they do not consider them to be harmless birds (probably because of the presence of recognizable raptor features). This would suggest different cognitive capacities for blue and great tits, which have never been documented (Healy & Krebs 1996; McGregor & Healy 1999; Lind et al. 2003). (3) The most probable explanation more likely resides in the differing motivation of the two species in visiting the feeder than in their recognition abilities. The great tit is the dominant species in winter flocks, while, by contrast, the blue tit appears to be interspecifically submissive (Ekman 1989; Haftorn 1993). The blue tits may therefore use the absence of great tits at the feeder when a predator is present and risk visiting the feeder. If we consider the perceptual abilities of both titmice species as equivalent, we may argue that both species perceive the modified dummies as strong generalizations of a sparrowhawk approximating the realistic-appearing sparrowhawk dummy (Stankowich & Coss 2007). Nevertheless, great tits are less likely to approach them.

All the presented modified dummies were unfamiliar to the tested tits, so that some level of neophobia towards them could be expected. In our experiments, we were not able to set apart the effect of fear when a sparrowhawk (raptor) is recognized and the effect of neophobia when a novel object is encountered. Nevertheless, neophobia is usually considered to be rather a short-term event (disappears within minutes – Marples & Kelly 1999), and tits in our experiments had 15 min to become accustomed to novel stimuli. Moreover, the level of feeder attendance significantly differed among dummies, according to the similarity to the unmodified sparrowhawk. No fear/neophobia response of tits was recorded towards the strangest dummy, the sparrowhawk with the chequered pattern, which also speaks against the presence of neophobia.

Our most interesting result is that without a doubt the equally less inhibited response of both species in approaching the sparrowhawk painted with a violet-white chequered pattern. This result can be explained by the existence of a general concept of a bird, which has been repeatedly documented to be formed in birds (Ghosh et al. 2004; Matsukawa et al. 2004; Shettleworth 2010; Cook et al. 2013). A violet-white chequer-coloured sparrowhawk obviously does not match this concept. This is why the raptor features present on this dummy do not elicit similar responses in tits as they do when present on other modified dummies.

An alternative explanation is based on the importance of the perception of the general shape of the predator. The lack of avoidance of the feeder during the presentation of the chequered dummy might be based on the visual disruption of continuously smooth sparrowhawk contours by the contrasting violet chequered diamonds. The importance of the figure shape was shown, for example, by Curio (1975). In his experiments, flycatchers gave a high rate of alarm calls to a simplified owl dummy without feathers and coloration (except for the eyes). They showed this response only after being primed by pre-exposure to a realistic owl model; nevertheless, this was not the case for the red-backed shrike dummy. The owl dummy obviously has a typical body shape useful in recognition. The conspicuous chequered pattern might have disrupted the general body contours and prevented its recognition as a sparrowhawk. This type of contour disruption has been numerously described in the literature (reviewed by Stevens et al. 2009). Thus, despite the presence of eyes and a beak, the general appearance of the chequered dummy would not likely appear as bird-like.

Both tits showed a high level of feeder avoidance in the presence of the sparrowhawk with the harmless robin coloration. This result suggests that dummies combining any real coloration with the presence of raptor/sparrowhawk features like the curved beak, conspicuous eyes, or long legs with talons are recognized as potentially dangerous. This result agrees with studies testing the effect of particular raptor features (Beránková et al. 2014, 2015). Moreover, the coloration of the robin might be mistaken for the coloration of an adult male sparrowhawk, having rusty to orange barred pattern on the breast (Mullarney et al. 1999). Neophobia could also have significantly affected the titmice responses to this dummy. Another possibility is that the orange colour was perceived as a warning signal, which has been demonstrated in blue and great tits in relation to their prey (Prokopová et al. 2010; Tesařová et al. 2013; Veselý et al. 2013; Cibulková et al. 2014); nevertheless, warning signals may also act in relation to avian predators (Götmark

1994). This might explain why, in a study involving great tits in laboratory conditions, the robin-coloured sparrowhawk was considered to be a threat while the pigeon-coloured sparrowhawk was not (Beránková et al. 2015). The coloration of a pigeon was probably recognized correctly and overwhelmed the presence of raptor beak, eye and talons in the experiments of Beránková et al. (2015).

Avoidance of the sparrowhawk dummy with the barred pattern on the underparts removed agrees with the results of Davies & Welbergen (2008). They showed that the presence of the barred belly pattern significantly increases the peril represented by a cuckoo or dove, but in case of the sparrowhawk, both forms, with and without the barred belly, elicited equal feeder avoidance in tits. This trait is obviously important but not essential for sparrowhawk recognition.

To sum up, our results showed that the ability of wild birds to recognize a predator is quite flexible. There are traits within the coloration, which can be important for the predator recognition; nevertheless, these are not essential and birds may take also other features into consideration. Recognition of two familiar real predators like sparrowhawk and kestrel is obviously enabled by details in the coloration (kestrel lacking the barred belly pattern); nevertheless, when faced to a novel predator (sparrowhawk without this barred pattern), it is too risky to behave the same way as when facing a harmless bird. Even when the coloration is completely changed, but provides some suspicious features (orange underparts), such a predator is treated as a threat. Only when the coloration is unfamiliar, such a predator is not recognized and treated as harmless.

Acknowledgements

We thank Killu Timm for help with data collection. We thank Christopher Mark Steer for his proof-reading services and two anonymous reviewers for their helpful comments. MB was funded by Grant Agency of the University of South Bohemia (151/2016/P). Experiments carried out in this research comply with the guidelines for the use of animals in research as published in Animal Behaviour and comply with the current laws of the Czech Republic. Authors are licensed for animal experimentation (Ministry of Agriculture, CZ 01629 and CZ 02766) and for conducting experiments with birds (Ministry of Education, Youth and Sports, licence no. 833/630/15). The authors declare that they have no conflict of interest.

Literature Cited

Amat, J. A. & Masero, J. A. 2004: Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Anim. Behav. **67**, 293—300.

Arnold, K., Pohlner, Y. & Zuberbuehler, K. 2008: A forest monkey's alarm call series to predator models. Behav. Ecol. Sociobiol. **62**, 549—559.

Ash, J. 1970: Observations on a decreasing population of red-backed shrikes. Br. Birds **63**, 185—205.

Beránková, J., Veselý, P., Sýkorová, J. & Fuchs, R. 2014: The role of key features in predator recognition by untrained birds. Anim. Cogn. **17**, 963—971.

Beránková, J., Veselý, P. & Fuchs, R. 2015: The role of body size in predator recognition by untrained birds. Behav. Process. **120**, 128—134.

Bujoczek, M. & Ciach, M. 2009: Seasonal changes in the avian diet of breeding sparrowhawks *Accipiter nisus*: how to fulfil the offspring's food demands? Zool. Stud. **48**, 215—222.

Caro, T. 2005: Antipredator Defenses in Birds and Mammals. The Univ. of Chicago Press, Chicago.

Cibulková, A., Veselý, P. & Fuchs, R. 2014: Importance of conspicuous colours in warning signals? The Great tit's (Parus major) point of view. Evol. Ecol. **28**, 427—439.

Cook, R. G., Wright, A. A. & Drachman, E. E. 2013: Categorization of birds, mammals, and chimeras by pigeons. Behav. Process. **93**, 98—110.

Curio, E. 1975: The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim. Behav. **23**, 1—115.

Davies, N. B. & Welbergen, J. A. 2008: Cuckoo–hawk mimicry? An experimental test. Proc. Biol. Sci. **275**, 1817—1822.

Ekman, J. 1989: Ecology of non-breeding social system of Parus. Wilson Bull. **101**, 263—288.

Exnerová, A., Štys, P., Fučíková, E., Veselá, S., Svádová, K., Prokopová, M., Jarošík, V., Fuchs, R. & Landová, E. 2007: Avoidance of aposematic prey in European tits (Paridae): learned or innate? Behav. Ecol. **18**, 148—156.

Ghosh, N., Lea, S. E. & Noury, M. 2004: Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. J. Exp. Anal. Behav. **82**, 125.

Götmark, F. 1994: Does a novel bright colour patch increase or decrease predation? Red wings reduce predation risk in European blackbirds. Proc. R. Soc. Lond. B **256**, 83—87.

Haftorn, S. 1993: Is the Coal Tit Parus-Ater Really the Most Subordinate of the Scandinavian Tits. Ornis Scandi. **24**, 335—338.

Healy, S. D. & Krebs, J. R. 1996: Food storing and the hippocampus in Paridae. Brain Behav. Evol. **47**, 195—199.

Hill, G. E. 1986: The function of distress calls given by tufted titmice (Parus bicolor). Anim. Behav. **34**, 590—598.

Hogstad, O. 2005: Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition. Ibis **147**, 375—380.

Krätzig, H. 1940: Untersuchungen zur Lebensweise des Moorschneehuhns (*Lagopus l. lagopus* L.) während der Jugendentwicklung. J. Ornit. **88**, 139—165. (in German).

Lind, J., Hollen, L., Smedberg, E., Svensson, U., Vallin, A. & Jakobsson, S. 2003: Detection distance influences escape behaviour in two parids, Parus major and P-caeruleus. J. Avian Biol. **34**, 233—236.

Lorenz, K. 1939: Vergleichende verhaltensforschung. Verhandlungen der Deutschen Zoologischen Gesellschaft Zoologischer Anzeiger, Supplementband **12**, 69—102.

Marples, N. M. & Kelly, D. J. 1999: Neophobia and dietary Conservatism: two distinct processes? Evol. Ecol. **13**, 641—653.

Matsukawa, A., Inoue, S. & Jitsumori, M. 2004: Pigeon's recognition of cartoons: effects of fragmentation, scrambling, and deletion of elements. Behav. Process. **65**, 25—34.

McGregor, A. & Healy, S. D. 1999: Spatial accuracy in food-storing and nonstoring birds. Anim. Behav. **58**, 727—734.

McLean, I. G. & Rhodes, G. 1991: Enemy Recognition and Response in Birds. Cur. Ornit. **8**, 173—211.

Mullarney, K., Svensson, L., Zetterström, D. & Grant, P. J. 1999: Bird guide: The Most Complete Field Guide to the Birds of Britain and Europe. HarperCollinsPublishers Ltd., London.

Němec, M., Syrová, M., Dokoupilová, L., Veselý, P., Šmilauer, P., Landová, E., Lišková, S. & Fuchs, R. 2015: Surface texture plays important role in predator recognition by Red-backed Shrikes in field experiment. Anim. Cogn. **18**, 259—268.

Prokopová, M., Veselý, P., Fuchs, R. & Zrzavý, J. 2010: The role of size and colour pattern in protection of developmental stages of the red firebug (*Pyrrhocoris apterus*) against avian predators. Biol. J. Lin. Soc. **100**, 890—898.

Scaife, M. 1976: The response to eye-like shapes by birds. I. The effect of context: a predator and a strange bird. Anim. Behav. **24**, 195—199.

Shettleworth, S. J. 2010: Cognition, Evolution and Behaviour, 2nd edn.. Oxford Univ. Press, Oxford, UK.

Stankowich, T. & Coss, R. G. 2007: The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. Proc. Biol. Sci. **274**, 175—182.

Stevens, M., Winney, I. S., Cantor, A. & Graham, J. 2009: Outline and surface disruption in animal camouflage. Proc. Biol. Sci. **276**, 781—786.

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.

Tesařová, M., Fric, Z., Veselý, P., Konvička, M. & Fuchs, R. 2013: European checkerspots (Melitaeini: Lepidoptera, Nymphalidae) are not aposematic – the point of view of great tits (Parus major). Ecol. Entomol. **38**, 155—163.

Trnka, A. & Grim, T. 2013: Color plumage polymorphism and predator mimicry in brood parasites. Front. Zool. **10**, 25.

Trnka, A., Prokop, P. & Grim, T. 2012: Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? PLoS One **7**, e37445.

Trnka, A., Trnka, M. & Grim, T. 2015: Do rufous common cuckoo females indeed mimic a predator? An experimental test. Biol. J. Lin. Soc. **116**, 134—143.

Tvardíková, K. & Fuchs, R. 2010: Tits use amodal completion in predator recognition: a field experiment. Anim. Cogn. **13**, 609—615.

Tvardíková, K. & Fuchs, R. 2011: Do birds behave according to risk assessment theory? A feeder experiment. Behav. Ecol. Sociobiol. **65**, 727—733.

Tvardíková, K. & Fuchs, R. 2012: Tits recognize the potential dangers of predators and harmless birds in feeder experiments. J. Ethol. **30**, 157—165.

Veselý, P., Veselá, S., Fuchs, R. & Zrzavý, J. 2006: Are gregarious red-black shieldbugs, Graphosoma lineatum (Hemiptera: Pentatomidae), really aposematic? An experimental approach. Evol. Ecol. Res. **8**, 881—890.

Veselý, P., Veselá, S. & Fuchs, R. 2013: The responses of Central European avian predators to an allopatric aposematic true bug. Ethol. Ecol. Evol. **25**, 275—288.

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. Anim. Cogn. **5**, 253—259.

Welbergen, J. A. & Davies, N. B. 2011: A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav. Ecol. **22**, 574—579.

Článek IX.

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.

Anim Cogn (2015) 18:259–268
DOI 10.1007/s10071-014-0796-2

ORIGINAL PAPER

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

Michal Němec · Michaela Syrová · Lenka Dokoupilová · Petr Veselý · Petr Šmilauer · Eva Landová · Silvie Lišková · Roman Fuchs

Received: 16 January 2014 / Revised: 29 July 2014 / Accepted: 30 July 2014 / Published online: 9 August 2014

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.

Keywords Anti-predator behaviour · Artificial dummies · Surface texture · Categorization · Recognition · Priming

M. Němec · M. Syrová (✉) · L. Dokoupilová · P. Veselý · P. Šmilauer · R. Fuchs
Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic
e-mail: syrova.michaela@seznam.cz

M. Syrová
Ethology Department, Institute of Animal Science, Prague, Czech Republic

E. Landová · S. Lišková
Faculty of Sciences, Charles University, Prague, Czech Republic

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. 2010), 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; Buitron 1983; Curio et al. 1983; Jacobsen and Ugelvik 1992; Clemmons and Lambrechts 1992; Rytkönen and Soppela 1995; Kleindorfer et al. 2005; Tvardíková and Fuchs 2011; Strnad et al. 2012; Nemec and Fuchs 2014). One way to study 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, b). 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, 1996, 1997; Katz and Cook 2000; Kelly and Cook 2003; Young et al. 2001) 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 1965), 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; Nemec 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 2008–2010.

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 and 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; Nemec 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 than 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 min, starting from the appearance of at least one parent. If neither parent appeared within 20 min, the trial was terminated and included in the dataset as a zero response. We used this approach because shrikes tend to visit the nest relatively rarely (the feeding frequency is 5–10 min) 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 min. The experimenter interrupted the experiment after 20 min. The time interval until the presentation of the next dummy was 1 h.

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.

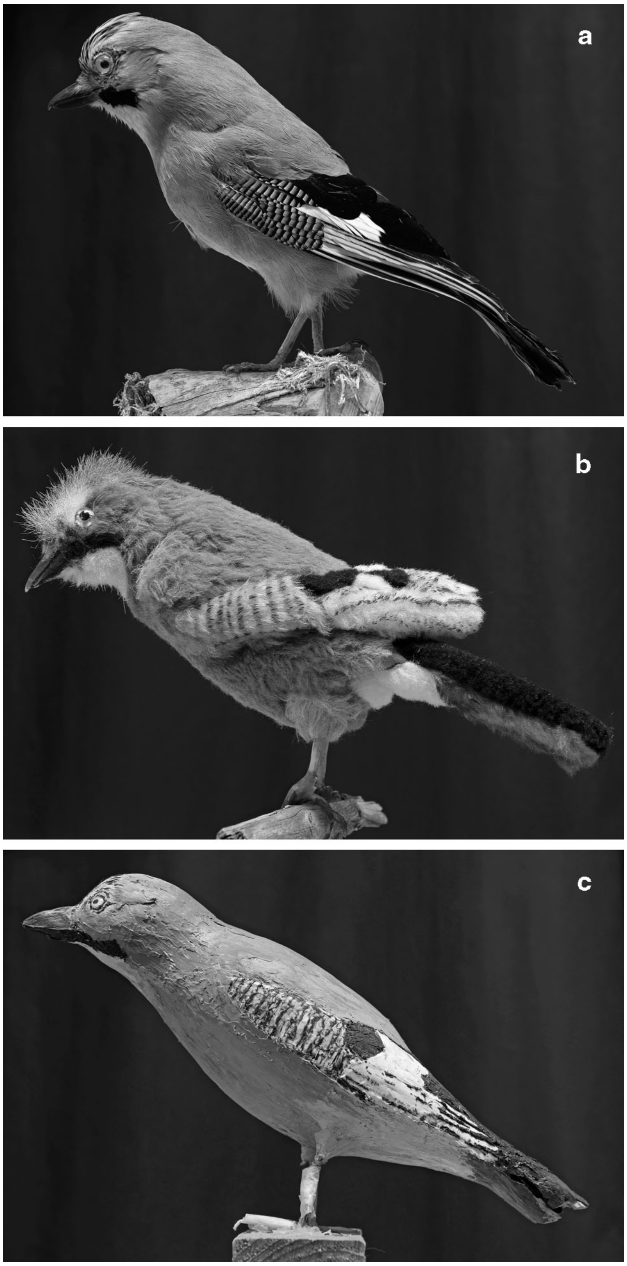


Fig. 1 Three dummy types of the Eurasian jay presented close to the red-backed shrikes' nests. **a** Stuffed dummy; **b** plush dummy; **c** silicone dummy

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.'s (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 in 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 min, scored dichotomously for each trial (0/1). Secondly, we used the number of attacks against the dummy performed during the 20 min. This variable was log-transformed [log (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 in the 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 X^2 or F test, respectively) were used to assess the effect of particular variables. The Tukey's HSD post hoc test (in case of normal data) or Fisher's LSD post hoc test (for binomial data) was 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 prespecified 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 ($X^2 = 15.94$, $df = 2$ and 126, $P < 0.001$; Fig. 2), by the sequence of the dummy ($X^2 = 10.18$, $df = 2$ and 126, $P = 0.006$, Fig. 2) and by the sex of the parent ($X^2 = 8.87$, $df = 1$ and 126, $P = 0.003$). The silicone dummy was attacked by fewer birds than the stuffed (Fisher's LSD post hoc test, $P < 0.001$) or the plush dummy (Fisher's LSD post hoc test, $P = 0.020$). Dummies were attacked by fewer birds in the first trial than in the second (Fisher's LSD post hoc test, $P = 0.033$) or than in the third trial (Fisher's LSD post hoc test, $P = 0.007$). More males than females attacked the presented dummies at least once.

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 silicon dummy (Tukey's HSD post hoc test:

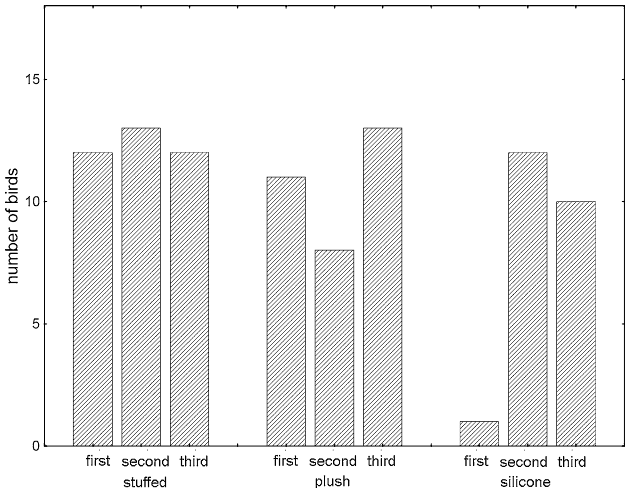


Fig. 2 Numbers of birds performing attacks against particular dummies, exposed in various order in the sequence

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; Table 1). There were no significant effects of sequence within the stuffed and plush dummies (Fig. 3; Table 1).

First attack latency

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

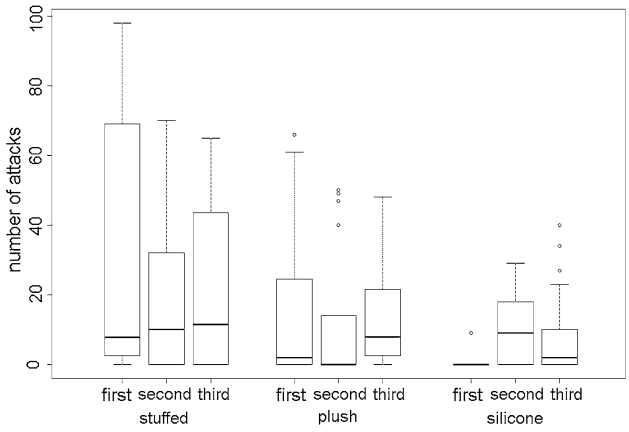


Fig. 3 Number of attacks performed by the red-backed shrikes against particular dummies, exposed in various order in the sequence. The *thick line* within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to upper quartile; the range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

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's HSD post hoc test: $z = 2.73$, $P = 0.017$) as well as than in the third trial (Tukey's 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 (Table 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 (1) significantly distinct in one dummy only (silicone throat or plush tail) or (2) quite similar among all dummies (back, neck, belly, moustaches). Only the colouration of the

Table 1 Results of multiple comparisons on the interaction terms for dummy type and the order of its exposure, using linear contrasts

	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.)

The statistic is followed by a parenthesized estimate of type I error

Table 2 Distances (ΔS) between particular spots on each dummy type based on the reflectance data in respect to the avian visual system

Body part	Comparison		
	Stuffed–plush	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

Presented units are dimensionless just noticeable differences. Values lower than 1 should not be recognizable for birds under optimal light conditions stuffed and silicone tail should not be recognizable by birds according to statistical significance within the avian visual model (see Table 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.

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, 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

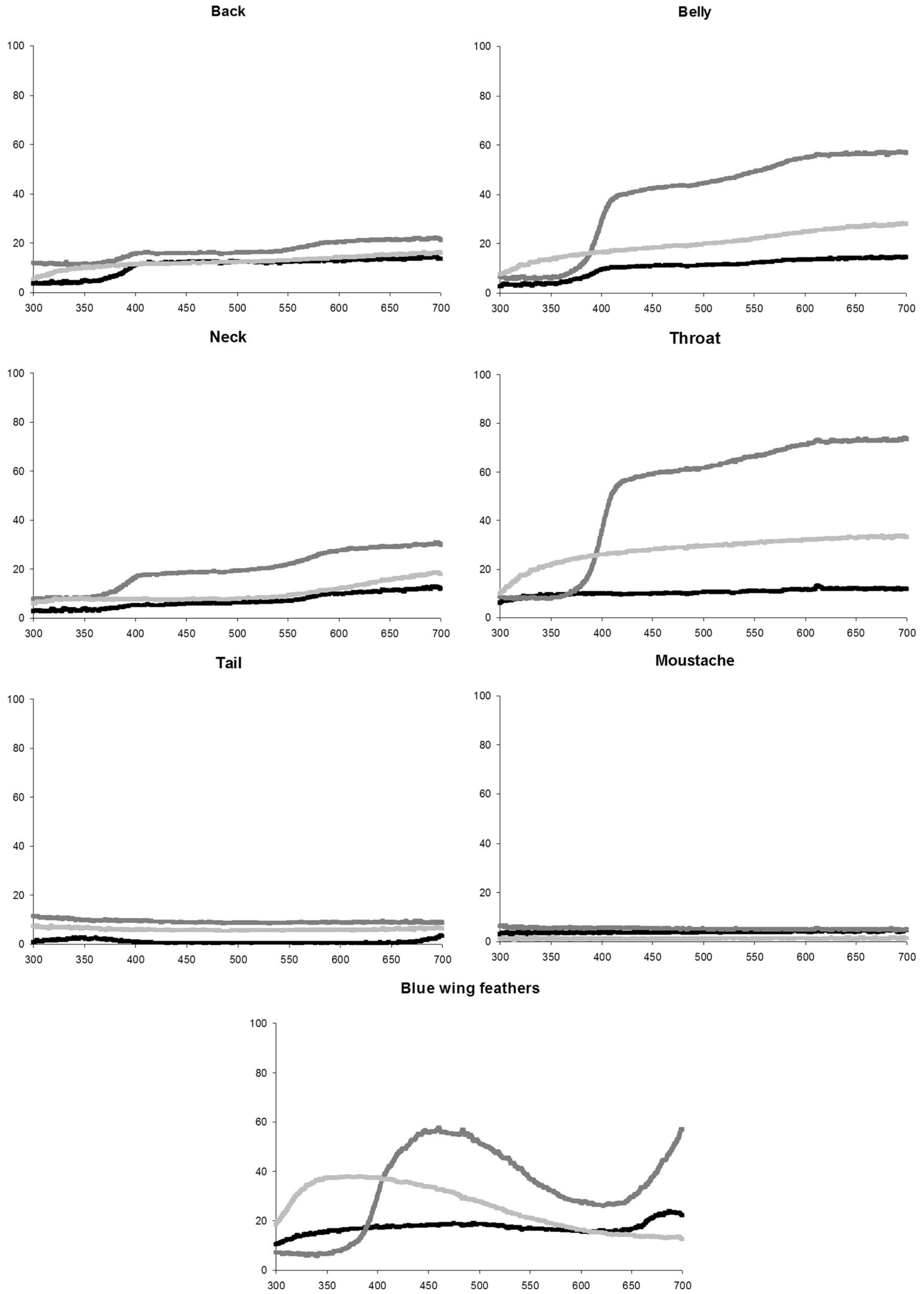


Fig. 4 Average spectral reflectance (mean of five independent measurements on each body part) of seven body parts on each dummy type as depicted in Fig. 1. One hundred percent of reflectance is defined as the light reflected from ‘white standard’ (WS-2, Ocean Optics). *Light grey line* refers to the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

of sensitization 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 (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 categorization of ecologically relevant objects by wild nontrained birds in the field.

Acknowledgments We would like to thank the Academy of Sciences of the Czech Republic (IAA601410803), the Czech Science Foundation (206/08/H044), and the Grant Agency of the University of South Bohemia (04-142/2010/P and 144/2010/100) for their financial support. We also thank the Hradiště Military Regional Office for allowing us to conduct experiments within their training area. Special thanks also to Martin Strnad for help in the field, Petr Kos and Corey Stringer from North Carolina, USA, for a linguistic revision of the manuscript, and to Simona Poláková for consultations.

Conflict of interest The authors declare they have no conflict of interest.

Ethical standard 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).

References

Arroyo B, Mougeot F, Bretagnolle V (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). Behav Ecol Sociobiol 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. Anim Learn Behav 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. J Exp Psychol Anim B 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 Res 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. Behav Process 93:50–61. doi:10.1016/j.beproc.2012.08.005

Blough PM (1989) Attentional priming and visual search in pigeons. J Exp Psychol Anim B 15:358–365. doi:10.1037/0097-7403.15.4.358

Blough PM (1991) Selective attention and search images in pigeons. J Exp Psychol Anim B 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. Anim Learn Behav 20:293–300. doi:10.3758/BF03213383

Blumstein DT (2006) The multipredator hypothesis and the evolutionary persistence of antipredator behaviour. Ethology 112:209–217

Bovet D, Vauclair J (2000) Picture recognition in animals and humans. Behav Brain Res 109:143–165. doi:10.1016/S0166-4328(00)00146-7

Brodbeck DR (1997) Picture fragment completion: priming in the pigeon. J Exp Psychol Anim B 23:461–468

Brown GE, Ferrari MCO, Malka PH, Russo S, Tressider M, Chivers DP (2011) Generalization of predators and non-predators by juvenile rainbow trout: learning what is and what is not a threat. Anim Behav 81:1249–1256

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, Chicago

Clemmons JR, Lambrechts MM (1992) The waving display and other nest site antipredatory behaviour of the black-capped chickadee. Wilson Bull 104:749–756

Cook RG (1992a) Dimensional organization and texture discrimination in pigeons. J Exp Psychol-Anim Behav Proc 18:354–363

Cook RG (1992b) Acquisition and transfer of visual texture discriminations in pigeons. J Exp Psychol-Anim Behav Proc 18:341–353

Cook RG (1993) The experimental analysis of cognition in animals. Psychol Sci 4:174–178

Cook RG, Cavoto KK, Cavoto BR (1995) Same-different texture discrimination and concept learning by pigeons. J Exp Psychol-Anim Behav Proc 21:253–260

Cook RG, Cavoto KK, Cavoto BR (1996) Mechanisms of multidimensional grouping, fusion and search in avian texture discrimination. Anim Learn Behav 24:150–167

Cook RG, Cavoto BR, Katz JS, Cavoto KK (1997) Pigeon perception and discrimination of rapidly changing texture stimuli. J Exp Psychol-Anim Behav Proc 23:390–400

Curio E, Klump G, Regelmann 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 Pigeons Perspective. P Roy Soc Lond B Bio 251:195–200

Dukas R (1998) Cognitive ecology: the evolutionary ecology of information processing and decision making. University of Chicago Press, Chicago

Dukas R, Kamil AC (2001) Limited attention: the constraint underlying search image. Behav Ecol 12:192–199. doi:10.1093/beheco/12.2.192

Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, New York

Ferrari MCO, Gonzalo A, Messier F, Chivers DP (2007) Generalization of learned predator recognition: an experimental test and framework for future studies. Proc Roy Soc B 274:1853–1859. doi:10.1098/rspb.2007.0297

Ferrari MCO, Brown GE, Messier F, Chivers DP (2009) Threat-sensitive generalization of predator recognition by larval amphibians. Behav Ecol Sociobiol 63:1369–1375. doi:10.1007/s00265-009-0779-5

Friedman A, Spetch ML, Lank I (2003) An automated apparatus for presenting depth-rotated three-dimensional objects in human and animal object recognition research. Behav Res Meth Ins C 35:343–349. doi:10.3758/BF03202563

Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. Anim Behav 62:577–589. doi:10.1006/anbe.2001.1781

Hart NS, Partridge JC, Cuthill IC, Bennett ATD (2000) Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus*) and the blackbird (*Turdus merula*). J Comp Physiol A 186:375–387

Hartley P (1950) An experimental analysis of interspecific recognition. Symp Soc Exp Biol 4:313–336

Jacobsen OW, Ugelvik M (1992) Antipredator behaviour of breeding Eurasian wigeon. J Field Ornit 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, Tokyo, pp 269–293

Katz JS, Cook RG (2000) Stimulus repetition effects on texture-based visual search by pigeon. J Exp Psychol Anim Behav Process 26:220–236

Kelly DM, Cook RG (2003) Differential effects of visual context on pattern discrimination by pigeons (*Columba livia*) and humans (*Homo sapiens*). J Comp Psychol 117:200–208

Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. Anim Behav 69:307–313

Knight R, Temple S (1988) Nest-defense behavior in the red-winged blackbird. Condor 90:193–200

Krätzig H (1940) Untersuchungen zur Lebensweise des Moorschneehuhns, Lagopus l. Lagopus, während der Jugendentwicklung. Jour für Ornith 88:139–166

Kullberg C, Lind J (2002) An experimental study of predator recognition in great tit fledglings. Ethology 108:429–441

Lack D (1965) The life of the robin. Collins, London

Langley CM, Riley DA, Bond AB, Goel N (1996) Visual search for natural grains in pigeons (*Columba livia*): search images and selective attention. J Exp Psychol Anim Behav 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 Behav 6:34–40

Lorenz K (1940) Vergleichende Verhaltensforschung. Verh deutsch Zool Gesellsch 1939:69–102

Maia R, Eliason CM, Bitton PP, Doucet SM, Shawkey MD (2013) pavo: an R Package for the analysis, visualization and organization of spectral data. Methods Ecol Evol 4:906–913. doi:10.1111/2041-210X.12069

Němec M, Fuchs R (2014) Nest defense of the red-backed shrike *Lanius collurio* against five corvid species. Acta Ethol 1–6. 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. Anim Cogn 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. Behav Ecol Sociobiol 7:227–231

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

Rytkönen S, Soppela M (1995) Vicinity of sparrowhawk nest affects willow tit nest defense. Condor 97:1074–1078

Shettleworth SJ (1993) Where is the comparison in comparative cognition? Alternative research programs. Psychol Sci 4:179–184. doi:10.1111/j.1467-9280.1993.tb00484.x

Shettleworth SJ (2010) Cognition, evolution, and behavior, 2nd edn. Oxford University Press, New York

Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K (2004) Interspecific and intraspecific views of color signals in the strawberry poison frog Dendrobates pumillo. J Exp Biol 207:2471–2485

Spetch ML, Friedman A (2006) Comparative cognition of object recognition. Comp Cogn Behav Rev 1:12–35

Stankowich T, Coss RG (2007) The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. Proc Roy Soc B 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 Bull 60:6–51

Troje NF, Huber L, Loidolt M et al (1999) Categorical learning in pigeons: the role of texture and shape in complex static stimuli. Vision Res 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. J Ethol 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 Ornithol 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. Anim Cogn 13:609–615. doi:10.1007/s10071-010-0311-3

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 (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

Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. Proc Roy Soc Lon B 265:351–358

Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill C (1998) Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol A 183:621–633

Wasserman EA, Zentall TR (2009) Comparative cognition: experimental explorations of animal intelligence. Oxford University Press, New York

Webb JK, Pike DA, Shine R (2010) Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. Behav Ecol 21:72–77

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. Anim Learn Behav 29:97–106. doi:10.3758/BF03192819

Zentall TR, Wasserman EA, Lazareva OF, Thompson RKR, Rattermann MJ (2008) Concept learning in animals. Comp Cogn Behav Rev. doi:10.3819/ccbr.2008.30002

Článek X.

Tvardíková K., Fuchs R. (2010): Tits use amodal completion in predator recognition: a field experiment. Animal Cognition 13: 609-615.

Anim Cogn (2010) 13:609–615
DOI 10.1007/s10071-010-0311-3

ORIGINAL PAPER

Tits use amodal completion in predator recognition: a field experiment

Kateřina Tvardíková · Roman Fuchs

Received: 16 November 2009 / Revised: 9 January 2010 / Accepted: 14 January 2010 / Published online: 4 February 2010

Abstract Amodal completion enables an animal to perceive partly concealed objects as an entirety, and to interact with them appropriately. Several studies, based upon either operant conditioning or filial imprinting techniques, have shown that various animals (both mammals and birds) can perform amodal completion. Before this study, the use of amodal completion by untrained animals in the recognition of objects had not been considered. Using two feeders, we observed in a field experiment the reaction of tits to the torso of a sparrowhawk (partly occluded or an 'amputated' dummy) in two different treatments (sparrowhawk torso vs. complete dummy pigeon; and torso vs. complete dummy sparrowhawk). It is clear that the birds considered the two torso variants as predators and kept away from both of them when the second feeder offered a 'pigeon' instead. On the other hand, when a 'complete sparrowhawk' was present on the second feeder, the number of visits to the occluded torso remained low; while the number of visits to the amputated one increased threefold. Birds risked perching near what was clearly an amputated torso; while the fear of a "hiding" (occluded) torso remained unchanged, when the second feeder did not provide a safe alternative. Such discrimination between torsos requires the ability for amodal completion. Our results demonstrate that in their recognition process, the birds not only use simple sign stimuli, but also complex cognitive functions.

Keywords Occluded predator · Amputated predator · Amodal completion · Sign stimuli · Pair-wise experiments · Feeders · Winter · Sparrowhawk · Accipiter nisus · Tit species

Introduction

In the three-dimensional natural environment, objects frequently occlude portions of themselves, as well as other objects. Humans seem to have little difficulty recognizing a person who is sitting in a car or standing behind a counter, and casual observations suggest that animals can do the same (Vallortigara 2006). For example, a chick can recognize the mother hen even if it is partially hidden in the grass (Vallortigara 2004).

This adaptive ability is the phenomenon called amodal completion: the cognitive completion of an object that remains partially hidden behind another (Kanizsa et al. 1993). However, it is possible to recognize a partially occluded object without perceiving it as complete (Lazareva et al. 2007). Several studies have shown that mammals (mice: Kanizsa et al. 1993; rhesus macaques: Bakin et al. 2000; Fujita 2001; baboons: Deruelle et al. 2000, Fagot et al. 2006; squirrel monkeys: Nagasaka and Osada 2000; Japanese macaques: Sugita 1999; and chimpanzees: Sato et al. 1997) all can perform amodal completion.

Evidence for amodal completion has also been obtained in some species of birds. Chicks clearly recognized a triangle when faced with a partly occluded triangle, but could not recognize an amputated one (Regolin and Vallortigara 1995; Lea et al. 1996). This confirmed that chicks perceive object uniformity soon after hatching. Similarly, adult hens had the ability for recognition of overlapping squares and circles (Forkman 1998) or chromatically homogenous overlapping figures (Vallortigara and Tommasi 2001).

K. Tvardíková (✉) · R. Fuchs
Department of Zoology, Faculty of Biological Science,
University of South Bohemia, Branišovská 31,
370 05 České Budějovice, Czech Republic
e-mail: katerinatvardikova@seznam.cz

The evidence surrounding amodal completion in pigeons (the most studied species) is equivocal. Some findings seem to indicate that pigeons can compensate for an incomplete image (Watanabe 1999; Aust and Huber 2006). However, there are many other experiments suggesting that they are not able to perceive the unity and coherence of partly occluded objects. Watanabe and Furuya (1997) concluded that birds did not see the hidden figure in a video image. This finding was supported by the work of Fujita (2001) and Sekuler et al. (1996). By contrast, Lazareva et al. (2007) and DiPietro et al. (2002) suggest that pigeons can recognize partially occluded objects without amodal completion if they are given sufficient training.

Inappropriate stimuli may cause those biases. More ecologically valid objects and setting might better trigger the bird's ability to perceptual complete occluded items, as shows the work on courtship displays of Bengalese finches (Okanoya and Takahashi 2000). Most prior studies dealing with amodal completion in animals have been based upon operant techniques (Vallortigara 2006). The animals were trained to respond to a complete object (typically a geometric shape) (Vallortigara 2006), and then were tested as to whether they recognized the object in its amputated and occluded versions (Fig. 1). If the animal's responses suggested that only partially occluded objects looked to them like a complete object, it was considered that they were aware of the continuance of the object behind the obstruction.

Prior to this study, the possible use of amodal completion by untrained animals in their recognition of natural objects (e.g. animals) had been studied only exceptionally (Okanoya and Takahashi 2000). We designed an experiment in which an unambiguous recognition reaction of the experimental animals could be measured. The recognition of predators was one possibility. The ability of birds to recognize and discriminate predator dummies has been shown in many studies (for review, see Caro 2005); therefore these stimuli could be used for the amodal completion research. Experiments at a feeder have proven to be an effective tool to test a bird's ability in the discrimination of predator dummies in the field (Gentle and Gosler 2001; Desrochers et al. 2002; MacLeod et al. 2005). If a predator is recognized in the surroundings adjacent to the feeder, birds do not come near and prefer to stay within the cover provided in the environs without food intake. The more dangerous the predator, the stronger is this response.

In this paper, we report on the ability of tits (Paridae) for the visual completion of the upper half of an avian predator (Accipiter nisus). We observed the numbers of arrivals to a pair of feeders. On one of the pair, either an occluded or amputated sparrowhawk dummy was installed; the other paired experimental feeder was provided with either a dummy of a sparrowhawk or a harmless pigeon.

We set out to test two hypotheses: (1) If the number of arrivals between the amputated or occluded sparrowhawk

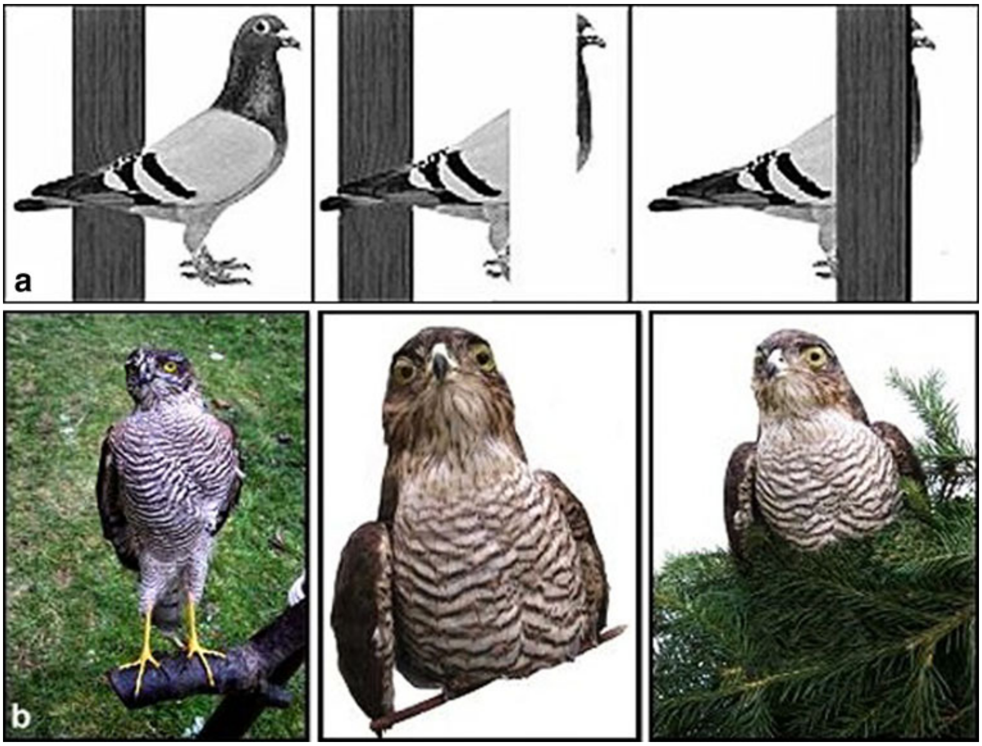


Fig. 1 **a** Complete, amputated, and occluded pigeon (according to Aust and Huber 2006). **b** Dummies used in this experiment: complete, amputated, and occluded sparrowhawk

would likely differ, when a pigeon was presented on the alternate feeder. Ethologists have long assumed that sign stimuli, alone, functioned for the recognition of both predators and sexual partners (e.g. Tinbergen 1951; Chantrey and Workman 1984; Carbaugh et al. 1962; Schein and Hale 1957; Shoettle and Schein 1959). Therefore, we assumed that the birds would recognize a sparrowhawk with both torso alternatives (occluded and amputated); yet give priority to the perceived safer alternate feeder. (2) If the number of arrivals to an amputated sparrowhawk would be higher than to an occluded sparrowhawk, when a complete sparrowhawk was present on the alternate feeder. We assumed that the birds attempt and prefer to avoid any alternative feeder that is perceived as dangerous. Nevertheless, they will risk arrivals near an amputated (incomplete) sparrowhawk on the experimental feeder, in preference to one with an occluded sparrowhawk (thus perceived as continuing behind the obstruction, and perceived as being as/almost as dangerous as a complete sparrowhawk).

Methods

Experimental site and species

The experiment was done during the winter of 2007/2008 in an area of broad-leaved trees growing near the village of Chodská Lhota (49°21′15″, 30°47′25″), Czech Republic. The site is 640 m above sea level and is located in a comparatively cold portion of Bohemia. The winter of 2007/2008 was quite a severe one. We studied three species of tits that predominated on the feeders: the great tit (Parus major), the blue tit (Cyanistes caeruleus), and the “marsh” tit. The “marsh” tits were represented by two species: the marsh tit (Poecile palustris) and the willow tit (Poecile montanus). As these two species are indistinguishable on videotape, they were lumped together as one species.

Experimental design

The feeders were established in a small clearing, surrounded by mixed deciduous woodland and scrubland. The shortest distance from feeder to cover was ca. 4 m. The two feeders were 25 m apart, and the space between the feeders was free of trees. The feeders were surrounded by shrubs and trees on three sides. These served as both a shelter and surveillance position for the birds. The feeders were boards (45 cm by 45 cm) lying upon the ground, with raised edges to avoid food scattering. Between the experiments, the feeders were covered with a roof. Sunflower seeds were used as the food. To attract the birds, before the first experimental series the feeders were filled with sunflower seeds for 4 weeks. Any remaining sunflower seeds were attentively removed and replaced with grated walnuts just before the trials. The grated walnuts were used because they required the birds to remain longer at the feeder (Desrochers et al. 2002). As the tits were not able to carry the grated walnuts away to consume them in the surrounding cover, they had to stay on the feeder longer in order to obtain a sufficient food intake.

Stuffed models were used as both the test sparrowhawk and pigeon. They were placed on a 75-cm-high stake on the outer right corner of the feeder (as seen from the camera), and always faced toward the center of the feeder. Throughout the paper, we have used the terms occluded (for the upper torso hidden in the shrubs) and amputated (for only the upper torso on the perch) sparrowhawks. Either an amputated or occluded sparrowhawk model was tested on the experimental feeder, juxtaposed to a complete pigeon or a sparrowhawk on the alternate feeder. Two empty feeders were used in the last tested trial (as a reference control) and it always preceded two experimental trials. This amounted to four different trials in one series: two experimental (amputated/occluded sparrowhawk vs. sparrowhawk, amputated/occluded sparrowhawk vs. pigeon) and two reference controls. The reference control trials had fixed positions within the series (the 1st and 4th trials). The sequence of the dummy pairs (experimental trials) within each series was randomly arranged. Additionally, the placement of a dummy (on the left or the right feeder) was randomly arranged within a trial.

Each experimental day started 1 h after daybreak. Individual trials lasted 30 min, and the experimental feeders were videotaped continuously throughout the duration of the experiments. The camera was set up in a fixed position, facing the experimental feeder, at a distance of 8 m. Snow cover and temperature were noted for each experimental day. Between each series, there was usually a 6 or 7 days pause. Thirteen series were conducted during the winter of 2007/2008, amounting to a total of 78 half-hours of trials, from which a total of 14,672 tit visits were analyzed.

In this study, the birds additionally were trapped using mist-nests, in order to reveal the rate of pseudo replications. The experiment was designed so that the trapping level was constant (about 50 birds were ringed per day) throughout the study. Mist-nets were used 1 day before each series. A total of 568 birds were ringed during the winter. Each trapped individual bird was fitted with a standard metal leg-ring with a unique number. Additionally, an individual combination of color-rings was then fitted under license (Czech Bird Ring Association, #1062). Each bird was thus uniquely identifiable on the videotape.

Statistical calculations showed that of those birds which were ringed during individual mist-nettings (approximately 50 birds) 51.23 ± 2.55% ($X \pm$ SD) returned to the feeder

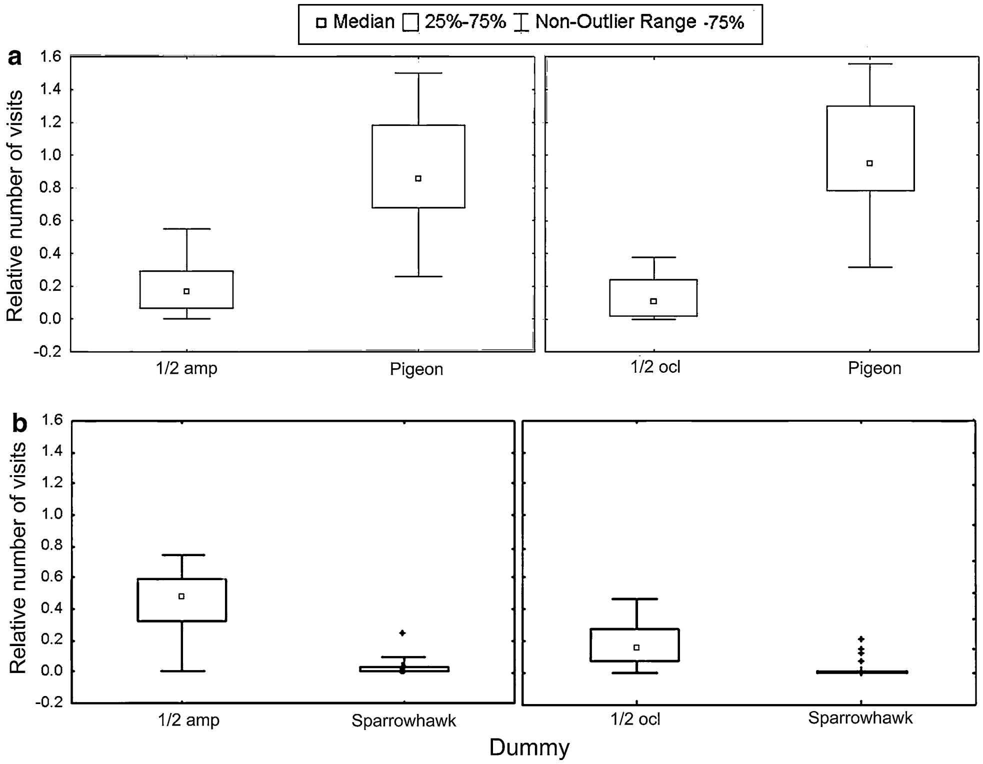


Fig. 2 **a** Relative number (compared to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with a pigeon on the alternate feeder. **b** Relative number (compared to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with a sparrowhawk (sp. hawk) on the alternate feeder

1 day after ringing. Only 37.33 ± 2.09% ($X \pm$ SD) of these stayed onto be in the next experiment (8 days later), and 18.51 ± 5.2% ($X \pm$ SD) stayed through the third experiment (15 days later). Less than 1.61 ± 0.7% ($X \pm$ SD) of the ringed birds appeared 4 weeks later. The average individual bird usually visited the feeder in 1.26 ± 0.51 ($X \pm$ SD) trials (3 trials, at most) during one series. Once a bird appearing for the first time in the trial, on average they arrived at the feeder 1.93 ± 1.08 ($X \pm$ SD) times.

Statistical analysis

During the trials, the numbers of individual visits of tit species to the experimental feeders with the sparrowhawk torsos were analyzed. To remove the effects of a fluctuating pool of tits in the study area during the winter, we calculated the relative number of visits (the number of visits at the experimental feeder; the mean number of visits at one control feeder). The arithmetic means of the visits at both control feeders were used, because the number of arrivals to left and right feeders did not differ (One-way Anova: $F_{1,12} = 0.14$, $P = 0.713$).

The following explanatory variables were used: dummy combination (amputated sparrowhawk vs. complete pigeon, occluded sparrowhawk vs. pigeon, amputated sparrowhawk vs. complete sparrowhawk, and occluded sparrowhawk vs. complete sparrowhawk); the sequence of the series (1–13); tit species (only interactions between dummy and species were important); temperature (°C); and snow cover (cm). GLMM was constructed; the data had a normal distribution, and the link function identity was used. The Tukey post hoc test in R (Hothorn et al. 2008) was performed in multcomp package of R software (R Development Core Team 2008), for the variable dummy combination.

Non parametric tests (Wilcoxon) were used when the data did not reach normality, and when appropriate. These statistical calculations (and all graphs) were made using STATISTICA 8 for Windows (Statsoft Inc. 2007).

Results

Both sparrowhawk torso variants decreased the number of visits, when compared to the pigeon being present on the alternate feeder. (Wilcoxon test, relative number of visits; occluded: $T = 75$, $N = 36$, $P < 0.001$, amputated: $T = 107$, $N = 36$, $P = 0.001$, Fig. 2a). On the other hand, both sparrowhawk torso variants had less of an effect on the number of visits than did a complete sparrowhawk presented on the alternate feeder (Wilcoxon test, relative number of visits; occluded: $T = 4$, $N = 36$, $P < 0.001$, amputated: $T = 0$, $N = 36$, $P < 0.001$, Fig. 2b).

The combination of which dummies were presented on the two feeders significantly affected the relative number of arrivals to the feeder. No significant effects were found for snow layer, temperature, series sequence, or the interaction between dummy and the tit species (Table 1).

Table 1 Effects of the dummies, weather, and experimental design on the relative changes in the number of visits to a feeder

	Df	*F*	*P*
Dummy comb.	1	13.18	<0.001
Temperature	1	2.42	0.102
Snow layer	1	0.95	0.332
Series	1	0.09	0.758
Dummy: species	2	0.37	0.693

Error *Df* = 135

The results of GLM show *Df*, *F* and *P* values for each predictor and some interactions (see "Methods")

The Tukey post hoc test shows that the difference between the two torsos was only significant in those treatments when a complete sparrowhawk was on the alternate feeder (sparrowhawk as alternate dummy: $P < 0.001$; pigeon as alternate dummy: $P = 0.849$). The relative number of visits to the occluded torso did not differ between treatments with a sparrowhawk, and a pigeon as the alternate dummy ($P = 0.850$); whereas the relative number of visits to the amputated torso was higher in those treatments with a sparrowhawk vs. one with a pigeon ($P < 0.001$) on the alternate feeder (Fig. 3).

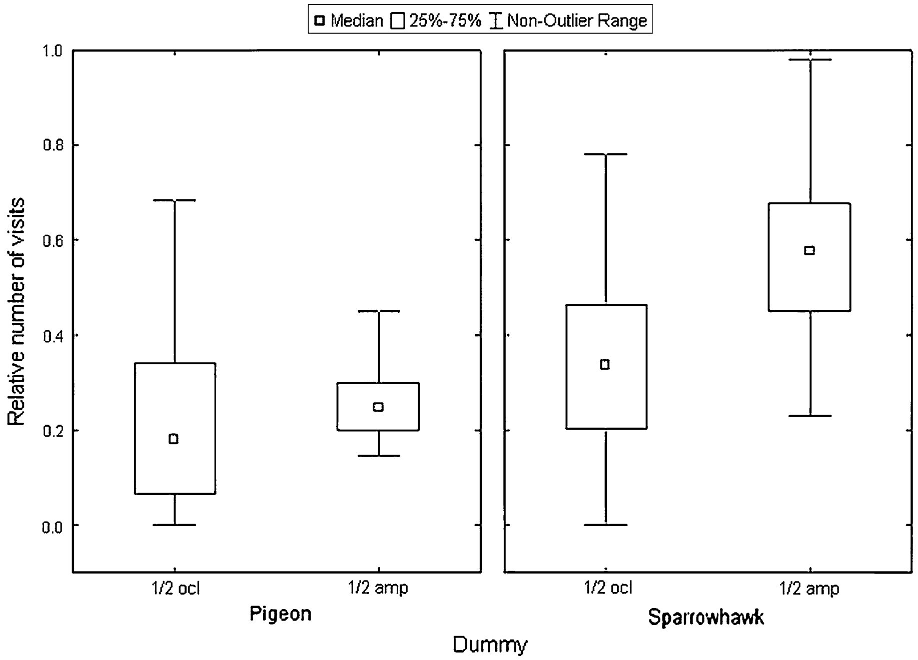
Discussion

The tits recognized both of the sparrowhawk torsos (amputated, as well as occluded), as the decrease in the number of visits did not differ for either of the torso treatments with a pigeon on the alternate feeder. This could well be interpreted as the tits not using amodal completion, but that instead they recognize a predator according to sign stimuli (i.e. on the head region it could be eyebrow stripe, hooked bill, and yellow eye), and thus keep away. However, in those treatments with a complete sparrowhawk on the alternate feeder, the relative numbers of visits to an amputated sparrowhawk increased intensively; up to nearly 100% of the reference controls in some trials.

This should be interpreted as the tits recognizing a predator in both torso variants; however, only the occluded one is perceived as "fully-featured". On the other hand, the amputated torso is perceived as "partly-featured". The birds keep away from both torsos when a safe choice (pigeon) at the alternate feeder exists. Nonetheless, when the alternate feeder offers only a dangerous complete sparrowhawk, they risked visiting the "partly-featured" amputated torso; while the fear of a "full-featured" occluded one remained unchanged. This kind of discrimination requires the ability for amodal completion. The birds seem to be sentient that the occluded sparrowhawk continues behind the branches, while an amputated sparrowhawk is clearly recognized as being incomplete.

The interesting result of our study was that the birds arrived near the occluded sparrowhawk dummy more often than to the complete sparrowhawk dummy. There may be some birds that do not recognize an occluded torso as a predator. This could be due to either limited experience (e.g. of young birds) or a lack of attentiveness. Sometimes when a bird landed at the feeder and was pecking at the food, it suddenly looked as if horrified and emitted an alarm call, as though it had seen the predator too late. A possible alternative explanation could be that a bird is more likely to approach a

Fig. 3 Relative change in the number of visits (compared to control trial) to a feeder with the occluded (1/2 ocl) and amputated (1/2 amp) sparrowhawk when a pigeon or sparrowhawk are present on the alternate feeder



predator which has some occluding obstacle in front of it, in preference to a predator which has no obstacle blocking it, which could attack straight toward the potential prey.

Study of the occlusion phenomena has been extended from infants onto nonhuman species, and has become a popular topic in the last few decades. All of these groups of animals were trained to discriminate between various occluded and amputated objects (see reviews Vallortigara 2006 and Vallortigara 2006). Only occasionally, courtship behaviour to amputated or occluded con-specific female was studied (e.g. Okanoya and Takahashi 2000). The results of our study demonstrate, for the first time, that amodal completion is used as a part of object recognition in the natural discrimination and categorization processes of birds.

In particular, several comparative studies, using operant techniques, on amodal completion with birds have yielded inconsistent results. These operant technique studies have shown that domestic fowl can perceive amodal completion (Regolin and Vallortigara 1995; Lea et al. 1996; Forkman 1998; Forkman and Vallortigara 1999; Vallortigara and Tommasi 2001; Regolin et al. 2004). Conversely, other studies have not yielded any clear evidence that the pigeons can perceive amodal completion to distinguish between occluded and amputated objects (Cerella 1980; Fujita 2001; Sekuler et al. 1996; Ushitani and Fujita 2005; Aust and Huber 2006). In spite of this, previous results have been dismissed by the mounting evidence that pigeons can perceive partly occluded objects as complete, under the appropriate testing conditions (Nagasaka et al. 2005; Nagasaka et al. 2007), especially if the stimuli looks more natural (DiPietro et al. 2002; Nagasaka and Wasserman 2008). Generally, pigeons appear to be able respond to amodal completion or to subjective contours (closely linked to amodal completion) but only if they are strongly encouraged to do it so (Vallortigara 2006).

The results of our study show that field experiments, in which the predicted reactions (e.g. escape) of birds to real objects (e.g. predators) can be used as a suitable alternative for conditioning techniques. At the same time, our results show that discrimination and categorization in nature are not a simple process, and that amodal completion is only a part of that process. Birds recognize predators according to sign stimuli. Therefore, both occluded and amputated torsos of a predator are judged as dangerous; and incompleteness (with concomitant lesser danger sensed) of an amputated torso only appears in the situation where it is compared with a complete predator by the bird. Such complexity in the recognition processes should be taken into account even in conditioning experiments.

Acknowledgments The study was supported by grants of the Academy of Sciences of the Czech Republic (IAA601410803), and the Ministry of Education, Youth, and Sports (MSM6007665801).

References

Aust U, Huber L (2006) Does the use of natural stimuli facilitate amodal completion in pigeons? Perception 35:333–349. doi:10.1068/p5233

Bakin JS, Nakayama K, Gilbert CD (2000) Visual responses in monkeys areas V1 and V2 to three-dimensional surface configurations. J Neurosci 1(20–21):8188–8198

Carbaugh BT, Schein MW, Hale EB (1962) Effects of morphological variations of chicken models on sexual responses of cocks. Anim Behav 10(3–4):235–238. doi:10.1016/0003-3472(62)90046-5

Caro TM (2005) Antipredator defences in birds and mammals. The University of Chicago Press, London, p 591

Cerella J (1980) The pigeon's analysis of pictures. Pattern Recogn 12:1–6. doi:10.1016/0031-3203(80)90048-5

Chantrey DF, Workman L (1984) Song and plumage affects on aggressive display by the European Robin *Erithracus rubecula*. Ibis 126:366–371

Deruelle C, Barbet I, Dépy D, Fagot J (2000) Perception of partly occluded figures by baboons (*Papio papio*). Perception 39:1483–1497

Desrochers A, Belisle M, Bourque J (2002) Do mobbing calls affect the perception of predation risk by forest birds? Anim Behav 64:709–714. doi:10.1006/anbe.2002.4013

DiPietro NT, Wasserman EA, Young ME (2002) Effects of occlusion on pigeon's visual object recognition. Perception 31:1299–1312

Fagot J, Barbet I, Parron C, Deruelle C (2006) Amodal completion by baboons (*Papio papio*): contribution of background depth cues. Primates 47(2):145–150. doi:10.1007/s10329-005-0165-5

Forkman B (1998) Hens use occlusion to judge depth in two-dimensional picture. Perception 27:861–867. doi:10.1068/p270861

Forkman B, Vallortigara G (1999) Minimization of modal contours: an essential cross-species strategy in disambiguating relative depth. Anim Cogn 2:181–185. doi:10.1007/s100710050038

Fujita K (2001) Perceptual completion in rhesus monkeys (*Macaca mulatta*) and pigeons (*Columba livia*). Percept Psychophys 63:115–125

Gentle LK, Gosler AG (2001) Fat reserves and perceived predation risk in the great tit, *Parus major*. P Roy Soc Edinb B 268(1466):487–491. doi:10.1098/rspb.2000.1405

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical J 50(3):346–363

Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L (1993) Amodal completion in mouse vision? Perception 22:713–721

Lazareva FO, Wasserman AE, Biederman I (2007) Pigeons' recognition of partially occluded objects depends on specific training experience. Perception 36:33–48. doi:10.1068/p5583

Lea SEG, Slater AM, Ryan CME (1996) Comparison of object unity in chicks: a comparison with the human infant. Infant Behav Dev 19:501–504. doi:10.1016/S0163-6383(96)90010-7

MacLeod R, Gosler AG, Cresswell W (2005) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. J Anim Ecol 74(5):956–964. doi:10.1111/j.1365-2656.2005.00993.x

Nagasaka Y, Osada Y (2000) Subjective contours, amodal completion and transparency in animals. JPN J Anim Psychol 50:61–73

Nagasaka Y, Wasserman EA (2008) Amodal completion of moving objects by pigeons. Perception 37(4):557–570

Nagasaka Y, Hori K, Osada Y (2005) Perceptual grouping in pigeons. Perception 34:625–632. doi:10.1068/p5402

Nagasaka Y, Lazareva OF, Wasserman EA (2007) Prior experience affects amodal completion in pigeons. Percept Psychophys 69(4):596–605

Okanoya K, Takahashi M (2000) "Shikaku-teki hokan e no seitaigakuteki apuroochi" [Ecological approach to visual completion]

Kokoro no Hattatsu: Ninchi-teki Seicho no Kikoo 1999 (Reports of the Grant-in-aid for Scientific Research for Priority Areas)

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Regolin L, Vallortigara G (1995) Perception of partly occluded objects by young chicks. Percept Psychophys 57(7):971–976

Regolin L, Marconato F, Vallortigara G (2004) Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). Anim Cogn 7:162–170. doi:10.1007/s10071-004-0208-0

Sato A, Kanazawa S, Fujita K (1997) Perception of object unity in chimpanzee (*Pan troglodytes*). JPN Psychol Res 39:191–199

Schein MV, Hale EB (1957) The head as a stimulus of orientation and arousal of sexual behaviour in male turkeys. Anat Rec 128:617–618

Sekuler AB, Lee JAJ, Shettleworth SJ (1996) Pigeons do not complete partly occluded figures. Perception 25:1109–1120. doi:10.1068/p251109

Shoettle HET, Schein MW (1959) Sexual reaction of male turkeys to deviations from a normal female head model. Anat Rec 134:635

StatSoft Inc (2007) STATISTICA, version 8.0. www.statsoft.com

Sugita Y (1999) Grouping of image fragments in primary visual cortex. Nature 401:269–272

Tinbergen N (1951) The study of instinct. Oxford University Press, London

Ushitani T, Fujita K (2005) Pigeons do not perceptually complete partially occluded photos of food: an ecological approach to the "pigeon problem". Behav Process 69:67–78. doi:10.1016/j.beproc.2005.01.002

Vallortigara G (2004) Visual cognition and representation in birds and primates. In: Lesley JR, Kaplan G (eds) Comparative vertebrate cognition. Chap 2, Kluwer/Plenum publishers, New York

Vallortigara G (2006) The cognitive chicken: visual and spatial cognition in a nonmammalian brain. In: Wasserman EA, Zentall TR (eds) Comparative cognition: experimental explorations of animal intelligence. Oxford University Press, Oxford, pp 41–58

Vallortigara G, Tommasi L (2001) Minimization of modal contours: an instance of an evolutionary internalized geometric regularity? Brain Behav Sci 24:706–707. doi:10.1017/S0140525X01670080

Watanabe S (1999) Effects of hippocampal lesion on spatial discrimination in pigeons. Behav Brain Res 103(1):77–84. doi:10.1016/S0166-4328(00)00358-2

Watanabe S, Furuya I (1997) Video display for study of avian cognition: from psychophysics to sign language. Int J Comp Psychol 10:111–127