Škola doktorských studií v biologických vědách
Jihočeská univerzita v Českých Budějovicích
Přírodovědecká fakulta

Antipredační chování ptáků

Disertační práce

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České Budějovice 2021

Doporučená forma citace:

Syrová, M. (2021) Antipredační chování ptáků. (Antipredation behaviour of birds. Ph.D. Thesis in Czech.) Ph.D. Series, No. 7, University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 122 pp.

Annotation

This thesis is focused on the antipredation behaviour of birds, factors that influence differences in their behaviour, and it shows different approaches to study manners of behaviour. In general, all studies included in the thesis are related to antipredation behaviour of three bird species – Red-backed shrike (*Lanius collurio*), Arctic tern (*Sterna paradisaea*) and Common raven (*Corvus corax*). The first study describes possibilities of using dummies of nest predator that are made from different materials. Further, the effect of priming for cognitive abilities of Red-backed shrikes is discussed. The second and the fourth studies show the problem of multiple predator conflict and alternative strategies in nest defence of Red-backed shrikes. The third study is focused on Arctic terns and their reaction to human disruption in two colonies with varying frequency of contact with people. Moreover, the study addresses the ability of Arctic terns to adapt to a new predator (human) in the high Arctic. Finally, the last study compares the reaction of Common ravens to conspecific and various heterospecific alarm calls.

Prohlášení

Prohlašuji, že jsem autorem této disertační práce a že jsem ji vypracoval(a) pouze s použitím pramenů a literatury uvedených v seznamu použitých zdrojů.

České Budějovice, 15.4.2021

Michaela Syrová

Afiliace

Tato práce vznikla na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

Přírodovědecká fakulta
Faculty of Science

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

Finanční podpora

Výzkum byl během let podpořen z následujících zdrojů:

Grantová agentura Jihočeské univerzity v Českých Budějovicích, projekt 159/2013/P, prof. RNDr. František Sedláček, CSc.: Kognitivní schopnosti a jejich prediktory u modelových skupin živočichů. 2013-2015.

Grantová agentura Jihočeské univerzity v Českých Budějovicích, projekt 048/2019/P, prof. Mgr. Radim Šumbera, Ph.D.: Biodiverzita obratlovců: od chování jedinců až po společenstva. 2019-2021.

CzechPolar2, projekt LM2015078, Ministerstvo školství, mládeže a tělovýchovy České republiky, doc. Ing. Josef Elster, CSc.: Česká arktická vědecká infrastruktura Jihočeské univerzity v Českých Budějovicích – stanice Josefa Svobody. 2016-2019.

Rozpočet RVO, Katedra zoologie, Přírodovědecká fakulta Jihočeské univerzity v Českých Budějovicícich, doc. RNDr. Roman Fuchs, CSc. 2012-2020.

Poděkování

Na tomto místě bych chtěla poděkovat především svému školiteli Romanu Štetke Fuchsovi za jeho trpělivost, za veškeré rady, za ochotu vyslechnout, za lidskost, kterou vůči mně nikdy nešetřil, a za to, že mě vzal zpátky.

Dále děkuji Petru Veselému za to, že dokázal být šéfem, kolegou i kamarádem zároveň, za občasné vyškolování, za moudrost, humor, za konference, exkurze i psaní pejprů, za stabilitu, nadhled, i za to, že si mě nechal v kanclu.

Děkuji Michalu Majklu Němcovi, který mě přivedl k ťuhýkům, ukázal mi krásy Doupovek a díky kterému jsem si terénní výzkum se všemi jeho klady i zápory zamilovala.

Poděkování patří i minimálně třem generacím studentů Štetkeho pracovní skupiny, bez kterých by nebyl terén, nebylo by chytání, budky ani hospody po seminářích. Děkuju za zážitky, pohodu, pomoc i možnost se přiučit.

Ráda bych vyzdvihla i polárníky, kteří mě vzali k sobě, ukázali mi dalekou Arktidu a naučili mě, že si člověk zkrátka občas musí umět poradit a že velké přátele může najít i na 78° severní zeměpisné šířky.

Děkuji celé své alma mater za vše, co mě naučila od bakaláře až sem. Děkuji, že mi dopřála studentského života a že mi umožnila vyrůst. Děkuji mnoha zaměstnancům i studentům fakulty za jejich znalosti a rady, za pomocnou ruku, za úsměvy i konstruktivní kritiku. Děkuji, že mi má alma mater ukázala, že i stres a nervy se dají zvládnout a že mi dávala do cesty jen takové překážky, které jsem dokázala překonat.

Děkuji zaměstnancům Výzkumného ústavu živočišné výroby v Uhříněvsi za to, že mi ukázali taje a krásy akustického výzkumu, že mě zasvětili do práce s hospodářskými zvířaty a dali mi možnost vidět, jak se dělá věda jinde než v univerzitním prostředí. Této zkušenosti si nesmírně vážím.

Na tomto místě bych chtěla poděkovat své rodině, která mě podporovala po celou dobu studia (a že to byla doba…) a to i přes to, že jsem často nebyla úplně nejvzornější dcera/sestra/teta. Velký dík patří Jakubu Ondruchovi za to, že mě pouštěl do terénu, že mě podporoval a měl se mnou trpělivost, a to i v těch posledních měsících, které byly hektičtější. Teď už to snad se mnou bude lepší…

Na úplný závěr ale neméně bych chtěla poděkovat všem spoluautorům, bez nichž by jednotlivé publikace nevznikly.

Seznam publikací a autorský podíl

Disertační práce je založena na následujících publikacích (řazeno chronologicky):

I. Němec M, **Syrová M**, Dokoupilová L, Veselý P, Šmilauer P, Landová E, Lišková S, Fuchs R (2015) Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. Animal Cognition 18: 259-268. DOI: 10.1007/s10071-014-0796-2; IF_{2018} = 2,488; Q1

Michaela Syrová provedla část terénních prací, podílela se na sepsání manuskriptu a byla korespondenčním autorem. (Celkově 40%)

II. **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; IF_{2018} = 2,776; Q2

Michaela Syrová navrhla experiment, provedla terénní práce, podílela se na analýze dat, sepsala většinu manuskriptu. (Celkově 80%)

III. **Syrová M**, Hromádková T, Pavel V, Veselý P (2020) Responses of nesting Arctic terns (*Sterna paradisaea*) to disturbance by humans. Polar Biology: 43(5): 399-407. DOI: 10.1007/s00300-020-02641-2; IF_{2018} = 2,002; Q2

Michaela Syrová se podílela na navržení experimentu, provedla většinu terénního sběru dat, zanalyzovala data a podílela se na sepsání manuskriptu. Zároveň je korespondenčním autorem. (Celkově 70%)

IV. Davídková M, Veselý P, **Syrová M**, Nácarová J, Fuchs R (2020) Ravens respond to unfamiliar corvid alarms. Journal of Ornithology 161: 967-975. DOI: 0.1007/s10336-020-01781-w; IF_{2018}= 1,472; Q2

Michaela Syrová se podílela na navržení experimentu, přípravila přehrávané stimuly, provedla část terénní práce a přispěla k sepsání manuskriptu. (Celkově 30%)

V. Veselý P, **Syrová M**, Voháňková M, Havlíček J, Nácarová J, Fuchs R (manuskript) Cowards or clever guys: an alternative strategy of shrikes defending nests against magpies.

Michaela Syrová se podílela na navržení experimentu, provedla část terénní práce a přispěla k sepsání manuskriptu. (Celkově 40%)

Prohlášení o autorském podílu

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V Českých Budějovicích dne 15.4.2021

doc. RNDr. Roman Fuchs, CSc.

RNDr. Petr Veselý, Ph.D., který je spoluautorem článků III a V, plně souhlasí s uvedenými podíly Michaely Syrové na těchto článcích.

V Českých Budějovicích dne 15.4.2021

RNDr. Petr Veselý, Ph.D.

Obsah

Kapitola 1

Úvod do problematiky antipredačního chování ptáků

Michaela Syrová

Antipredační chování čili odpověď na hrozbu predace je jeden z nejdůležitějších a při případné chybě i nejvíce nebezpečných behaviorálních projevů. Antipredační chování může být rozděleno na tzv. aktivní a pasivní. Zatímco pasivní obrana spočívá ve snaze vyhnout se objevení predátorem a pokud se to nepodaří, tak v útěku, aktivní obrana zahrnuje projevy od varování (*alarm calls, warning calls*) až po fyzické útoky na predátora, tzv. *mobbing* (Shields 1984; review Caro 2005).

Energeticky náročnější a současně nebezpečnější aktivní obrana je nejčastěji využívána při obraně potomků (Shedd 1982, Pavel 2006). Mláďata na hnízdě jsou totiž velmi cenná, ale zároveň bezbranná, bez možnosti útěku před predátorem. Jejich vlastní obrana spoléhá především na krypsi, tedy na ukrytí hnízda a nenápadné chování mláďat, avšak v případě objevení je jedinou záchranou aktivní obrana rodičů (Biermann & Robertson 1981).

Při obraně musí jedinci neustále zvažovat náklady a zisky (*cost & benefit*) a volit její optimální intenzitu. Intenzita obrany by měla odrážet především hodnotu potomstva (počet potomků, jejich stáří), investice do potomků (která se mění v různých fázích hnízdění – samice má větší investice do snůšky během snášení vajec, samec pak investuje během krmení, a to jak krmením samice při inkubaci vajec nebo později krmením mláďat po jejich vylíhnutí), dále pak jedinec zohledňuje i šance náhrady snůšky v daném roce (náhradní hnízdění) nebo v dalších letech (*life history*). Na druhé straně jedinec zohledňuje i aktuální nebezpečí predátora pro snůšku, tedy jeho preferovanou kořist, a dospělce, tedy pravděpodobnost vlastního zranění, ale také svoji šanci na odehnání predátora (viz níže) a šanci, že predátor hnízdo neobjeví.

Asi nejčastěji studovaným faktorem, který ovlivňuje aktivitu rodičů při obraně, je hodnota snůšky (= *brood value hypothesis*; Curio 1987; Redondo & Carranza 1989; Onnebrink & Curio 1991). Rodiče intenzivněji brání hnízdo, do kterého již více investovali. Tzv. *parental investment theory* říká, že z důvodů časových i energetických investic do snůšky rodiče více brání mláďata než vajíčka, která právě snesli (Anderson et al. 1980; Greig-Smith 1980; Redondo 1989; Brunton 1990; Rytkönen et al. 1990; Viñuela et al. 1995; Dale et al. 1996; Rytkönen 2002; Albrecht & Klvaňa 2004). Tato teorie byla ještě upřesněna o tzv. *feedback theory*, která říká, že intenzita obrany vzroste skokově v okamžik, kdy se vylíhnou mláďata a pak následně lineárně roste se stářím mláďat. Lineární nárůst u vylíhnutých mláďat autoři vysvětlují jejich vizuální proměnou. Tato proměna u vajíček nenastává (vajíčka vypadají stále stejně), a proto rodiče brání vajíčka po celou dobu inkubace stejně intenzivně (McLean & Rhodes 1992; Pavel & Bureš 2001). Všechny tyto teorie se nicméně doplňují a říkají totéž – čím více času a energie dospělci investovali do snůšky, tím ochotněji je budou bránit.

Na podobném vztahu je založena i korelace mezi intenzitou obrany hnízda a velikostí snůšky. Páry, které mají větší snůšku, jí hodnotí jako cennější, a proto do její obrany investují víc (Wiklund 1990). Na druhou stranu Curio et al. (1984) ukázal, že u sýkor koňader (*Parus major*) koreluje intenzita obrany s velikostí snůšky jen u některých párů. Větší vliv na investice do obrany mělo opět stáří mláďat. S tím se shodují i další práce studující vliv velikosti snůšky (e.g. Lazarus & Inglis 1986; review Caro 2005). Univerzální význam hodnoty snůšky pro rozhodování o intenzitě obrany hnízda zpochybňuje Söderström (1999), který ve svém review nenašel žádný rozdíl v intenzitě obrany mezi tropy a mírným pásmem bez ohledu na to, že se průměrná velikost snůšky se zeměpisnou šířkou mění. To znamená, že absolutní velikost snůšky zpravidla není rodiči vnímána jako významný faktor pro změnu intenzity obrany.

Z nepochybného pozitivního vztahu mezi intenzitou obrany a hodnotou snůšky plyne, že investice do obrany hnízd je závislá na pohlaví bránícího rodiče. V práci Hogstad (2005) byly v souladu s *offspring value hypothesis* v době inkubace nejprve agresivnější samice a po vylíhnutí mláďat byli agresivnější samci. Zvýšená agresivita samců po vylíhnutí mláďat je odůvodněna zvýšením jejich investic do potomstva, když začínají samci krmit mláďata a zároveň je jako proxi vyšší agresivity obvykle uváděna zvyšující se hladina testosteronu na agresivitu (např. Kryštofková et al. 2011; review Caro 2005). Vliv pohlaví rodiče není ovšem vždy závislý jen na jejich investicích a může ho ovlivňovat i větší či menší jistota rodičovství (Weatherhead 1989; Tryjanowski & Golawski 2004).

V některých pracích je variabilita v reakcích na ohrožení hnízda predací natolik veliká, že autoři nezjistili žádný nebo jen velmi slabý vztah mezi hodnotou snůšky či pohlavím bránícího rodiče a intenzitou obrany. Vysvětlují to velkou individuální variabilitou způsobenou perzonalitou (Vrublevska et al. 2015, ale Couchoux & Cresswell 2012), věkem jedince (Shields 1984), či jeho aktuální kondicí (Greigh-Smith 1980; Abolins-Abols & Ketterson 2017).

Uvažujeme-li o hodnotě snůšky, je třeba brát v úvahu i *life history* daného druhu, tzn. kolik daný druh investuje do aktuální snůšky a její obrany a kolik do přežití sebe sama a do budoucích reprodukčních pokusů. Podle *optimality theory* v obecné rovině platí, že behaviorální odpověď závisí na enviromentálním a sociálním kontextu a zároveň na kondici jedince, stejně jako na jeho pohlaví a věku (Michl et al. 2000; Avilés & Bednekoff 2007; Krams et al. 2014). Podle teorie *risk–taking* i *residual reproductive value* (*RRV)* by proto měli méně mobbovat mladší jedinci a ti, kteří jsou v lepší kondici, tzn. ti jedinci, kteří mohou nejvíce ztratit tím, že by se při obraně současné snůšky zranili a nemohli by využít možnosti náhradního hnízdění v dané sezoně nebo hnízdění v dalších letech (Clark 1994; Ghalambor & Martin 2000, 2001).

Curio (1988) ve své teoretické práci zabývající se *life history* předpokládá, že investice do aktuální snůšky je vyšší se snižující se *residual reproductive value* (poměr mezi investicemi do současné snůšky a do budoucí). To znamená, že čím vyšší tento poměr je, tím spíš rodič investuje do současné snůšky než do budoucí, a tedy je i víc ochoten riskovat při obraně mláďat. Zároveň pokud je pravděpodobnost predace rodiče vyšší než pravděpodobnost predace mláďat, tak by u takového druhu mělo dojít ke snížení *residual reproductive value* a rodiče by měli spíš riskovat svůj život a s menší pravděpodobností snůšku opouštět (Dale et al. 1996).

Předpoklad, že by měli rodiče více investovat do obrany hnízda v pozdějších fázích hnízdní sezóny, kdy se snižuje nebo zcela mizí možnost náhradního zahnízdění však není vždy naplněn. Např. Curio et al. (1984) testovali rozdíl v obraně u první a druhé snůšky sýkory koňadry. Jejich výsledky ovšem nedokázaly, že by byl rozdíl v investicích mezi první a druhou snůškou. Nicméně na obranu hnízda měla vliv postupující fáze sezóny, věk mláďat a v případě druhé snůšky i počet mláďat. Tato změna ve vlivu velikosti snůšky mezi první a druhou snůškou byla autory hodnocena jako nejzajímavější, a to z toho důvodu, že na investice do obrany má vliv *life history* i v měřítku jedné hnízdní sezóny. Hodnota snůšky pro ptáky vzrůstá, až tehdy, kdy ji v aktuální sezóně nelze nahradit. Weatherhead (1989) pak ukázal, že vrabci bránili svá hnízda dokonce méně aktivně s postupující hnízdní sezónou. Vysvětluje to tím, že se u vrabců nezvyšuje pravděpodobnost predace s jejich věkem, a proto jsou ochotni obětovat snůšku v daném roce pro vlastní přežití do další sezóny.

Příkladem experimentální studie vlivu *life history* na antipredační chování je práce autorů Ghalamobr & Martin (2000) porovnávající dva druhy brhlíků (brhlíka amerického, *Sitta canadensis* a brhlíka běloprsého, *Sitta carolinensis*). Oba druhy sice rozeznávali od sebe predátora hnízd a dospělců a adekvátně na ně reagovali, nicméně jejich reakce byly protichůdné. Tyto dva druhy se liší ve své mortalitě. Brhlík běloprsý je vystaven vyšší míře predace a investuje více do obrany aktuální snůšky, zatímco brhlík americký je méně predován a investuje víc do ochrany sebe sama a tím i do budoucích snůšek (Martin & Ghalambor 1999; Ghalambor & Martin 2000).

Vliv predačního tlaku na dospělce a jejich investice do obrany hnízda byl jinak studován především ve spojitosti s velikostí snůšky (review Lima 2009). Výsledky těchto prací však nejsou příliš přesvědčivé. Zatímco v některých oblastech s vyšším predačním tlakem na dospělé ptáky (typicky s vyšším výskytem krahujců, jestřábů apod.) došlo ke snížení velikosti snůšky, což autoři vysvětlují tím, že rodiče nemusí následně krmit mláďata s tak vysokou frekvencí a tím snižují pravděpodobnost konfrontace s predátorem (Julliard et al. 1997; Doligez & Clobert 2003; Zanette et al. 2006), v jiných oblastech k takovému efektu nedochází (Fontaine & Martin 2006b). Tento rozpor není tak překvapující s ohledem na fakt, že velikost snůšky není sama o sobě zásadním faktorem ovlivňující chování rodičů (viz výše).

Vedle hodnoty snůšky by měla rozhodování o formě a intenzitě obrany určovat míra hrozícího nebezpečí, a to nejen pro snůšku ale i pro bránící rodiče. Jedním z faktorů, které proto musí ptáci uvažovat, je tedy kvalita ukrytí hnízda a s ním bezprostředně spjatá nalezitelnost pro predátory. V případě, že jde o hnízdo vhodně ukryté, je možné namísto aktivní obrany využít pasivní, tedy tu energeticky méně náročnou a méně nebezpečnou, kde bránící jedinec spoléhá na krypsi a snaží se na přítomnost hnízda neupozorňovat.

Důležitost dostatečného ukrytí hnízda na intenzitu predace popsal Söderström (1999) ve své review porovnávající hnízda ukrytá ve vegetaci a umístěná volně na zemi v temperátu a v tropech. Podle jeho výsledků jsou hnízda umístěna na zemi pod signifikantně vyšším predačním tlakem než ta ukrytá ve vegetaci, a to bez ohledu na podnebný pás. Při porovnání jen hnízd umístněných na zemi jsou více predována ta v tropech než ta v temperátu. U hnízd ukrytých ve vegetaci se tento rozdíl stírá a míra predace je v obou regionech srovnatelná.

Vliv ukrytí hnízda na přežití snůšky byl experimentálně studován např. Remešem (2005) u pěnice černohlavé (*Sylvia atricapila*). Ten ukázal, že přirozená, ale špatně ukrytá hnízda nejsou predována víc než ta dobře ukrytá a zároveň jsou predována méně než umělá špatně ukrytá hnízda, což vysvětlil vyšší aktivitou rodičů při obraně špatně ukrytých hnízd. Podobné byly závěry Kleindorfer et al. (2005), v jejíž práci rostla intenzita obrany hnízd rákosníků proti pozemním predátorům s klesající výškou umístnění hnízda, a tedy s jeho lepší dosažitelností ze země. Stejné byly výsledky dalších prací na rákosníku tamaryškovém, *Acrocephalus melanopogon* (Kleindorfer et al. 2003) i rákosníku velkém, *Acrocephalus arundinaceus* (Mérö & Žuljević 2017). Zajímavé na tom je, že malý rákosník tamaryškový má nepochybně menší schopnost zahnat predátora než rákosník velký. U ťuhýka obecného (*Lanius collurio*) byla prokázána pozitivní korelace mezi ukrytím hnízd a přežitím snůšky (Jakober & Stauber 2002). Ťuhýk agresivně brání hnízdo proti většině vetřelců (Tryjanowski & Goławski 2004; Strnad et al. 2012). Výsledek práce Jakober & Stauber (2002) by ovšem svědčil pro to, že přinejmenším v některých případech nemusí mít tato obrana pozitivní efekt. To by pak vysvětlovalo, proč ťuhýk proti některým predátorům volí alternativní strategii (Syrová et al. 2016)

I když podle výše uvedených prací je vyšší aktivita při obraně hnízda spojena s nižší predací, u některých druhů byla prokázána pozitivní korelace mezi celkovou aktivitou rodičů a vyšší pravděpodobností objevení hnízda, což naopak způsobuje vyšší míru predace (Martin et al. 2000a,b). V oblastech s vyšším predačním tlakem proto může být aktivita rodičů naopak celkově snížena, aby rodiče svou aktivitou neupozorňovali na hnízdo, a to i během krmení mláďat, kdy rodiče navštěvují hnízdo s nižší frekvencí ale s vyššími dávkami potravy (Martin et al. 2000a).

Aktuální ohrožení snůšky je ovlivněno i vzdáleností predátora od hnízda. Shields (1984) ukázal, že rodiče koloniálně hnízdících vlaštovek (*Hirundo rustica*), jejichž hnízdo je bezprostředně ohroženo, reagují daleko aktivněji ve srovnání s rodiči sousedních hnízd, kteří využívají jen pasivní obranu. Kleindorfer et al. (2005) tento poznatek zobecnila v tzv. *dynamic risk assessment hypothesis*, která předpokládá, že vyhodnocení nebezpečnost predátora není jednorázovým aktem ale dynamickým procesem. Ten byl potvrzen i v dalších pracích (Burhans & Thompshon 2001; Kleindorfer et al. 2005; Kryštůfková et al. 2011), které ukazují, že se zvyšující se vzdáleností predátora od hnízda prudce klesá obranná reakce rodičů. Tento efekt prokázala i Falkenauerová (2008), v jejíž práci ťuhýk obecný snižuje intenzitu obrany proti krahujcovi (*Accipiter nisus*) se vzrůstající vzdáleností od hnízda.

Naše práce (Syrová et al. 2016) ukázala, že i přes to, že ťuhýci reagují na vzdálenou atrapu signifikantně méně, věnují širšímu okolí hnízda stále pozornost, a i takto vzdálený predátor má silný vliv na jejich chování. V této práci byla do bezprostřední vzdálenosti od hnízda umístěna atrapa poštolky obecné (*Falco tinnunculus*) a do vzdálenosti deseti metrů (tj. do vzdálenosti, kde na krahujce ťuhýk už vůbec nereaguje –

Falkenauerová 2008) druhá atrapa (straka – *Pica pica*, sojka – *Garulus glandarius*, holub – *Columna livia* f. *domestica*, či prázdná kontrola). Reakce na predátora u hnízda byla signifikantně ovlivněna právě atrapou umístěnou v deseti metrech. Tato práce tak navíc ukazuje, že ťuhýci řeší nejen nebezpečnost jednotlivého druhu predátora, ale i jejich kombinace, a v případě predátorů, vůči kterým využívají různé strategie (tzv. *multiple predator conflict*, Sih et al. 1998), jsou schopni alternativní obranné reakce (blíže viz kapitola III).

Aktuální nebezpečnost predátora významně ovlivňuje jeho velikost, a to hned dvojím způsobem. Různě velcí predátoři se obvykle liší svoji potravní specializací a velikost predátora do značné míry určuje i pravděpodobnost, že se jej bránícím ptákům podaří zahnat. Vliv velikosti predátora na obrannou reakci byl přesto studován jen okrajově. V pracích autorů Klump & Curio (1983) či Palleroni et al. (2005), kde byly testovány sýkory modřinky (*Cyanistes caeruleus*), resp. kur domácí (*Gallus gallus* f. *domestica*), v reakci na letící siluetu krahujce, respektive živé zástupce rodu Accipiter, byl vliv velikosti významný. Nicméně autoři první práce ovšem předpokládají, že sýkory interpretovaly různou velikost jako informaci o jeho vzdálenosti. I v pracích Templeteon et al. (2005) a Soard & Ritchison (2009) testující vliv velikost predátora tentokrát na intenzitu varování byla frekvence varování nižší při reakci na menší druhy dravců než při prezentaci větších druhů. Oproti tomu práce Beránkové et al. (2015) prokázala, že pouhá velikost predátora nemá vliv na reakci sýkory. Sýkory koňadry reagovaly stejně na krahujce obecného, ať už byl ve standardní velikosti či zmenšený. Zdá se tedy, že velikost funguje jen, je-li spojena s konkrétním druhem. Odlišný přístup k problematice velikosti zvolili Larsen et al. (1996), kteří porovnávali literární údaje o antipredačním chování různě velkých bahňáků. Výskyt aktivní obrany v jejich studii pozitivně koreloval s jejich rostoucí hmotností, což odráželo zvyšující se pravděpodobnost úspěšného zahnání predátora. Schopnost zahnat predátora ale zřejmě nezávisí jen na poměru fyzických sil mezi ním a bránícími ptáky. Strnad et al. (2012) zjistil u ťuhýka obecného naprosto odlišnou formu obrany proti dvěma obdobně velkým predátorům hnízd strace a sojce. Zatímco sojku velmi razantně zaháněli vůči strace se chovali zcela pasivně. Jediné vysvětlení je, že se snaží straku neupozornit na přítomnost hnízda. To jsem potvrdila i ve své studii se dvěma predátory (Syrová et al. 2016). Obdobně pak Burhans (2000) otestoval alternativní strategii obrany hnízda u vrabců polních (*Passer montanus*), kteří se při prezentaci hnízdního predátora, sojky chocholaté (*Cyanocitta cristata*), přestali přibližovat k hnízdu. Stejně jako vzdálenost predátora a jeho velikost ptáci zohledňují i jeho aktuální aktivitu. Mathot et al. (2009) prokázal rozdíl v reakci jespáka rezavého (*Calidris canutus*) na letícího a sedícího krahujce obecného. Přidání pohybu jako důležitého aspektu využili i Deppe et al. (2003), Cockrem & Silverin (2002) či Zaccaroni et al. (2007), ačkoli ve svých pracích přímo neporovnávali pohybující se podnět s nehybným. Ve většině antipredačních prací se však pohyb, jakožto efekt zvyšující dojem akutního nebezpečí, nevyužívá (review Caro 2005; Ibañez-Álamo et al. 2015).

Investice do obrany by měla odrážet nebezpečí, které hrozí nejen potomkům ale i rodičům. Toto nebezpečí je ovlivněno potravní ekologií predátora – hnízdní predátoři nejsou pro rodiče tak nebezpeční jako predátoři dospělců a naopak. Řada prací (Ash 1970; Curio 1975; Gottfried 1979; Patterson et al. 1980; Nijman 2004; Sordahl 2004; Hogstad 2005; Strnad et al. 2012) ukazuje, že ptáci brání hnízdo intenzivněji proti predátorům hnízd než proti predátorům dospělců. Zde se ovšem nedá rozhodnout, které nebezpečí zohledňují. Jednoznačný doklad, že berou zřetel na nebezpečí hrozící jim samým poskytuje Strnad et al. (2012). V jeho studii ťuhýci obecní reagovali agresivněji na poštolku, živící se převážně drobnými savci či vzletnými mláďaty než na krahujce obecného, specialistu na lov malých ptáků.

Pokud má obrana adekvátně zohlednit míru nebezpečí, které predátor představuje, musí ho bránící pták co nejpřesněji rozpoznat, přinejmenším odlišit od neškodného druhu, ale i odlišit predátory vajec od predátorů hnízd a nejlépe pak jednotlivé druhy mezi sebou. Není vhodné reagovat na neškodné podněty, protože tak dochází ke zbytečným ztrátám energie, stejně tak reagovat na velmi nebezpečné podněty riskantním chováním může predátorovi usnadnit útok, před kterým již nebude obrana (Montgomerie & Wheatherhead 1988).

Tuto schopnost potvrdila řada prací porovnávajících reakce na různé skupiny a druhy predátorů. Rodiče bránící hnízdo zohledňují nebezpečnost predátora pro ně samotné a pro potomky (Curio 1975; Curio & Regelmann 1985; Hogstadt 2005). Strnad et al. (2012) prokázal, že rodiče ťuhýků obecných při obraně hnízd rozlišují nebezpečné predátory od neškodných vetřelců, navíc odlišně reagují na predátora nebezpečného pro hnízdo a pro dospělce. Podobně pak byla tato schopnost odlišit různé typy predátorů a adekvátně na ně reagovat prokázána i v dalších studiích (Ghalamobr & Martin 2000; Tvardíková & Fuchs 2011; review Fuchs et al. 2019).

Rozpoznávání predátorů (stejně jako jiných objektů) je založeno především na dvou kognitivních procesech – diskriminaci a kategorizaci (Shettleworth 2010). Diskriminace je využívána k rozlišení daného podnětu od ostatních a kategorizace pomáhá k přiřazení podnětů do skupin podle společných znaků. V případě rozpoznávání v antipredačním chování je diskriminace využívána k rozlišení predátorů od neškodných druhů a kategorizace je využívána pro konfrontaci s již známými predátory.

Při rozpoznávání predátorů využívají ptáci převážně vizuální a akustické signály (výjimečně i olfaktorické – Amo et al. 2008). Většina experimentálních prací, které tento proces studují, se tedy zabývá vizuálními podněty a jejich vyhodnocováním. Bylo provedeno množství studií, ve kterých autoři manipulovali s tzv. klíčovými znaky (tvarem zobáku, pařáty, okem; review Fuchs et al. 2019), popř. celkovým zbarvením (Curio 1975; Němec 2015) a snažili se tak vysvětlit detailní způsob rozpoznávání predátorů od neškodných ptáků, jednotlivých druhů predátorů mezi sebou, popřípadě známých druhů predátorů od neznámých (např. Veen et al. 2000; Němec et al. in press).

Testování známých a neznámých druhů bylo využito např. u timalie šedé (*Turdoides squamiceps*). Ta je schopna rozpoznat míru nebezpečí i u predátorů, kteří se v jejím okolí pravidelně nevyskytují, ale jen protahují, a adekvátně na ně reagovat (Edelaar & Wright 2006). Csermely et al. (2006) oproti tomu pozoroval u poštolky obecné (*Falco tinnunculus*) rozdílnou reakci na známého predátora – vránu (*Corvus corone cornix*), a neznámého predátora – krkavce (*Corvus corax*). Vrána byla napadána intenzivněji než neznámý krkavec. Bohužel nebyla v této práci zohledněna velikost predátora, a tak výsledek může být ovlivněn více než familiárností, reálným nebezpečím, kteří predátoři představují, či jejich velikostí, podobně jako v práci Němec & Fuchs (2013).

Práce Syrová et al. (2020) diskutuje známost predátora (člověka) pro dvě různé kolonie rybáků dlouhoocasých (*Sterna paradisaea*) na Svalbardu. Tyto dvě kolonie se lišily právě přítomností lidí v těsné blízkosti hnízdících rybáků. První kolonie se nacházela přímo ve městě Longyearbyen, druhá pak na poloostrově v předpolí ledovce Nordenskiöldbreen vzdálené asi 60 km od Longyearbyen. Autoři měřili čas, který rodiče potřebují k tomu, aby se vrátili po vyrušení zpátky k inkubaci. Tento čas byl signifikantně delší v kolonii na předpolí ledovce, která na přítomnost člověka nebyla zvyklá (cca 50 s vs. 7 min).

S problematikou známosti predátora je spojena i dědičnost antipredačního chování. Tím se u ptáků zabývali Bize et al. (2012), kteří testovali vrozenost reakce na predátora u rorýsů velkých (*Apus melba*). Jejich výsledky z pokusů s *cross-fosteringem* (výměnou mláďat) ukazují, že antipredační chování je více vrozené než naučené. V jejich práci však není zřejmé, zda jde o vrozenost reakce na konkrétní predátory nebo vrozenou celkovou vyšší míru agresivity, neboť sledovanou proměnnou byla jen reakce na člověka při jeho přiblížení do kolonie a během vlastních odchytů.

Při studiu antipredačního chování ptáků by z metodického hlediska bylo vhodné pro lepší věrohodnost predátorů využívat živé jedince. Tento přístup je však vzhledem k možnému zranění všech pokusných zvířat neetický, a proto se v současnosti nevyužívá. Většina prací tak pracuje s vycpaninami. Tento přístup se zdá být vhodný vzhledem k věrohodnosti atrapy a zároveň díky snížení pravděpodobností poranění bránících jedinců i predátorů, ovšem při studiu rozpoznávacích procesů, kdy je třeba manipulovat s jednotlivými znaky jako jsou pařáty, zobák či barva oka, je omezující. Modifikování vycpaných atrap je možné provádět např. na mrazem vysušených modelech (Gill et al. 1997). V takovém případě se dá manipulovat se zobákem, ovšem manipulace se zbarvením peří je opět problematická. Několik prací využívalo zcela uměle vytvořené atrapy. Nejčastěji se pracovalo s modely hadů vytvořených z gumy (Gottfried at al. 1985; Maklakov 2002; Kleindorfer et al. 2005), ve výjimečnějších případech i s gumovými (Knight & Temple 1988), plastovými (Arroyo et al. 2001) či dřevěnými (Deppe et al. 2003) modely ptáků. Autoři některých prací využili dokonce jen 2D siluety ptáků (Deppe et al. 2003, Zaccaroni et al. 2007). Všechny tyto práce kombinovali využití vycpaných a uměle vyrobených atrap bez ohledu na jejich věrohodnost. Pouze práce Hartley (1950) a Němec et al. (2012) se pokouší porovnat reakci ptáků na jeden podnět zhotoven z různých materiálů. Hartley (1950) nenašel rozdíl v reakci na dřevěný model a vycpanou atrapou kulíška amerického (*Glaucidium gnoma*), což vzhledem k absenci statistického zhodnocení není zcela směrodatné. Němec et al. (2012) rozdíl v reakcích na vycpanou sojku obecnou a její model vyrobený ze silikonu prokázali. Mezi vycpaninou a atrapou vyrobenou z plyše ale rozdíl nebyl, umožňuje využívání plyšových atrap v antipredačních pokusech (blíže viz kapitola II).

Ptáci na objevení predátora reagují velmi často varováním. Varování čili *alarm call* má za cíl především upozornit konspecifické jedince na přítomnost nebezpečí, nicméně ptáci dokážou alarmy předávat i další informace. Díky využívání různých typů varování na vzdušné a na pozemní predátory předávají informaci o směru, ze kterého nebezpečí čekat a mohou tak na ně rychleji a lépe reagovat (např. Knight & Temple 1988; Rainey et al. 2004; Colombelli-Négrel & Robertson 2010; Magrath et al. 2010; Suzuki 2011). Zároveň umí ptáci reagovat na predátory v různých vzdálenostech buď zvýšením intenzity varování (modropláštník nádherný, *Malurus cyaneus* – Colombelli-Négrel & Robertson 2010) nebo změnou varování (Soard & Ritchison 2009). Některé druhy jsou schopny zakódovat do varování i velikost predátora (Templeton et al. 2005; Courter & Ritchison 2010).

Studium *alarm calls* je většinou zaměřeno na konspecifickou komunikaci, tedy tu, která se využívá mezi jedinci stejného druhu ať už jde o komunikaci mezi dospělci navzájem nebo mezi rodiči a jejich mláďaty. Práce zaměřené na využívání varovování při obraně hnízda navíc podporují i *brood value hypothesis,* neboť rodiče využívají intenzivnější varování u starších mláďat než u mladších (Montgomerie & Weatherhead 1988; Redondo 1989). U ptáků byla poměrně podrobně studována i komunikace mezi rodiči a mláďaty na hnízdě. Kleindorfer et al. (1996) ukázali, že mláďata rákosníků jsou schopna reagovat na varování rodičů, a to adaptivně, v přítomnosti vzdušného predátora přikrčením v hnídě, v přítomnosti velmi blízko se nacházejícího pozemního predátora vyskákáním z hnízda. I Suzuki (2011) ukázal, že rodiče sýkory koňadry využívají různé typy *alarm calls* podle toho, zda jde o predátora, před kterým je možné se v hnízdní dutině schovat či nikoli a mláďata na hnízdě dokážou na tyto dva různé *alarm calls* bezchybně reagovat, tedy buď se v hnízdě přikrčit, nebo naopak vyskákat ven.

Kromě reakce na konspecifické *alarm calls* je výhodné rozpoznat i ty heterospecifické. Tlak na schopnost reagovat na cizí varování je především mezi druhy, u kterých dochází ke sdílení predátorů (Shriner 1998; Goodale & Kotagama 2008). K reakci na heterospecifické *alarm calls* dochází v některých případech i jen díky podobnosti v akustických parametrech *alarm calls* jednotlivých druhů (Johnson et al. 2003; Randler 2012; Fallow et al. 2013; Nácarová et al. 2018). V mnoha pracích bylo však prokázáno, že jsou ptáci schopni reagovat na druhy, jejíž *alarm calls* se od vlastních liší (Magrath et al. 2009; Wheatcroft & Price 2013). Například modropláštníci nádherní jsou schopni reagovat na *alarm calls* širokého spektra druhů, se kterými sdílí biotop (Magrath et al. 2009), ale navíc jsou schopni se naučit reagovat i na *alarm calls* druhu, se kterým nemají žádnou předchozí zkušenost (Magrath et al. 2015). Zajímavé závěry jsou pak v práci Davídková et al. (2020), kde nejenže krakavci (*Corvus corax*) reagovali na konspecifické varovné hlasy stejně jako na varování sympatricky se vyskytující sojky obecné (*Garrulus glandarius*), ale zároveň i na americkou sojku chocholatou, přičemž nereagovali na varování evropského ani amerického racka (*Chroicocephalus ridibundus*, resp. *Leucophaeus atricilla*). Tyto závěry naznačují, že krkavcovití sdílí některé akustické parametry ve varovných hlasech, díky kterým jsou schopni reagovat i na varování neznámých druhů.

Při studiu antipredačního chování je pozoruhodná i tendence k tvorbě agregací (hejn, stád, neanonymních societ, kolonií), která je nejen u ptáků poměrně silná, a to i přes to, že agregace jsou daleko lépe detekovatelné a tím i častěji napadané než solitérně žijící jedinci. Výhody života ve skupině pro antipredační chování byly intenzivně studovány, popsány v množství experimentálních studií a zobecněny v několika teoriích.

První z teorií popisuje tzv. *dilusion effect* (=efekt zředění, Hamilton 1971), který predikuje výhodu pro jedince žijící ve skupině, pokud dojde k setkání s predátorem, který na jeden útok je schopen ulovit pouze jednu kořist. V takovém případě je žití ve skupině vždy výhoda. Ta navíc roste s velikostí skupiny, protože pravděpodobnost ulovení jedince je jí nepřímo úměrná (1/n, kde n je velikost skupiny).

S tímto efektem je spojen i fakt, že ve větších skupinách jsou jedinci během mobbování aktivnější (Curio & Regelmann 1986; Krams et al. 2009). Tato vyšší aktivita je vysvětlována opět tím, že ve skupině se stává mobbing pro jednotlivce méně riskantním díky efektu zředění (Hamilton 1971). Obdobně Cresswell (1994a) popsal, že ohrožení jedince klesá s rostoucí velikostí skupiny. Podobné závěry uvádí i Krams et al. (2009) u semikoloniálně hnízdících lejsků černohlavých (*Ficedula hypoleuca*), kde prokázali, že intenzita mobbingu stoupá s velikostí skupiny. Moták lužní (*Circus pygargus*) ve větší kolonii napadá predátory ve větším počtu jedinců, ale s nižšími náklady na jedince (Arroyo et al. 2001).

Druhá teorie je popsána jako *confusion effect* (Miller 1922). Tato teorie říká, že díky pohybu jedinců v rámci hejna dochází u predátora ke zmatení a dezorientaci, a ten tak není schopen se zaměřit na jednoho jedince a napadnout ho.

Godin & Morgan (1985) ukázali další výhody žití ve skupině v podobě předávání informace o blížícím se nebezpečí. Jedinci, kteří sami nevidí predátora reagují na jedince, kteří predátora již detekovali, a tím signifikantně zvyšují svou šanci na útěk (tzv. *Trafalgar effect*; Treherne & Foster 1981). Obě výše zmíněné práce však ukazují tento efekt v mořském ekosystému, a to na plošticích (*Halobates robustus*) nebo rybách (*Fundulus diaphanu*). U ptáků tento efekt nebyl takto pojmenován, ale zároveň je nepřímo popisován při studiu *alarm* (resp. *warning*) *calls* (Lima 1995a,b; Hilton et al. 1999). Také Møller (1987) ukázal, že větší hejno vlaštovek reaguje na sýčka obecného (*Athene noctua*) dřív, stejně tak podle Harkin et al. (2000) vrabci reagují na blížícího se člověka ve větších skupinách dříve. Větší skupiny mají vyšší šanci jako takovou predátora detekovat (Lima & Bednekoff 1999), a to i přes to, že dochází se zvětšující se skupinou u každého jedince k významnému poklesu vigelance (Avilés & Bednekoff 2007).

Specifickým typem ptačích agregací jsou hnízdní kolonie. Během jejich tvorby dochází k pravidelným bojům o pozici hnízda, a to především proto, že jednotlivá místa pro hnízdění jsou signifikantně rozdílně vystavena predačnímu tlaku. Je známo, že jedinci hnízdící na okrajích kolonie jsou častěji napadáni a predováni než ti, kteří hnízdí v centrální části (Hamilton 1971). Zároveň i tráví daleko více času vigilancí než jejich centrálněji hnízdící sousedé (Elgar 1989). Je proto výhodné být v rámci kolonie spíše v jejím centru než při okraji.

Na druhou stranu při testování reakce koloniálně hnízdících tučňáků uzdičkových (*Chinstrap penguin*) byla testována nejen fáze hnízdění a pohlaví bránícího rodiče, ale opět konkrétní umístnění hnízd v rámci kolonie. Výsledky pak ukazují, že jedinci hnízdící dál od okraje kolonie útočí na člověka agresivněji (a tedy s větší energetickou náročností) než ti, kteří jsou na periférii (Viñuela et al. 1995). To může být způsobeno i tím, že místa uvnitř kolonie jsou obsazována silnějšími, a tedy pravděpodobně i agresivnějšími jedinci (Ehrlich et al. 1988).

Hejna ptáků mohou být složena z více druhů, které obvykle mají stejné potravní nároky či stejné predátory. V takovýchto skupinách na sebe jsou schopny druhy reagovat a identifikovat navzájem svá *alarm calls* (Magrath et al. 2015). Např. americké sýkory rezavoboké (*Baeolophus bicolor*) a karolinské (*Poecile carolinensis*) vytváří mimo hnízdní období společná hejnka, která jsou schopna společné obrany před predátory. Sýkory rezavoboké jsou větší a jsou pravděpodobně častějšími terči predátorů kvůli své nižší schopnost manévrovat (Dial et al. 2008). Proto jsou ochotny při obraně více riskovat a bránit hejno aktivněji a přibližovat se víc k potenciálním predátorům (Courter & Ritchison 2010). Sýkory karolinské se k predátorům tolik nepřibližují a využívají výhodu obrany od sýkor rezavobokých. Zároveň oba druhy profitují ze společného výskytu díky včasnější detekci predátorů. Na druhou stranu však jsou sýkory karolinské pravděpodobně lépe detekovatelné v přírodě právě kvůli společnému výskytu s větším druhem (Courter & Ritchison 2012). Existují ale i agregace druhů, které se potkaly spíše náhodou a žádné další výhody (krom nižších nákladů na vigelanci na jedince) nemají (Mönkkönen et al. 1996).

U koloniálně hnízdících vlaštovek pestrých (*Petrochelidon pyrrhonata*) bylo prokázáno, že se jedinci liší v míře vigilance během hnízdění. Tyto rozdíly byly stabilní během celé doby hnízdění a neměly vliv na pravděpodobnost přežití vlastní snůšky. Více vigilantní jedinci ale s vyšší pravděpodobností narušovali hnízdění svých sousedů tím, že vyvolávali více konfliktů. Autoři tedy uzavírají, že vyšší vigilance může být více spojená s pozorováním konspecifických jedinců než predátorů (Roche & Brown 2013). Individuální rozdíly ve vigilanci byli dále studovány především u nehnízdících bahňáků (vodouš rudonohý, *Tringa totanus* – Couchoux & Cresswell 2012) či astrilidů (panenka muškátová, *Lonchura punctulata* – Rieucau et al. 2010).

Rostoucí velikost kolonie má i negativní důsledky. U koloniálně hnízdících drozdů kvíčal (*Turdus pilaris*) bylo prokázáno, že ve větších koloniích sice s vyšší pravděpodobností přežívají snůšky, ale zároveň stoupá riziko predace dospělců, stejně jako nebezpečí, že mláďata zemřou na nedostatek potravy (Wiklund & Andersson 1994). Autoři však uvádí zároveň i vyšší míru mobbingu u koloniálně hnízdících kvíčal, což je pravděpodobně největší výhoda jejich výskytu ve skupinách. Møller (1987) ukázal, že u vlaštovek obecných (*Hirundo rustica*) dochází ve větších koloniích k větší infanticidě, což je ovšem opět vyváženo rychlejší detekcí predátora.

Shrnutí výsledků

Antipredační chování ptáků jsme testovali na třech modelových druzí, a to během hnízdění i mimo ně.

V práci testující vliv známosti podnětu (člověka) na reakci koloniálně žijících rybáků dlouhoocasých (Syrová et al. 2020) jsme se přiblížili k ochranářské tématice, vzhledem ke stále rostoucí intenzitě turismu v arktických oblastech. Závěry naší práce ukazují, že rybáci jsou schopni se přizpůsobit lidské přítomnosti, nicméně ne tak, aby zcela vyloučili zvýšení energetických výdajů spojených s hnízděním, což je zvláště důležité v extrémních biotopech vysoké Arktidy. V navazující práci bychom chtěli od této problematiky trochu odhlédnout a zhodnotit efekt odlišné známosti vybraných ptačích predátorů v různých koloniích napříč rozsáhlým areálem výskytu tohoto vysoce filopatrického druhu.

V práci Němec et al. (2015) jsme testovali možnost využití atrap zhotovených z různých materiálů v pokusech testujících intenzitu antipredačního chování. Ověřili jsme, že je možné využívat nejen vycpaniny reálných zvířat, ale i atrapy vyhotovené z plyše. Méně vhodné se pak zdají být atrapy hladké a lesklé (v našem případě silikonové). V této práci jsme zároveň zjistili efekt primingu v reakci ťuhýků na jednotlivé podněty. Na nejméně věrohodnou, tedy silikonovou atrapu, ťuhýci reagovali jen v případě, kdy jí předcházela věrohodnější atrapa. Toto zjištění je zvlášť cenné vzhledem k faktu, že byl priming u ptáků poprvé prokázán v terénním výzkumu.

Při studiu antipredačního chování krkavců jsme se zaměřili na jejich reakci na heterospecifické *alarm calls*. V návaznosti na práce mých kolegů prováděné ve spolupráci s Vídeňskou univerzitou v minulosti (Bílá et al. 2017, Nácarová et al. 2018), jsme se rozhodli otestovat reakci krkavců na *alarm calls* dvou druhů sojek a dvou druhů racků, vždy jednoho evropského a jednoho amerického zástupce (Davídková et al. 2020). Krkavci překvapivě reagují na obě sojky, tedy i na *alarm call* neznámého druhu, ale na racky nereagují. Tento závěr byl překvapující i kvůli tomu, že sojky a krkavci nesdílí (až na výjimky) spektra svých predátorů. Zároveň jsou pak sojky a racci obdobné velikosti, takže její případný efekt lze vyloučit. Na základě těchto zjištění jsme se rozhodli pro metaanalýzu *alarm calls* všech druhů krkavcovitých a pokusíme se popsat, zda existují nějaké parametry definující univerzální *alarm call* krkavcovitých.

V předchozích experimentech bylo zjištěno, že ťuhýci nereagují mobingem na straku obecnou (Strnad et al. 2012). Byla vyslovena hypotéza, že se tak snaží neupozornit na přítomnost hnízda. Navrhla jsem experiment umožňující tuto hypotézu testovat (Syrová et al. 2016). U hnízda ťuhýka byl umístěn predátor, který je běžně napadán (poštolka obecná) a ve vzdálenosti deseti metrů pak druhý predátor – buď obvykle napadaný (sojka obecná) nebo nenapadaný (straka obecná). Reakce ťuhýka na atrapu umístěnou u hnízda byla ovlivněna přítomností druhé atrapy. Při současné prezentaci obvykle napadaného predátora byla atrapa u hnízda napadána. Pokud však byla prezentována atrapa predátora, na kterého ťuhýci standardně neútočí, neútočili ťuhýci ani na atrapu u hnízda. Tento výsledek poodkryl složitost rozhodování ťuhýků při obraně hnízda. To, že ťuhýci jsou schopni potlačit svou přirozenou reakci na bližší nebezpečí a nechají se ovlivnit přítomností vzdálenější atrapy, bylo překvapující. Inhibice reakce na aktuální nebezpečí byla tedy zjevně adaptivní a nabízí se vysvětlení, že je projevem značných kognitivních schopností ťuhýka.

Na tento výsledek jsme navázali prací Veselý et al. (submitted), ve které jsme ťuhýky vystavili přítomnosti predátora, na kterého nereagují aktivně, a zároveň jsme pouštěli varování z reproduktoru. V tomto uspořádání pokusu jsme zjistili, že ťuhýci jsou ochotni na straku zaútočit, pokud se již ozývá ťuhýčí varování, tzn. v situaci, kdy je již snaha na hnízdo neupozornit zhacena. Ťuhýci mají tedy vůči strace zvláštní strategii, která je silnější než jejich standardní aktivní reakce spočívající v agresivních náletech, kterou využívají vůči většině predátorům, a zároveň je ale možné tuto alternativní strategii potlačit v případě, kdy přestane být výhodné ji využívat. Důvod, proč je straka pro ťuhýka natolik nebezpečným predátorem, který si zaslouží alternativní strategii, však stále neznáme.

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Kapitola 2

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

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Abstract We compared the responses of the nesting redbacked 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

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; Němec 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 antipredator 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 presenc 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.

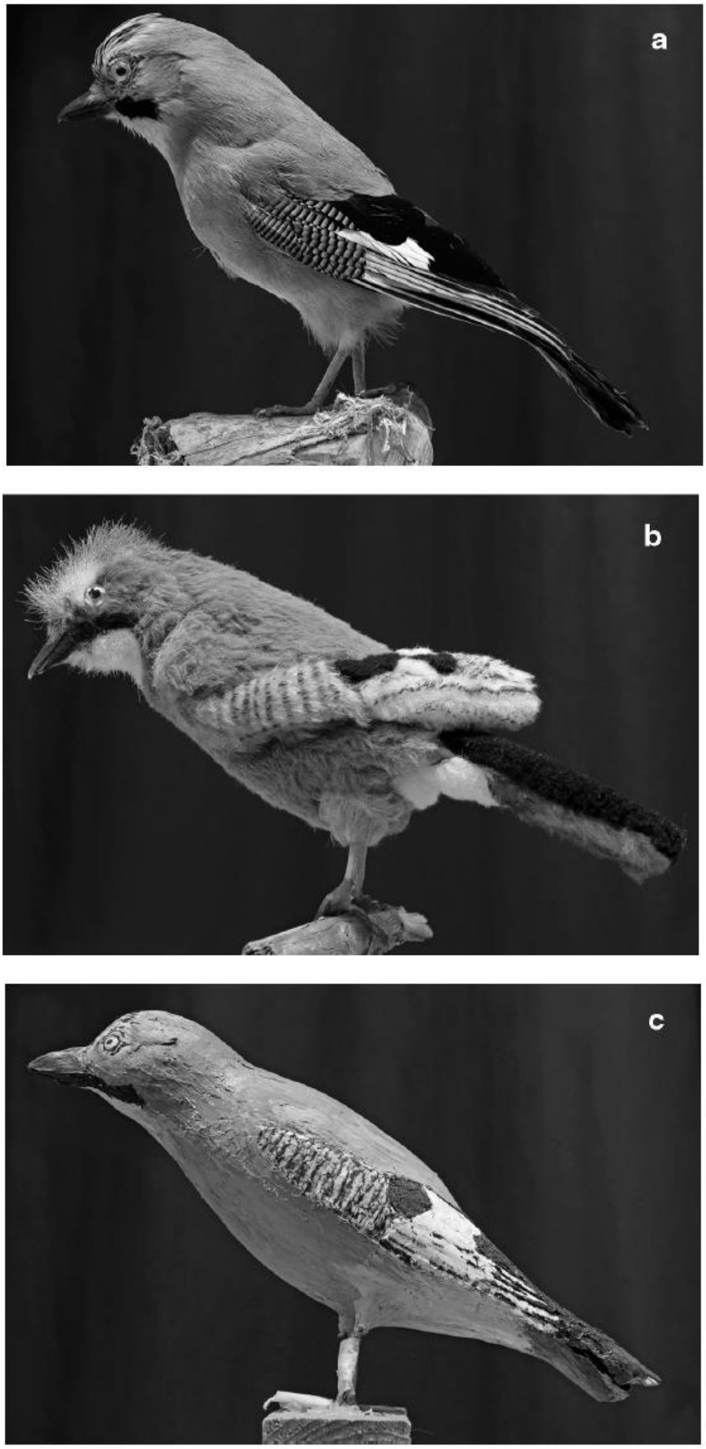


Fig. 1 Three dummy types of the European jay presented close to the red-backed shrikes´ nests. **a** Stuffed dummy; **b** plush dummy; **c** silicone dummy

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 redbilled leiothrix (*Leiothrix lutea*). The command coldist was used to count the distances (ΔS) between all measured body parts on all three dummies. Units of DS 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: $r = 0.718$, $t = 5.44$, $df = 52$, $P << 0.001$; number of attacks: $r = 0.678$, $t = 6.64$, $df = 52$, P << 0.001; attack latency: r = 0.325, t = 3.89, df = 52, P << 0.001; attack rate: r = 0.821, t = 8.85, df = 52, P << 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 V2 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 X 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).

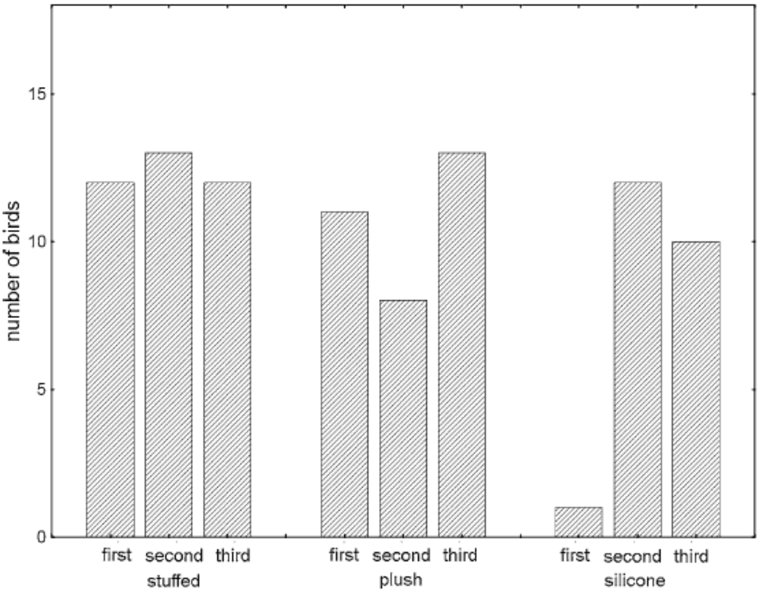


Fig. 2 Numbers of birds performing attacks against particular dummies, exposed in various order in the sequence

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: 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

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

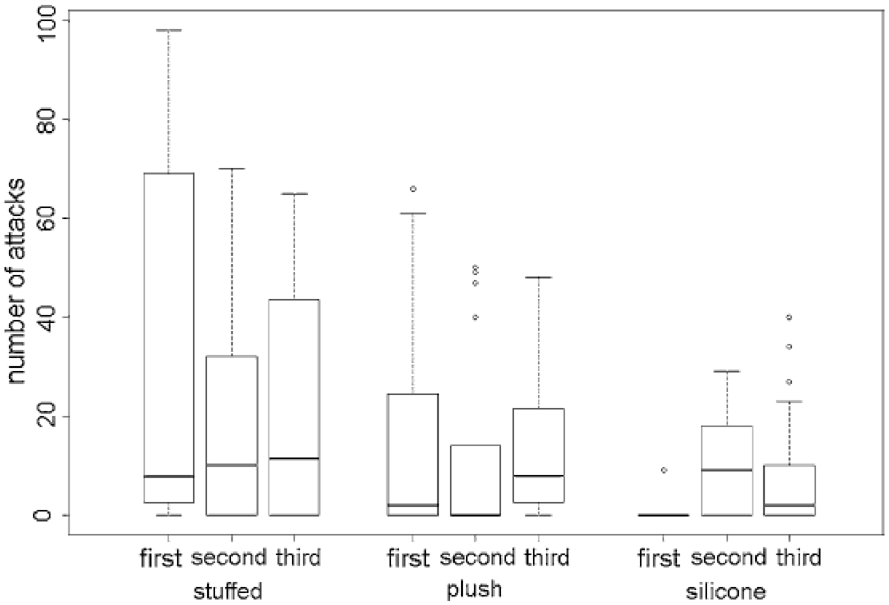


Fig. 3 Number of attacks performed by the red-backed shrikes against particular dummies, exposed in various order in the sequence. The thick line within each box-and-whisker drawing represents the median; the vertical span of the box represents the range from the lower to upper quartile; the range of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

similar among all dummies (back, neck, belly, moustaches). Only the colouration of the stuffed and silicone tail should not be recognizable by birds according to statistical significance within the avian visual model (see Table 2).

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

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

Table 2 Distances (ΔS) between particular spots on each dummy type based on the reflectance data in respect to the avian visual system

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

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.

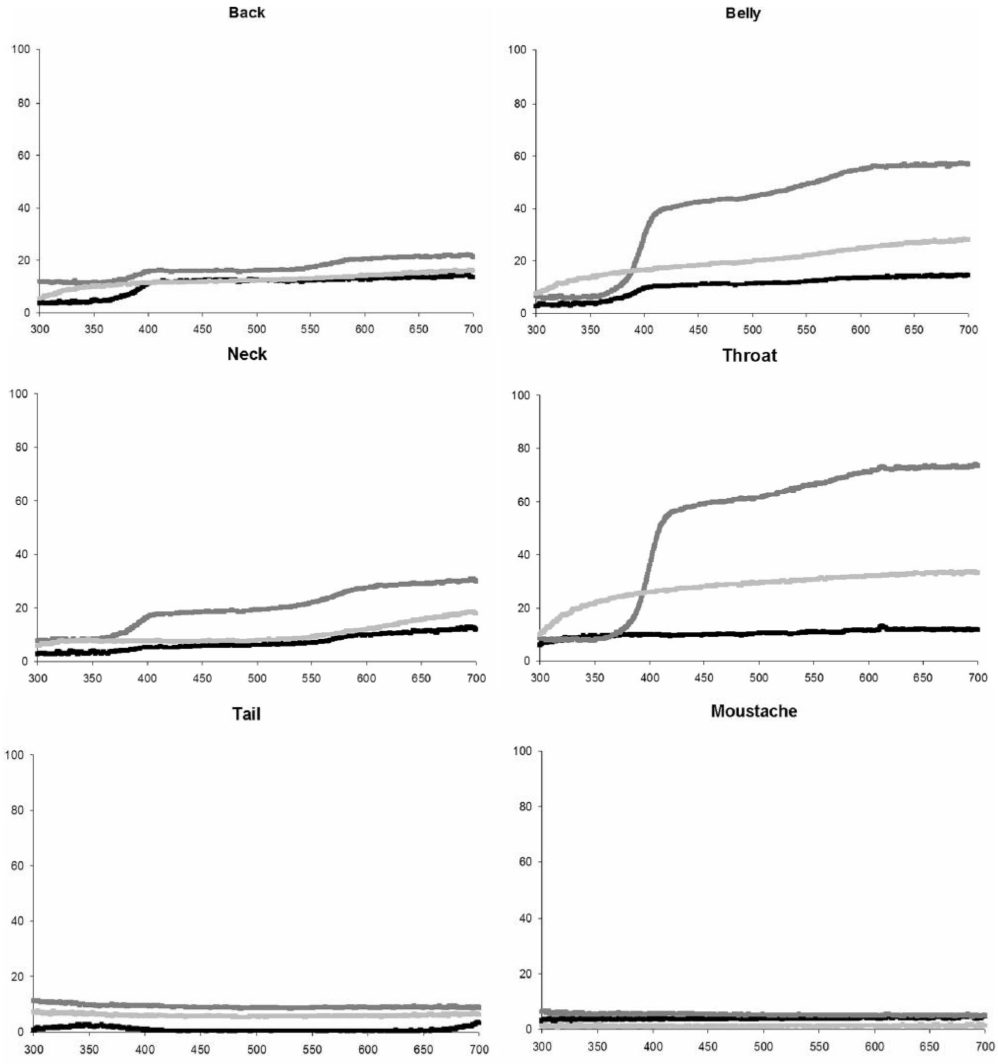
Experiments with pigeons (Cook 1992a) have shown a very high ability to learn to discriminate stimuli with homogenous internal texture, because they have the capacity for global perception of contrasting texture regions. This enables rapid visual perception during flight (Cook 1992b). Troje et al. (1999) 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 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



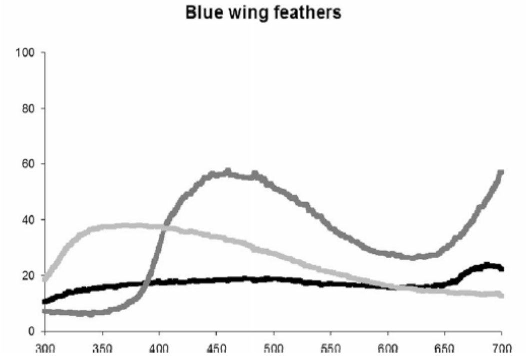


Fig. 4 Average spectral reflectance (mean of five independent measurements on each body part) of seven body parts on each dummy type as depicted in Fig. 1. One hundred percent of reflectance is defined as the light reflected from 'white standard' (WS-2, Ocean Optics). *Light grey line* refers to the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

(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 Polákova´ 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).

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Kapitola 3

Facing a clever predator demands clever responses – Red-backed shrikes (*Lanius collurio*) vs. Eurasian magpies (*Pica pica*)

Michaela Syrová, Michal Němec, Petr Veselý, Eva Landová, Roman Fuchs

Facing a clever predator demands clever responses – Red-backed shrikes (*Lanius collurio*) vs. Eurasian magpies (*Pica pica*)

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OPEN ACCESS
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.

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 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 ounterproductive. 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 nonattacked 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 redbacked 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 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 aussian distribution and partial F-test. The Tukey HSD post-hoc tests were used to evaluate the differences among the levels of categorical predictors.

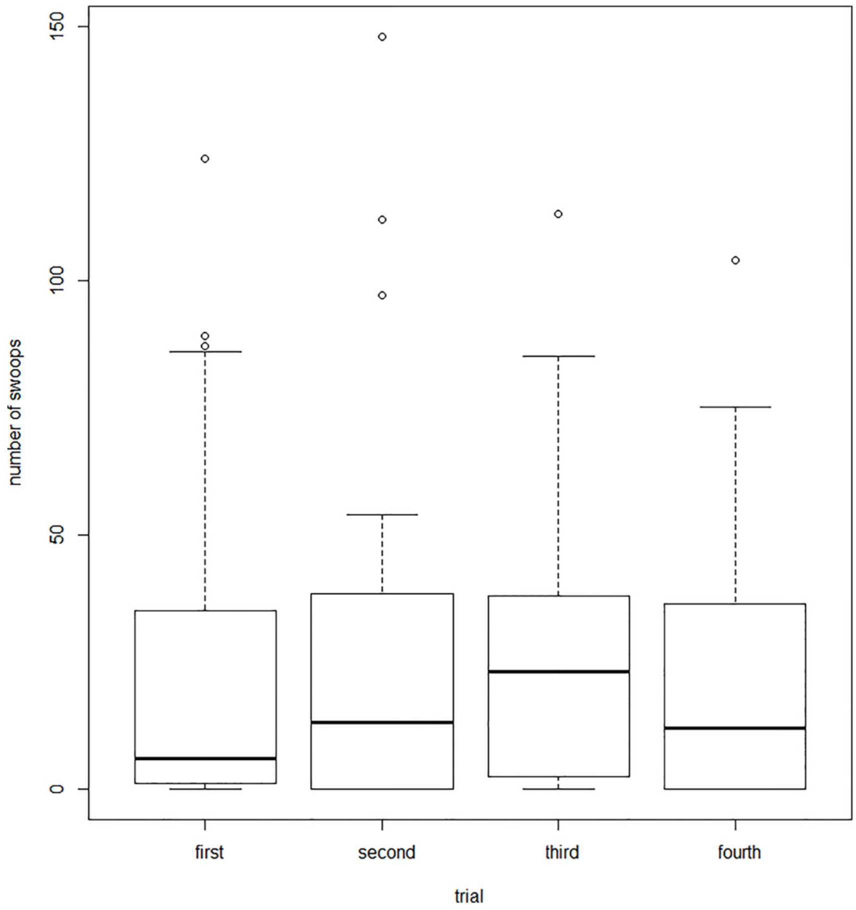

Fig 1. Number of swoops performed by shrikes against the kestrel dummies in particular trials. Line in the middle refers to median, box shows 25–75% of data, whiskers show 10–90% of data and dots are outliers.

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**
	Bystender+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.

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.

Our new results further show that 1) shrikes are able to solve the MPC arisen from the cooccurrence 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.

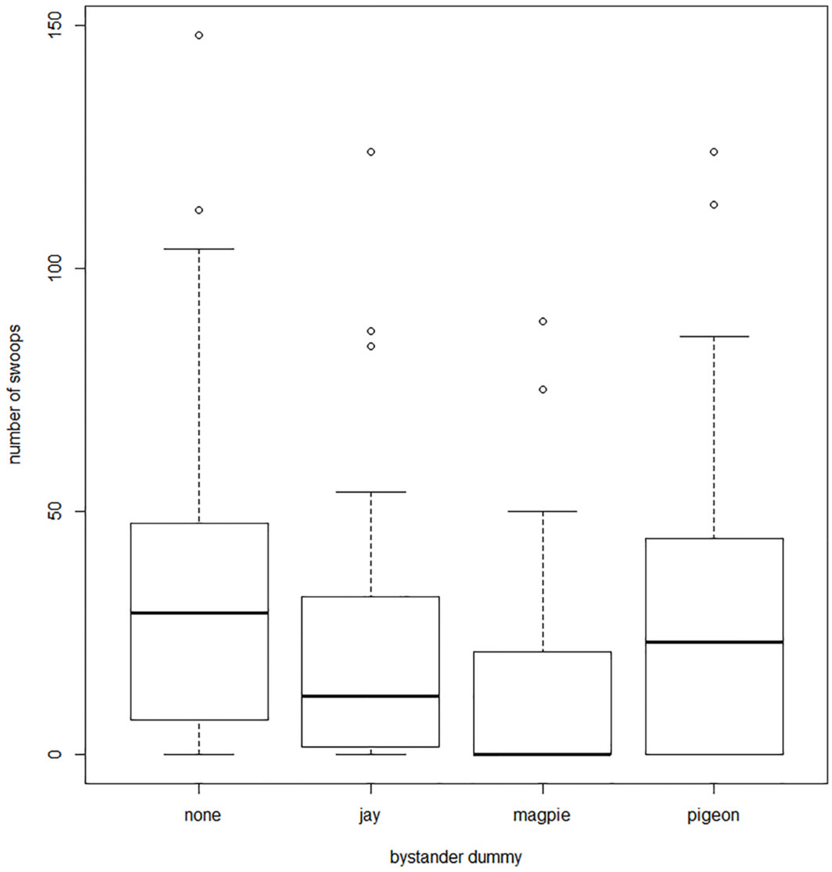

Fig 2. Number of swoops performed by shrikes against the kestrel dummies presented together with three bystander dummies (jay, magpie, pigeon) or alone during the 20-minutes lasting trial. Line in the middle refers to median, box shows 25–75% of data, whiskers show 10–90% of data and dots are outliers.

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].

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 nesting	1	242	0.08	0.91

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 whatwhere-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 result 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.

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Kapitola 4

Responses of nesting Arctic terns (*Sterna paradisaea*) to disturbance by humans

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Responses of nesting Arctic terns (Sterna paradisaea) to disturbance by humans.

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Abstract

Nesting birds often respond to human disturbance as to a predatory act. In the case of the high Arctic, the disturbance of incubating birds may bring further complications due to egg cooling. In addition, it is assumed that birds in the high Arctic are not shy and do not respond to human presence fearfully. We tested how quickly the Arctic terns (*Sterna paradisaea*) nesting in two colonies in Svalbard return to the nest after human disturbance. One colony was situated inside a town where the terns were regularly harassed by human presence. The second colony was on a glacial foreland where breeding terns have limited experience with humans. We found that terns without frequent experience with humans returned to the nest about 5 min after disturbance, while urban terns habituated to human presence returned within a few tens of seconds. The urban terns in this way likely solve the risk of spending too much time off the nest, which could lead under the conditions of the high Arctic to the stopping of embryogenesis. Terns from a remote colony do not show lower hatching success of their eggs than the urban ones, however, incubation and the whole population of terns could be threatened when there is more frequent disturbance by researchers or tourists.

Key words: antipredation behavior, Arctic tern, human impact, nesting behavior, Svalbard

Introduction

Breeding is a crucial period in the life of birds, especially in relation to the threat of predation. Adult animals can decide between a ‘fight or flight’ strategy when encountering a predator, but eggs and nestlings can usually rely only on their crypsis or defense from parents (Curio et al. 1969; Clutton-Brock 1991; Stearns 1992). Both antipredation strategies of the parent birds might have pros and cons (see Caro 2005 for review). If parents decide to be passive and not to defend the nest, relying on the nests’ crypsis, the parents minimize the threat to themselves and save energy, but they may expose the nest to the predator. If they decide to actively defend the nest, they may chase the predator away, but they risk being attacked and spend a lot of energy at the same time (Collias and Collias 1978; Dale et al. 1996; Scheuerlein et al. 2001).

Humans often act as predators of bird nests, or rather are often considered as predators by the breeding birds (e.g., Burger and Gochfeld 1988; Beale and Monaghan 2004; Smith-Castro and Rodewald 2010). Responses to humans may be different, including physical attacks (e.g., chinstrap penguins, *Pygoscelis antarcticus*—Viñuela et al. 1995; Eurasian kestrel, *Falco tinnunculus*—Carrillo and Aparicio 2001), alarm calling (e.g., Leavesley and Magrath 2005; Magrath et al. 2010), and injury pretending (e.g., zenaida dove, *Zenaida aurita*—Burger et al. 1989; lesser golden plover, *Pluvialis dominica dominica*—Byrkjedal 1989), but the most common response is flight. Therefore, one of the main measured behavioral response of birds to human presence at the nest is the flight-initiation distance (Blumstein 2003; Blumstein et al. 2003; Albrecht and Klvaňa 2004). Nevertheless, birds fleeing from the nest face a trade-off between safety for themselves and the threat to nest. Moreover, during their absence at the nest, the eggs and small chicks lack the thermal protection from the incubating parent, which may threaten successful nesting (e.g., Gillett et al. 1975; Piatt et al. 1990; Lord et al. 2001).

Each antipredation behavior may be affected by a set of variables, summarized within the ‘Optimal theory’ (McNamara and Houston 1986; Clark 1994). Differences in investments to nest defense might be caused by varying environmental and social contexts as well as by the condition, sex, and age of the defending parents (Gill et al. 2001; Beale and Monaghan 2004; Abolins-Abols and Ketterson 2017), different types of predators (Patterson et al. 1980; Brunton 1986; Sordahl 1990; King 1999; Strnad et al. 2012; Němec and Fuchs 2014), breeding stage (eggs vs. nestlings; Kruuk 1964; Lemmetyinen 1972; Shedd 1982; Becker 1984; Knight and Temple 1986; Pavel 2006; Strnadová et al. 2018), age of nestlings (Patterson et al. 1980; Curio and Regelmann 1985; Montgomerie and Weatherhead 1988; Redondo and Carranza 1989; Dale et al. 1996; Pavel and Bureš 2001; Pavel 2006; Lima 2009), and, in the case of colonially nesting birds, also by the colony size (Regelmann and Curio 1986; Wiklund and Andersson 1994; Krams et al. 2009) and position of the nest within the colony (Kruuk 1964; Krebs and Davies 1993). Moreover, the reaction to predator might be influenced also by the previous predatory and disturbance events (Fontaine and Martin 2006; Holm and Laursen 2009; Němec et al. 2015).

The familiarity of breeding birds with humans and the risk of being predated by them is also an important factor affecting their antipredation responses. Urban populations of birds have consistently shorter flight initiation distances than their rural counterparts (Møller 2008; Møller et al. 2013). Knight (1984) and Knight et al. (1987) showed that ravens and crows perform the most aggressive nest-defense behavior in areas of low persecution by humans even though the ravens were in an area of low human density and the crows were in an area of high human density. Other study systems suggest that the effect of human presence and persecution to birds decreases with increasing latitude, e.g., birds breeding in Finland and Sweden show lower flight initiation distances than in Spain (Díaz et al. 2013). On the other hand, the willingness of parental risk taking during nest defense in meadow pipits (*Anthus pratensis*) is higher in Norway than in Central Europe (Pavel et al. 2000). The question is to what extent can be these examples generalize to the situation of isolated populations in high Arctic, where the human disturbance is a novel and still relatively scarce phenomenon.

In the current study, we examined the impact of human presence on the behavior of nesting Arctic terns (*Sterna paradisaea*) in Svalbard. The Arctic tern is a colonially nesting bird known for its vigorous mobbing behavior used not only against bird predators, but also ground predators and even against humans (Burger and Gochfeld 1991; Clode et al. 2000). According to IUCN, Arctic tern is globally considered as decreasing (BirdLife International 2018), though detailed information is notoriously lacking. The main effects identified to be responsible for this decrease are predation (Nordström et al. 2002), egging (Gilchrist and Robertson 1999), and food shortage (Schreiber and Kissling 2005; Vigfúsdóttir 2012; Frederiksen et al. 2013; Vigfúsdóttir et al. 2013). According to the IUCN, the other important threatening factor is yachting and other leisure activities, which have led to a significant increase in disturbance of breeding terns (BirdLife International 2018).

In our study, we focused on the threat of human presence on the incubation behavior of Arctic terns in Svalbard. Nesting in the Arctic is very challenging due to severe weather conditions with daily mean temperatures lower than 10 °C during the breeding season (June–July) in Svalbard (Ambrožová and Láska 2017), which places higher demands on the parents in terms of thermo-regulation during incubation and foraging over breeding season in high latitudes (Piersma et al. 2003). Therefore, as a measure of the risk for the eggs in a nest, we decided to measure the latency of parents to return to the nest after being expelled by a human approaching the nest as a proxy of parental investment in the brood. In such an experimental design, the actual threat has already passed, and the parents should calm down and return to the nest as soon as possible to provide heat to the eggs. On the contrary, returning too early means that parents may expose themselves to the threat. Such risk-taking behavior was measured, e.g., by Dale et al. (1996) on pied flycatcher (*Ficedula hypoleuca*) as the time elapsed until the first parent returned to nest after the presence of a predator near the nest. At the same time, the acute necessity to quickly return to the nest could be in conflict with the generally low fear responses of breeding birds to humans in the high Arctic.

We studied the nest-defense behavior of the Svalbard population of Arctic tern in two colonies differing significantly in the presence of humans and disturbance. This allowed us to test the null hypothesis that terns breeding within the town and in the wild show equal latencies of return to the nest after human disturbance.

Material and Methods

Study area

We selected two Arctic tern colonies in Svalbard (the main island Spitsbergen). One colony with 50–60 pairs on the area of 500 m^2 was affected by the presence of humans, being situated within Svalbard´s main settlement, Longyearbyen (GPS: N78° 13.283′ E15° 35.868′; Fig. 1), where the colony is scattered between houses with only few meters to the closest building, road, or pathway. Humans encounter tern nests on a regular basis within this colony. Sometimes, eggs are accidentally damaged by a pedestrian.

The second colony with approximately 200 pairs on the area of 500 m^2 is situated on a glacial foreland on Retrettøya Island in Adolfbukta (GPS: N78° 39.368′ E16° 54.819′; Fig. 1). There is one occasionally inhabited cottage (approximately 10 people for 2 days twice a month) approximately 1800 m from the colony. The permanent human settlement is a polar station 12 km distant (oversea distance). Human visits at this locality are only sporadic (up to 10 persons per week during the breeding season, from June to August). During our stays at the locality, we met only once two canoeists, therefore, our visits were the main disturbance during recording the birds.

Experiments were conducted at the stage when Arctic terns incubate their eggs, in July 2015 and 2016, usually in the afternoon (16:39 ± 3:06, *n* = 66). Our previous

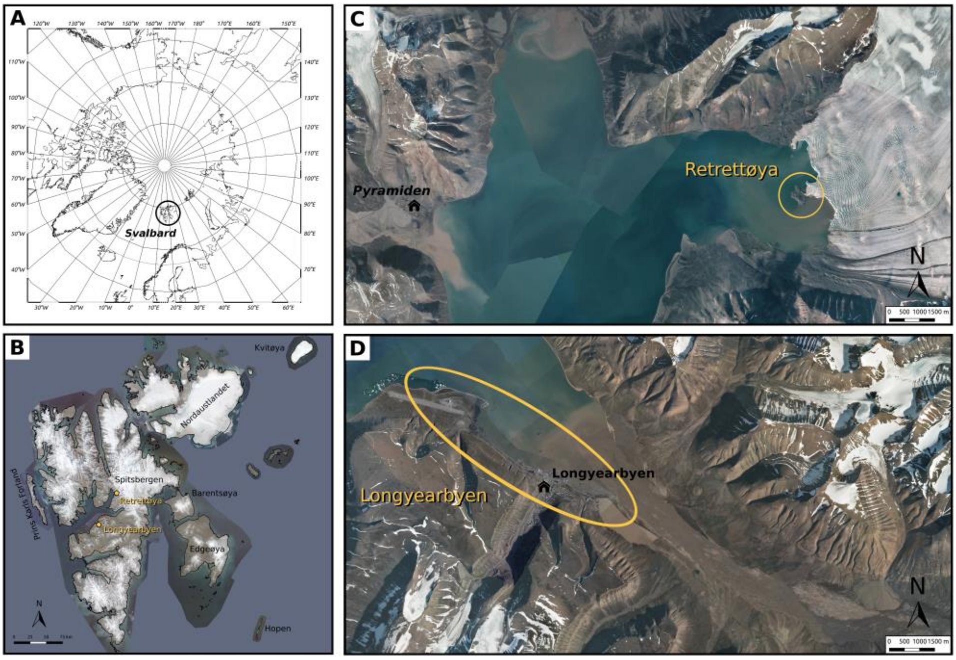

Fig. 1 Map of study locations. A) Svalbard archipelago in the Arctic; B) Svalbard archipelago with both studied colonies; C) Colony Retrettøya; D) Colony Longyearbyen.

research (Hromádková and Pavel personal observation), in which temperature data were collected from Arctic tern colonies at both these localities, showed that there is no difference in the mean daily air temperature between the study colonies (Fig. 2). Generally, the weather conditions were similar (and mild) during the days when we conducted the trials (wind speed: 2.95 ± 1.36 m/s; sum of precipitation: 0.01 ± 0.05 mm; temperature: 8.28 ± 1.58 °C; for detail information see Online Resource 1).

Study species

The Arctic tern is a medium-sized seabird of the family Sternidae without sexual dimorphism. The birds breed in either solitary nests to colonies of up to 500 pairs in Svalbard, on coast or islands, near the water (Burton and Thurston 1957; Lemmetyinen 1972; personal observation). Breeding is usually highly synchronized among pairs within a colony (although in poor season the synchronization can be broken down). In spite of the fact that Arctic terns undertake one of nature's longest migrations (from the Arctic to Antarctica and back—more than 70 thousand kilometers each year— Egevang et al. 2010;

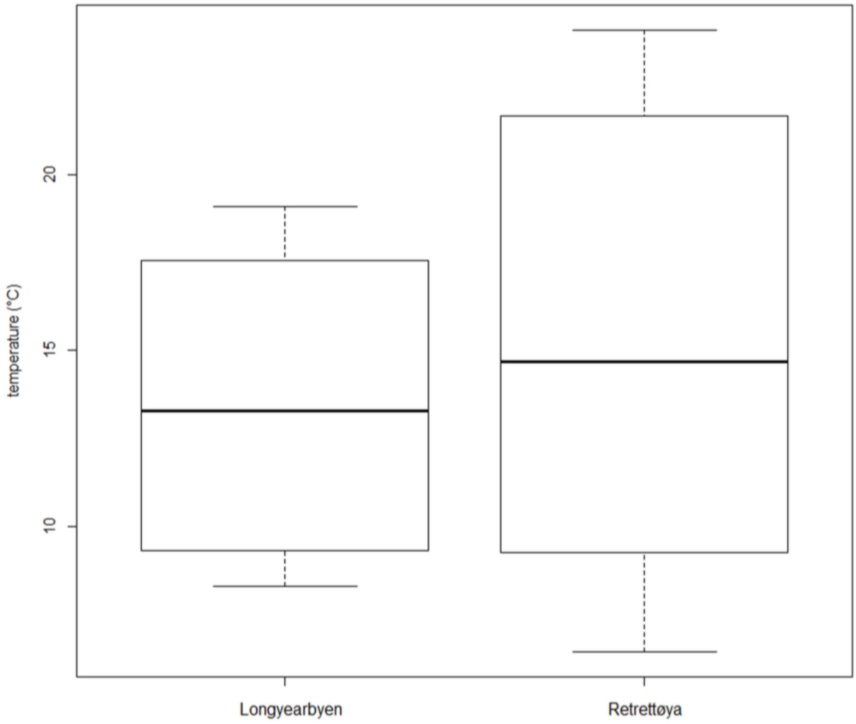

Fig. 2 Mean daily air temperature (°C) at the borders of Arctic tern (*Sterna paradisaea*) nests on two studied colonies in Retrettøya and Longyearbyen (Hromádková and Pavel, personal observation).

Fijn et al. 2013; Volkov et al. 2017; Hromádková et al. in press), they return to the same colony each year (Perrins 2003; Devlin et al. 2008). The nest is usually represented by a depression in the ground where terns lay one to three mottled and camouflaged eggs depending on food availability (Kilpi et al. 1992; Monaghan et al. 1992; Suddaby and Ratcliffe 1997).

Terns defend their nests and young very aggressively. They can attack humans and large predators, usually striking the top or back of the head and defecating. Although it is too small to cause serious injury to an animal of a human's size, it can efficiently repel many birds and mammalian predators (Cramp 1985).

Experimental design

We searched for nests within each colony and subsequently conducted the experiments at nests with a finished, already incubated clutch, before the chicks hatched. We assessed the approximate beginning of incubation using the egg floating test (measured in weeks: 1.91 ± 0.77, $n = 66$). The experimental method consisted first of an observer placing a video camera facing a tested tern's nest. The observer then went away from the nest to a distance of at least 30 m and waited till parents were habituated to the presence of the camera and the observer and sat on the eggs. After that, the human intruder (MS in 2015 and TH in 2016) went towards the nest, stopping directly above the nest, and then went back to the original distance of 30 m. The intruder walked slowly without any conspicuous behavior and movements. The reaction of the terns was recorded on the camera. We measured the time till the parent sat back on its nest (following Dale et al. 1996). The observation was ended after the parent bird either sat on the nest or after 15 min. If the parent did not return within 15 min, the latency was recorded as 900 s.

Each nest was recorded only once. For each trial, we noted the colony identity (Longyearbyen and Retrettøya), nest GPS location, number of eggs in the nest, stage of incubation (days), number of neighbors within 20 m, and date of experiment.

Statistical analyses

The response variable was the latency of getting back to the nest after a disturbance (measured as time in seconds). To meet the demands of normal distribution, these data were transformed by logarithmic transformation [log(latency)]. Firstly, we compared the logtransformed latency of getting back to the nest after disturbance between the experiments conducted at the Longyearbyen in 2015 and 2016. We showed that there is no difference ($F_{1,31} = 2.82$, $p = 0.10$) and therefore, we decided to lump these data together. We ran a linear mixed effect model (LMM) to assess the effect of the predictor variables (command lmer in R package lme4; Bates et al. 2015) with colony size as a random factor. The model included two categorical predictor variables, colony identity and the number of eggs (values 'one' and 'two'). There were also three continuous predictor variables:

stage of incubation (days), date, and number of neighbors within 20 m from the tested nest. The effect of particular predictors was assessed during stepwise forward selection using likelihood ratio test (*Chi*-square) to compare subsequent models.

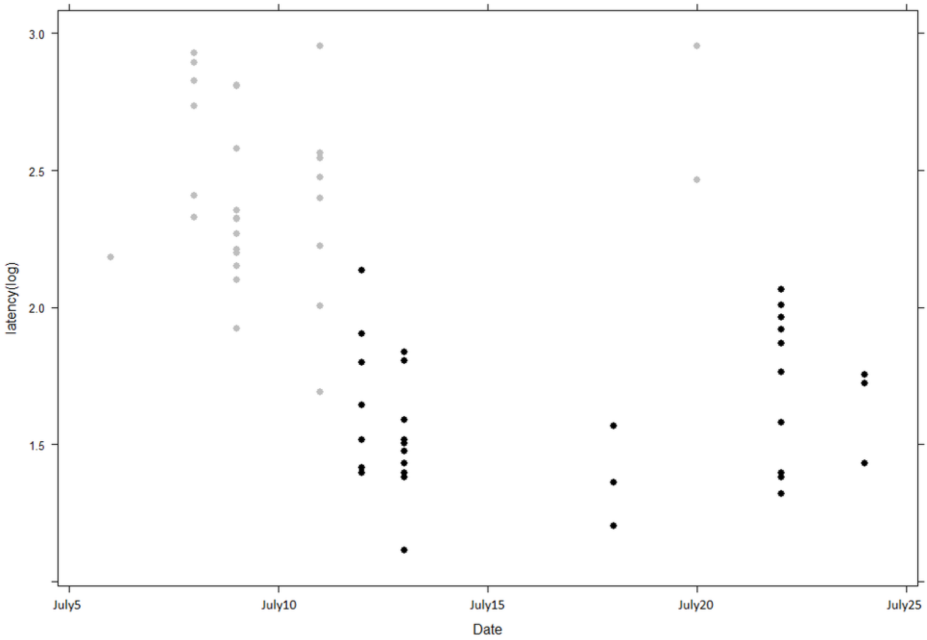

Fig. 3 Latency of the parent Arctic tern (*Sterna paradisaea*) to return to the nest after being disturbed by a human (measured in seconds, log transformed) in the course of the season starting with the day of the first trial conducted. Seasons 2015 and 2016 were lumped together. Black dots refer to the Longyearbyen colony and gray dots to the Retrettøya colony

Results

We recorded the reaction of parents for 33 nests in each colony for a total of 66 nests tested (Longyearbyen 23 + Retrettøya 33 in 2015 and Longyearbyen 10 in 2016, for more details see Online Resource 1).

We found a strong difference in the reaction of the terns between our two studied colonies. Terns in Longyearbyen returned to the nest faster after a disturbance than the birds in Retrettøya (Linear model, F1,59 = 146.67, $p < 0.01$, Fig. 3). We also found a weak effect of the date when the experiment was conducted (Table 1); terns returned to the nest faster with increasing date of the experiment (later in the breeding season; Fig. 4). Other factors (stage of incubation, number of eggs, stage of incubation, and number of neighbors within 20 m) had no effect (Table 1).

Table 1 Effect of particular predictor variables on the latency of return to the nest after human disturbance (Linear model)

	AIC	BIC	*Chi* value	*df*	*Pr* (>Chisq)
Intercept	45.590	52.159			
Colony identity	**37.12**	**45.88**	**10.47**	**1**	**<0.01**
Stage of incubation	39.59	52.73	1.53	2	0.47
Number of eggs	41.53	56.85	0.06	1	0.80
Date of experiment	**40.31**	**73.15**	**17.23**	**8**	**<0.05**
Number of neighbours within 20 m	40.00	75.03	2.31	1	0.13

Bold indicate variables with significant effect

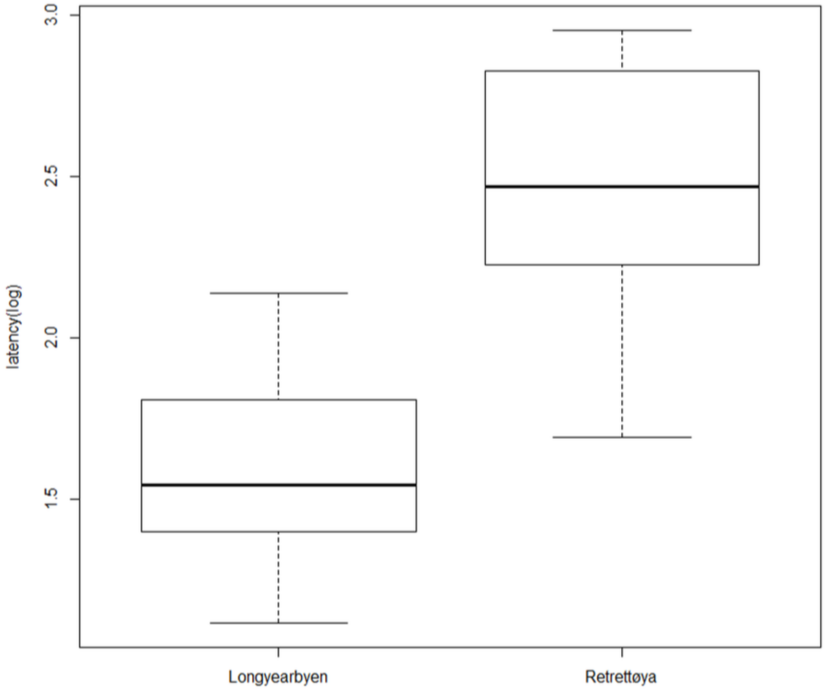

Fig. 4 Latency of the parent Arctic tern (Sterna paradisaea) to return to the nest after being disturbed by a human (measured in seconds, log transformed) in two colonies (Retrettøya and Longyearbyen)

Discussion

We found that terns from the colony within the human settlement returned to the nest significantly faster than terns breeding in pristine habitat at the edge of glacier. This difference is most probably caused by the habituation of the urban terns to human presence. Numerous studies have investigated the habituation of human presence in nesting behavior, e.g., Vennesland (2009) showed that breeding Great blue herons (*Ardea herodias*) reduced their behavior response by decreasing the response distance and habituated to the repeated approach of people, similarly Pfeiffer and Peter (2004) showed that south polar skuas (*Catharacta maccormicki*) are able to reduce aggressiveness in frequently visited areas. Moreover, Beale and Monaghan (2004) showed a habituation effect in nest occupancy patterns of the ruddy turnstone (*Arenaria interpres*), where young birds were forced into traditionally more disturbed areas. Burger and Gochfeld (1991) studied parameters correlated with flush distance of 138 species in India. They found that the flush distance is lower as the number and activities of near-by people are higher. On the other hand, ducks (*Anas platyrhynchos*) generally increase flushing distances in response to repeated human visits to the nest, most probably because these birds increasingly perceive a risk to themselves from the predator repeatedly approaching (Albrecht and Klvaňa 2004). Pfeiffer and Peter (2006) showed same increase of activity and nest defense in southern giant petrel (*Macronectes giganteus*), brown skua (*Catharacta antarctica lonnbergi*), and south polar skua (*Catharacta maccormicki*) in irregularly and unpredictably disturbed areas.

Nevertheless, crows and ravens show a lower rate of antipredation behavior when people persecute them, despite the level of urbanization of their locality (Knight 1984; Knight et al. 1987). This suggests that these birds might be more sensitive to a real disturbance than to simple human presence and urbanization level.

Breeding in human settlement confronts the terns with people approaching the tern nests on regular basis, which forces the parents to leave the nest too often. The parents needed to solve the trade-off between staying at the nest or leaving too early after the disturbance and exposing their eggs. Birds in the Arctic cannot afford to leave the nest for a too long period since there is a high risk of cooling. There were some studies showing that eggs of Arctic birds may survive cooling below 10 °C for many hours (Norton 1972; Roby and Ricklefs 1984); nevertheless, the embryos develop slowly (reviewed in Webb 1987) and there are high energy demands on the incubating parents (Tulp et al. 2012). It has been repeatedly shown that Arctic birds have almost 100% attentiveness on the nests with both parents incubating (e.g., Cresswell et al. 2003; Martin and Wiebe 2004; Bulla et al. 2014). As a consequence, the urban terns learned to overcome their natural fear of people and return to the nest quickly.

The terns from the colony without human presence returned to the nest approximately 5 min after a disturbance, which is ten times longer than the time needed by the terns from the colony in the main settlement. It is obvious that they are not used to such a disturbance and, since it is not common, they are not forced to return to the nest quickly to prevent the risk of their eggs cooling.

Food supply may be another, alternative explanation of the observed difference in the terns' behavior between the two studied colonies. Terns hunting near the glacier might have significantly richer food sources (krill, small fish— Lydersen et al. 2014), which may substantially affect their investment in offspring. Animals feeding in particularly rich habitats may be able to afford more of an interruption in the breeding behavior during a disturbance than those in poor feeding areas where individuals must devote all their available time to breeding (Gill et al. 2001). On the other hand, Beale and Monaghan (2004) showed that individuals in good conditions are less sensitive to disturbance. Anyway, we have no exact data on the foraging ground location of both studied localities. Based on personal observation, a significant portion of birds forages at the shores within several hundreds of meters from the colony; nevertheless, there may be local, more distant, and rich food sources, exploited by both colonies, which remain undiscovered.

Another possible explanation might be the generally higher predation pressure in colony Longyearbyen. It was well documented that birds living in more urbanized habitats suffer higher predation pressure (Jokimäki and Huhta 2000; Thorington and Bowman 2003; Jokimäki et al. 2005; López-Flores et al. 2009; Rivera-López and MacGregor-Fors 2016). Nevertheless, Svalbard is rather an exception in this case. Cats are forbidden in the town and dogs are kept in pens, so the higher predation pressure might be expected rather in the foreland of the glacier where polar bears and Arctic foxes are more common. On the other hand, the most common predators of tern nests are gulls and skuas, which occur at both localities. We have data of hatching success from both localities (Hromádková et al. personal observation), which can be to some extent understood as a proxy of predation pressure, and we showed no difference between both tested localities.

The weather conditions (temperatures and especially winds) are another factor affecting the nest attentiveness in Arctic birds (Bulla et al. 2015). Nevertheless, both our localities do not differ substantially in any measured weather conditions, at least during the days when the trials were conducted (Fig. 2, Online Resource 1). We can therefore suggest that the effect of weather on our results is low. Anyway, if the temperature near the glacier would be significantly lower than temperatures in the town (which one could expect), there would be higher pressure on the terns to return faster to their nests in the Retrettøya colony (as shown for other bird species—Larson 1960; Gramza 1967; Regelmann and Curio 1983), which is the very opposite of our results.

However, terns in the Retrettøya colony do not have a significantly lower degree of hatching success than terns in the Longyearbyen colony (Hromádková et al. personal observation). This suggests that there is no direct effect of the time spent incubating on the embryogenesis. In our study, we found a significant effect of date in the season when the experiment was conducted, in that terns returned to the nest faster at the end of the nesting season than at the beginning. This effect supports the reproductive value hypothesis (Patterson et al. 1980; Redondo 1989; Redondo and Carranza 1989; Viblanc et al. 2016), which posits that, with older clutches, parents have already a high amount invested and thus will continue to make further investments, e.g., nest defense. However, in our case, this effect was just a by-product of the fact that there was high synchronization of breeding between terns in both studied colonies. Terns in the Longyearbyen colony nested later in the season and, because their latencies were significantly lower than in the Retrettøya colony, the effect of date was pronounced as well (Fig. 4). However, there was no significant date effect in the case of the stage of incubation (i.e., age of clutch). It is obvious that behavior such as coming back to the nest does not reflect the existing level of parent investment in the clutch. This can be caused by the fact that all our experiments were conducted in the incubation stage. The variability in parental investment during the early stage of breeding is usually too low to affect the antipredation behavior of parents (see e.g., Strnadová et al. 2018).

The Arctic tern colonies in our two studied locations importantly differed in the number of breeding pairs. Both colonies were covering approximately equal area (around 500 m2); nevertheless, the colony in Longyearbyen housed approximately four times less nests (50 vs. 200). This suggests that the Longyearbyen colony was of much lower density, which could importantly affect the behavior of incubating birds when disturbed. Several studies showed that colonially breeding birds tend to respond more intensively to equal threat, when the colony is bigger. Burger and Gochfeld (1988) showed that, in general, the flush distance of Common ostrich (Struthio camelus) is negatively correlated with nest density, while the number of birds attacking the predator was positively correlated with nest density. In general, this suggests that birds feel safer in denser and larger colonies, with more neighbors to come to their aid. Anyway, there was no significant effect of the number of neighboring nests, i.e., the colony density on the latency of the return of incubating birds. The reason why we were not able to show this effect may reside in the fact that the variability of the densities was equally distributed within both colonies and the effect of this factor was far weaker than the difference between both colonies.

Conclusion

Terns breeding within human settlement returned to their nests more quickly than those breeding pristine environment. At the same time, the level of disturbance did not affect egg survival at these two colonies. Terns are able to adapt their incubation behavior to different disturbance levels to meet the optimal incubation performance and to overcome disturbances that may affect the survival of the clutch.

Acknowledgment

We would like to thank Keith Edwards for English language editing and Jakub Ondruch for help with the map of study area. We also thank all referees for helpful reviews of this manuscript.

Author contributions

MS participated on the design of experiments, collected most of the data, conducted the data analyses, and participated on the manuscript preparation. TH participated on the data collection and manuscript preparation. VP participated on the design of experiments and manuscript preparation. PV participated on the manuscript preparation. All authors have read the final version of the manuscript.

Funding

The study was supported by Grant Agency of University of South Bohemia 151/2016/P and 048/2019/P and from European Regional Development Fund-Project No. CZ.02.1.01/0.0/0.0/16_013 /0001708. Nevertheless, the authors wish to thank the Czech Arctic Scientific Infrastructure of the University of South Bohemia in České Budějovice—the Josef Svoboda Station in the Svalbard (CzechPolar2 project LM2015078 supported by Ministry of Education Youth and Sports of the Czech Republic).

Compliance with ethical standards

Conflict of interest

The authors declare no conflict of interests.

Ethical approval

All experiments were conducted in accordance with the valid laws and regulations of Norway. Behavioral experiments on the wild birds were enabled by license for research experiments in Svalbard (in 2015: RiS-ID 10363, and in 2016: RiS-ID 10394).

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s0030 0-020-02641 -2) contains supplementary material, which is available to authorized users.

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Kapitola 5

Ravens respond to unfamiliar corvid alarm calls

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Ravens respond to unfamiliar corvid alarm calls.

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Abstract

Eavesdropping on heterospecific alarm calls is a crucial source of information for many species (including corvids) and it is effective especially if these species form mixed-species flocks, have a similar spectrum of predators, and share habitat. Previous research on wild common ravens (*Corvus corax*) has shown that they react to the jackdaws' alarm call. We tested their responses to the heterospecific alarm calls of various bird species differing in familiarity and taxonomical relatedness to ravens. Two other corvid species (the blue jay *Cyanocitta cristata* and the European jay *Garrulus glandarius*) and two non-corvids (the black-headed gull *Chroicocephalus ridibundus* and the laughing gull *Leucophaeus atricilla*) were presented. We played back the tested alarm calls to free-ranging ravens at a feeding site and observed the ravens' responses to particular stimuli. We observed three behavioural responses made by the tested ravens: flying away, freezing (ceasing to move and crouching on the ground), and vigilance (observing the surroundings). The ravens responded to the Eurasian jay alarm call by freezing and flying away and to the blue jay alarm call by freezing and vigilance. The laughing gull alarm call induced mostly vigilance and the black-headed gull alarm call did not elicit any reaction. The responses to the alarm calls of both jays were similar to the responses to the playbacks of conspecific alarm calls, used as control (as well as to the response to a jackdaw alarm call from the previous study), which may point to the existence of a specific corvid characteristic in their alarm calls. The response to the alarm calls of both American species included vigilance, which suggests an uncertainty about the meaning of the call.

Keywords: Antipredator behaviour, Corvid, Gull, Heterospecific call, Jay, Raven

Zusammenfassung

Kolkraben reagieren auf Alarmrufe von anderen Rabenvögeln, selbst wenn diese unbekannt sind

Viele Vögel können über das Belauschen der Alarmrufe von anderen Arten wichtige Informationen über potentielle Gefahrensituationen sammeln, besonders wenn sie mit diesen Arten gemeinsame Gruppen bilden, ein ähnliches Spektrum von Raubfeinden haben, und sich ein Habitat teilen. Jüngste Forschung hat gezeigt, dass Kolkraben auf die Alarmrufe von Dohlen reagieren. Wir haben hier die Reaktion von Raben auf die Alarmrufe von mehreren Arten getestet, die den Raben unterschiedlich gut bekannt sind bzw. die mit Raben unterschiedlich eng verwandt sind. Wir verwendeten hierzu zwei Arten von Rabenvögeln (Blauhäher *Cyanocitta cristata* und Eichelhäher *Garrulus glandarius*) und zwei Möwenarten (Lachmöwe *Chroicocephalus ridibundus* und Aztekenmöwe *Leucophaeus atricilla*). Wir spielten die Alarmrufe dieser Arten freifliegenden Kolkraben vor, während diese sich an einem Futterplatz aufhielten und beobachteten folgende Reaktion der Raben auf die Alarmrufe: Abflug, Stillstand (Innehalten in Bewegung und Niederbücken Richtung Boden), oder Wachsamkeit (visuelles Erkunden der Umgebung). Auf Eichelhäheralarm reagierten Raben mit Stillstand und Abflug, auf Blauhäheralarm mit Stillstand und Wachsamkeit, auf Alarm von Aztekenmöwen mit Wachsamkeit, und auf Lachmöwen zeigten sie keine messbare Reaktion. Die Reaktionen auf beide Häherarten waren ähnlich wie die Reaktion auf arteigene Alarmrufe, die als Kontrolle dienten (ebenso wie die Reaktion auf Alarmrufe von Dohlen in der vorigen Studie), was auf spezielle Merkmale innerhalb der Alarmrufe von Rabenvögeln deutet. Die Reaktion auf die Alarmrufe der beiden amerikanischen Arten beinhaltete Wachsamkeit, was auf eine Unsicherheit in Bezug auf die Bedeutung der Rufe hinweist.

Electronic supplementary materialThe online version of this article (https://doi.org/10.1007/s1033 6-020-01781 -w) contains supplementary material, which is available to authorized users.

Introduction

The alarm call is an important antipredator strategy increasing the fitness of all species that eavesdrop on it (Marler and Slabbekoorn 2004; Caro 2005). We can divide alarm calls into three categories according to the relationship between the warning and the warned individuals: altruistic (profitable for the warned individual now, but reciprocal in the future), mutualistic (profitable for both) and selfish (profitable for the warning individual and harmful for the warned individual; Caro 2005). Besides conspecific alarm calls, which are usually driven and maintained by kin selection, we can also distinguish heterospecific alarm calls. Interspecific antipredator reactions have been described in more than 70 species including mammals, birds and reptiles (Magrath et al. 2015). Overall, both mammals and reptiles eavesdrop on birds more frequently than they do on other animal groups, as birds seem to be a trustworthy source of information due to their wide landscape view, excellent eyesight, and loud alarm calls (Magrath et al. 2015). While the use of heterospecific eavesdropping is typically based on a mutualistic relationship with all participants profiting from enhanced predator detection, it can also reflect forms of commensalism, with some species exploiting the skills of others (e.g. Lea et al. 2008; Ito and Mori 2010). Previous studies have identified several conditions influencing the alarm call information transfer between individual species: suffering from the same predators (Rainey et al. 2004; Kitchen et al. 2010), sharing the same habitat (Martínez and Zenil 2012), and/ or forming mixed-species groups (Goodale and Kotagama 2005; Griffin et al. 2005).

The sound of alarm call must encompass specific parameters to overcome deformation, attenuation, and obstacles caused by the given environment. An alarm call should be urgent, but also undetectable by predators—heterospecific alarm calls are often structured as narrow-frequency ranged, high-pitched tones, which are hard to localize (e.g. passerines' 'seet call'; Bradbury and Vehrencamp 2011). In contrast, a few heterospecific alarm calls are broadband calls which spread more easily through open spaces (e. g. *Corvus*, Corvidae). Due to these specific physical demands on alarm calls, evolutionary pressure has produced alarmcalls of similar parameters. This similarity often results in comprehension between species (Wiley and Richard 1982; Ghirlanda and Enquist 2003; Fallow et al. 2013). The recognition of a heterospecific alarm call could then be based on a comparison between the unknown call (heterospecific) and a conspecific alarm call and the detection of the same parameters (Ghirlanda and Enquist 2003), thus gaining the ability to react to a wider range of alarm calls and avoid the risk of ignoring an alarm (Searcy and Nowicki 2005). This may even result in comprehension between species that cannot meet in nature, but whose alarm calls have been formed similarly by evolution. For instance, European tits respond to the alarm calls of their American relatives (Randler 2012), Australian fairy-wrens (*Malurus cyaneus*) respond to those of some allopatric congeners (Fallow et al. 2011), and Australian apostlebirds (*Struthidea cinerea*) respond to the mobbing calls of non-relative North American Carolina wrens (*Thryothorus ludovicianus*; Johnson et al. 2003). Some alarm calls are easier to learn and remember (Guilford and Dawkins 1991) because they are similar to known alarms or because they have specific properties that are characteristic of alarm calls in general—harsh or high-pitched narrowband tones, which are hard to locate (Magrath et al. 2015).

Even though corvids are quite unusual passerines with respect to their song (it is usually quiet and inconspicuous), they are characterized by the exceptional wide range of varied calls they are able to modulate (Thompson 1982, Hoyo Calduch et al. 2009). The wide repertoire (inevitably including alarm calls) of their calls is the result of their unusually complex social life strategy. In contrast to this high variability, there are relatively few studies dealing specifically with corvid alarm calls. Some jay species are known for their conspicuous alarm calls (e.g. blue jay, *Cyanocitta cristata*; Dahl and Ritchison 2018). The calls of Eurasian jay (*Garrulus glandarius*) have been shown to be eavesdropped, e.g. by the red squirrel (*Sciurus vulgaris*; Randler 2006), European hare (*Lepus europaeus*; Klimšová and Policht 2011), roe deer (*Capreolus capreolus*; Klimšová and Policht 2011), as well as the allopatric impala (*Aepyceros melampus*; Klimšová and Policht 2015).

Several studies have shown the ability of corvids to produce alarm calls in response to a threat represented by various predators, e.g. Yorzinski and Vehrencamp (2009). While American crows (*Corvus brachyrhynchos*) emit the same types of vocalizations in response to the great horned owl (*Bubo virginianus*) and racoon (*Procyon lotor*), there are studies showing that other species with complex social structure use specific alarm calls when confronted with predators varying in the threat they represent (Veen 1977; Hailman 1989; Griesser 2008; Krama et al. 2008). A detailed study on the cooperatively breeding Siberian jay (*Perisoreus infaustus*) showed that they are able to differentiate between particular predator categories and communicate the threat they pose by altering their mobbing call (Griesser 2009). Siberian jays uttered 'perched hawk calls' and 'ki-ki calls' in the presence of a hawk mount and 'croaks' and 'gargles' mainly towards an owl mount (Griesser 2009). Corvids were shown to modify the speed, length and rate of their alarm calls according to the threat the particular predators represent (Griesser 2009; Yorzinski and Vehrencamp 2009; Dahl and Ritchison 2018).

Several corvid species have a high-pitched, harsh, and grating alarm call with high energy thus with high audibility. These parameters enhance the eavesdropping of these alarms by other species. For instance, owls and raptors (7 species) react to American crow and blue jay alarm calls (Consla et al. 2012). Contrary to the mobbing calls of smaller passerines (*Poecile atricapillus*, *Vireo solitarius*), the mobbing calls of corvids induced stress and behavioural changes in raptors, which may be a result of the more extensive sharing of predators by corvid and raptors than by small passerines and raptors. Moreover, raptors with experience of these alarm calls from the wild reacted to crow and jay calls (in playback) considerably more strong than individuals which were raised in captivity. Steller's jays (*Cyanocitta stelleri*) are able to differentiate between predators during visual and playback experiments using different alarm calls in response to them (Billings et al. 2017). Steller's jays modified their reaction on the basis of a combination of the predator's species and the type of stimuli.

An experimental study with wild carrion and hooded crows (*Corvus corone corone*, *Corvus corone cornix*; Bílá et al. 2017) tested their response to conspecific and heterospecific alarm call playbacks when groups of the crows were foraging in different enclosures of Vienna Zoo. Contrary to expectations, the crows (of either sub-species) were equally responsive to the playbacks of crows and jackdaws (*Corvus monedula*) in this setting. The two species sporadically co-occur in and around the city of Vienna (Wichman et al. 2010), but share their habitat and predators to a large extent, which would possibly explain this finding.

Using similar methods as Bílá et al. (2017), Nácarová et al. (2018) tested the response of wild common ravens to conspecific and heterospecific alarm call playback when groups of ravens were foraging in different enclosures of Cumberland Wildlife Park, near Grünau im Almtal, Austria (wild boars and wolves). As ravens are the largest of all corvids, they face only a few potential predators, and so it might be expected that their reaction to alarm calls would be rather poor. On the contrary, the common raven is a highly social species forming a large flock with a complex social structure and the use of alarm calls may thus be quite advanced. Ravens responded to jackdaw alarm calls even though they do not form mixed-species flocks and more importantly, they share only a small part of their respective predators' spectra (as a jackdaw is significantly smaller than a raven).

Based on this study on ravens, we decided to test the response of ravens to the alarm calls of other corvid species, but also to those of non-related gull species. We prepared our experimental design to test three hypotheses:

1. Ravens respond to any alarm.
2. Ravens respond only to corvid alarms.
3. Ravens respond only to familiar alarms.

To test these hypotheses, we presented free-ranging ravens with the alarm call playbacks of two corvid species (the familiar Eurasian jay and the unfamiliar blue jay) and two gull species (the familiar black-headed gull (*Chroicocephalus ridibundus*) and the unfamiliar laughing gull (*Leucophaeus atricilla*).

Methods

Experimental area and studied species

This study was performed at the Cumberland Wildlife Park, near Grünau im Almtal, Austria (47.8070° N, 13.9505° E). Our study species was a wild population of the common raven occurring in the park and its immediate surroundings. As an experimental area, we chose the wild boar (*Sus scrofa*) enclosure where ravens commonly forage. The wild boars enclosure (approximately 5200 m2, Supplement 3) is open, with several large coniferous trees on both sides of the fence. These trees provide a safe place for ravens and also high vantage points for surveying the surrounding.

We ran experiments from October 4, 2017 to October 15, 2017, from January 7, 2018 to February 4, 2018 and from September 17, 2018 to October 17, 2018. During the non-breeding season, 80–130 ravens per day visit the park (Drack and Kotrschal 1995). The population of ravens roaming within the zoo area consists mainly of juveniles, non-breeding subadults, and non-breeding adults. Breeding adults sometimes visit the feeding areas as well (Drack and Kotrschal 1995). Approximately one-third of the birds were marked with individually coloured wing tags and plastic rings.

Experimental procedure

We ran experiments between 8:00 and 10:00 (under appropriate weather conditions) immediately after the feeding of the wild boar in their enclosure, as many ravens appear during this time. Wild boar feed consisted mostly of bread, fruit, vegetables and various kitchen leftovers. On average 17 ravens (min. 3, max. 35) were present at the beginning of each experiment.

In total, 63 experiments were conducted with six types of playbacks—four of them were heterospecific and two were conspecific (control). Therefore, each playback was repeated 10–11 times. As heterospecific alarm calls, we used the playbacks of two jays and two gulls differing in familiarity to European ravens. The familiar playbacks were the laughing gull and the Eurasian jay, the unfamiliar were the black-headed gull and the blue jay. Two types of raven calls—alarm call and contact call—were used as conspecific, control playbacks. The recordings of the conspecific scolding call of ravens were recorded in a situation where captive ravens were scolding a human intruder (Haidlhof, Austria, Christian Blum). The recordings of heterospecific alarm calls of jays and gulls were downloaded from a freely accessible database (xenocanto.org). We selected responses to a flying hawk (see Supplement 2 for details). We prepared three different variations of

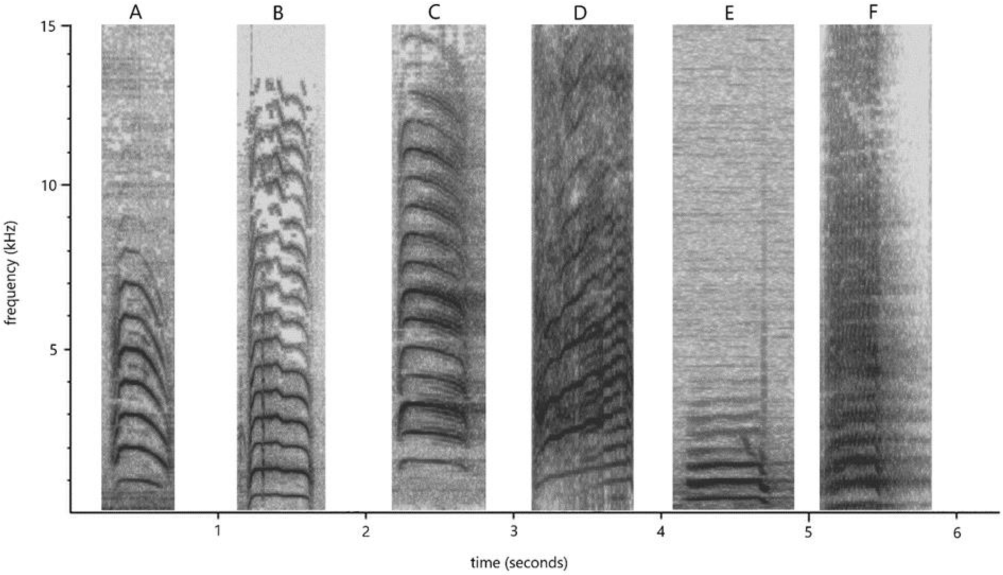

Fig. 1 Sonograms of representatives of all six presented playbacks. **a** Laughing gull (*Leucophaeus atricilla*)—alarm call, **b** black-headed gull (*Chroicocephalus ridibundus*)—alarm call, **c** blue jay (*Cyanocitta cristata*)—alarm call, **d** Eurasian jay (*Garrulus glandarius*)— alarm call, **e** common raven (*Corvus corax*)—contact call, **f** common raven—alarm call

each type of playback. All playbacks were prepared in the Audacity 2.0.6 software (2018 Audacity Team). All playbacks were adjusted to consist of three calls separated by silence, altogether lasting approximately 3 s (see Fig. 1 for sonograms of representative examples). We used the WAV file format to save the sound files.

To minimize possible habituation, we conducted only one trial a day. Moreover, the order of playbacks was randomized, and we never used the same type of playback 2 days in a row.

Each experiment consisted of two phases: (1) a 5- to 10-min-long observation after feeding and (2) the playback phase. The first phase ensured that the experimenters' presence did not cause any change in the ravens' behaviour and that the number of present birds was stabilized during this time. The second phase consisted of playing the playback and recording the ravens' reaction for 10 s directly following the playback. The playbacks were played from a loudspeaker (MIPRO MA-202B) placed approximately 3 m from the food source and 10 m from the observer using a remote control. The sound intensity off the loudspeaker at this distance ranged from 55 to 75 dB. The whole experiment was videotaped by two observers with camcorders (Canon Legria HF R506 and Sony Handycam DCR-SR78). One GoPro camera (HD HERO 2) was placed directly on a fence at the perimeter of the enclosure to record the situation at the feeding site. The observer closer to the feeding site (approximately 13 m from it) monitored the situation at the feeding site and the second observer monitored the behaviour of ravens in the rest of the enclosure (see Supplement Fig. 3 for layout of enclosure with observers).

Table 1 The differences in proportions of ravens (Tukey HSD post hoc test) showing freezing after particular playbacks from the number of ravens present on feeding site before the playback

Freezing	*Leucophaeus atricilla*	*Chroicocephalus ridibundus*	*Cyanocitta cristata*	*Garrulus glandarius*	*Corvus corax*—food call	*Corvus corax*—alarm call
Leucophaeus atricilla		Z = 0.06	Z = 3.02	*Z = 3.06*	*Z = 0.55*	*Z = 3.03*
Chroicocephalus ridibundus	*P* = 0.10		Z = 3.16	*Z = 3.20*	Z = 0.49	*Z = 3.17*
Cyanocitta cristata	*P = 0.03*	*P = 0.03*		Z = 0.58	*Z = −3.43*	Z = 0.60
Garrulus glandarius	*P = 0.03*	*P = 0.03*	*P* = 0.99		*Z = −3.34*	Z = 0.04
Corvus corax—food call	*P* = 0.99	*P* = 0.10	*P = 0.01*	*P = 0.02*		*Z = 3.33*
Corvus corax—alarm call	*P = 0.04*	*P = 0.02*	*P* = 0.99	*P* = 0.10	*P = 0.02*	

Left bottom corner of the table contains P values, right upper corner contains value of the test criterion Z. Statistically significant differences are highlighted in italics

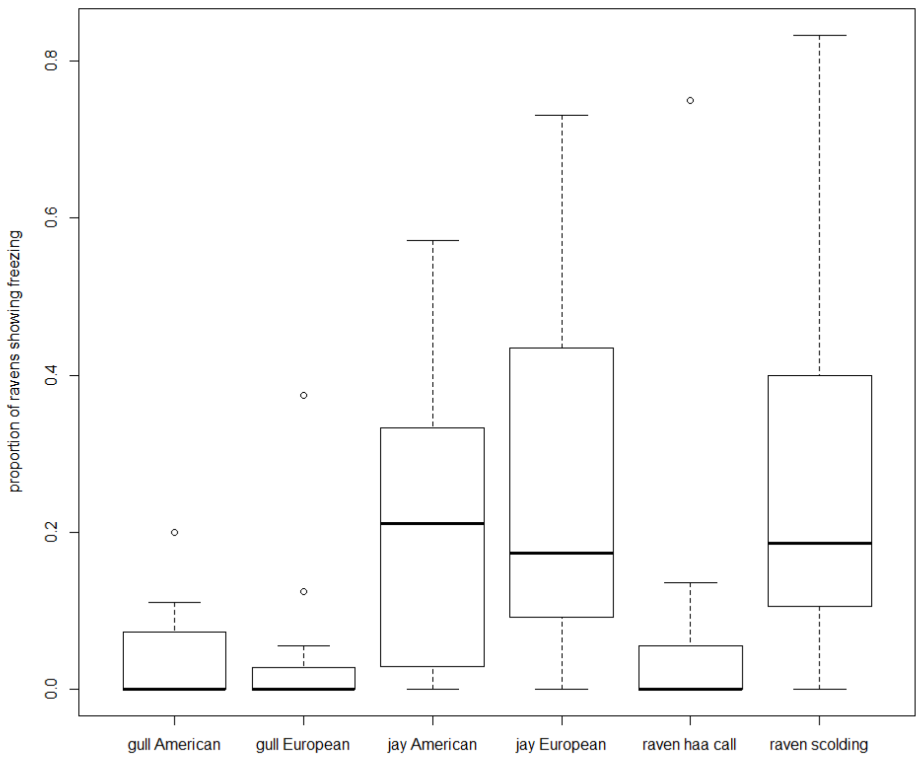

Fig. 2 The effect of particular playbacks on the proportion of ravens showing freezing, out of those present before the playback

We recorded three behavioural responses in the ravens present at the experimental site immediately following the playback: (1) a proportion of ravens (out of those present before the playback) showed freezing (ceasing to move and crouching on the ground); (2) a proportion of ravens (out of those present before the playback) showed vigilance (assuming an upright position and repeatedly checking/scanning the sky); (3) a proportion of ravens (out of those present before the playback) flew away from the feeding site (both, out of the enclosure or to another place within the enclosure).

Statistical analysis

As all three measured parameters were proportions, arcsin transformation was used to meet the demands of normality of the distribution of the variability of residuals. We ran three linear models to test the effect of the playback type with stimulus identity (three from each playback type) included as a covariate. A zero (empty) model was compared with a model including the predictor variable using the likelihood ratio F test. A Tukey HSD post hoc test with Tukey correction was used to compare particular conditions (playbacks). All statistical analyses were computed in R* 3.4.4 (R Development Core Team 2018).

Table 2 The differences in proportions of ravens (Tukey HSD post hoc test) showing vigilance after particular playbacks from the number of ravens present on feeding site before the playback

Vigilance	*Leucophaeus atricilla*	*Chroicocephalus ridibundus*	*Cyanocitta cristata*	*Garrulus glandarius*	*Corvus corax*—food call	*Corvus corax*—alarm call
Leucophaeus atricilla		*Z = −3.13*	Z =−1.46	*Z = − 2.97*	*Z = 3.86*	*Z* = − 2.01
Chroicocephalus ridibundus	*P = 0.03*		Z = 2.61	*Z = − 0.45*	Z = − 0.79	*Z* = 1.56
Cyanocitta cristata	*P* = 0.69	*P = 0.04*		Z = − 2.45	*Z = − 2.47*	*Z* = − 1.05
Garrulus glandarius	*P = 0.03*	*P* = 0.10	*P = 0.04*		*Z = − 0.35*	Z = 2.40
Corvus corax—food call	*P = 0.02*	*P* = 0.97	*P = 0.04*	*P* = 0.10		*Z = 2.42*
Corvus corax—alarm call	*P* = 0.36	*P* = 0.49	*P* = 0.60	*P = 0.06*	*P = 0.05*	

Left bottom corner of the table contains P values, right upper corner contains value of the test criterion Z. Statistically significant differences are highlighted in italics

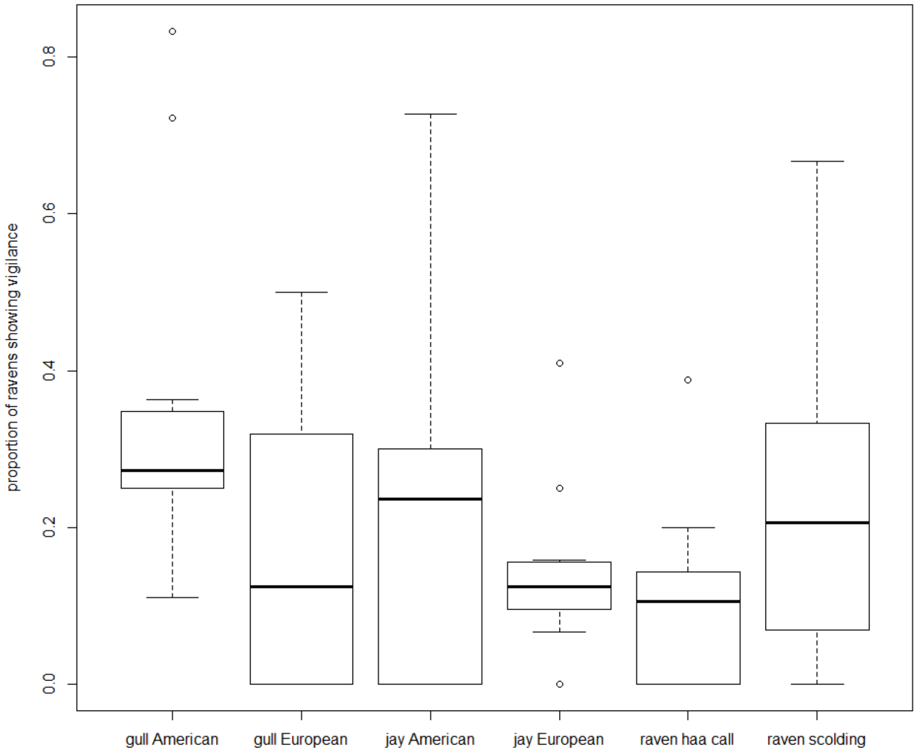

Fig. 3 The effect of particular playbacks on the proportion of ravens showing vigilance, out of those present before the playback

Table 3 The differences in proportions of ravens (Tukey HSD post hoc test) which flew away after the particular playbacks from the number of ravens present on feeding site before the playback

Fly away	*Leucophaeus atricilla*	*Chroicocephalus ridibundus*	*Cyanocitta cristata*	*Garrulus glandarius*	*Corvus corax*—food call	*Corvus corax*—alarm call
Leucophaeus atricilla		Z = 0.86	Z = 2.32	*Z = 2.61*	Z = − 0.40	Z = 0.57
Chroicocephalus ridibundus	P = 0.46		Z = 2.48	*Z = 2.75*	Z = − 0.63	Z = − 0,47
Cyanocitta cristata	P = 0.08	P = 0.09		Z = 0.65	Z = − 1.68	Z = − 0.44
Garrulus glandarius	*P = 0.05*	*P = 0.04*	*P = 0.75*		*Z = − 2.97*	Z = − 1.00
Corvus corax—food call	P = 0.10	P = 0.82	*P = 0.01*	*P = 0.03*		Z = 1.94
Corvus corax—alarm call	P = 0.89	P = 0.90	P = 0.98	P = 0.19	*P = 0.05*	

Left bottom corner of the table contains P values, right upper corner contains value of the test criterion Z. Statistically significant differences are highlighted in italics

Results

The proportion of ravens showing freezing was significantly affected by the type of playback presented (LM, F = 3.15, df = 5, P = 0.01). Ravens showed freezing behaviour significantly more often when both the jays alarm call and the raven scolding call were presented than when both the gulls alarm call and the raven contact call were presented (post hoc Tukey HSD, all Z > 3.00, all P < 0.04; Table 1; Fig. 2).

The playback type also significantly affected the proportion of ravens that showed vigilant behaviour (LM, F = 2.10, df = 5, P < 0.05). Ravens were significantly more often vigilant after the playback of both American species' (jay and gull) alarm calls and raven scolding call than after both European species' alarm calls and raven contact call (post hoc Tukey HSD, all Z > 2.40, all P < 0.05; Table 2; Fig. 3).

The proportion of ravens that flew away after the playback was significantly affected by the type of playback (LM, F = 1.84, df = 5, P < 0.05). Ravens flew away more frequently in reaction to both jay alarm calls and raven scolding call than to both gull alarm calls and raven contact call (post hoc Tukey HSD, all Z values above Z = 2.40, all P < 0.05; Table 3; Fig. 4).

Discussion

The reactions of ravens to the Eurasian jay alarm call included freezing, vigilance, and flying away. These reactions were, in all measured parameters, comparable to (or higher than) the reactions to the conspecific alarm calls. Ravens and jays do not create mixed-species groups and they share only a small spectrum of predators. Boarman and Heinrich (1999) showed that ravens of a North American population were usually killed by gyrfalcons (*Falco rusticolus*), great horned owls, golden eagles (*Aquila chrysaetos*), American martens (*Martes americana*), coyotes (*Canis latrans*), and wolves (*Canis lupus*). This is particularly in concordance with observation from the Alps (T. Bugnyar, personal observation) showing wolves, golden eagles and Eurasian eagle-owls (*Bubo bubo*) to be the main causes of raven death. Contrary to this, Eurasian jays are also killed by northern goshawks (*Accipiter gentilis*; Kennedy 1991; Boal and Mannan 1994; Manosa 1994) and sparrowhawks (*Accipiter nisus*; Griesser and Ekman 2005), and exceptionally also by Ural owls (*Strix uralensis*). As shown in experiments presenting stuffed dummies, ravens do not respond to the goshawk, the main predator of jays (M. Syrová, personal observation), which supports the theory that the spectra of threats perceived by jays and ravens differ. On the other hand, Eurasian jay alarm calls are commonly eavesdropped by multiple species including mammals (Randler 2006; Klimšová and Policht 2011; Klimšová and Policht 2015) as its alarm call is expressive, loud, and conspicuous. This fact might have been the reason for such a prominent reaction by the ravens to jays alarm calls.

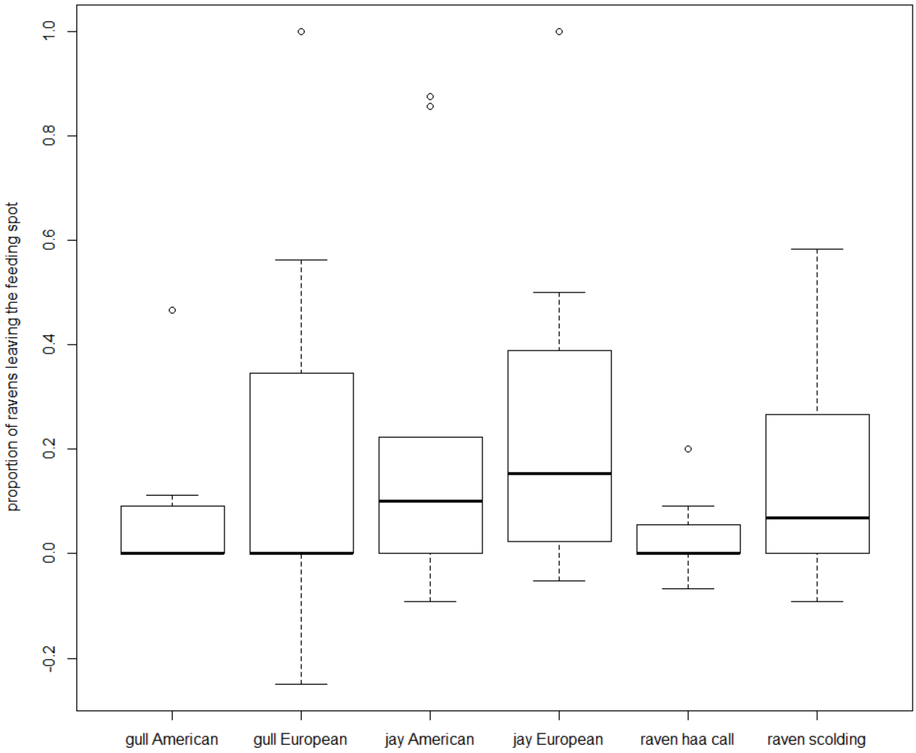

Fig. 4 The effect of particular playbacks on the proportion of ravens flying away, out of those present before the playback

The ravens’ reaction to the blue jay alarm call was not as prominent as to the Eurasian jay alarm call, but the reaction was still as strong as to the conspecific alarm calls. This is surprising since the blue jay is not a familiar species to Austrian ravens. We might speculate that there are acoustic features, common to blue jays and European corvids, which enable the generalization and comprehension of the blue jay alarm call. The recognition of heterospecific alarm calls via specific characteristics in calls has been repeatedly shown between continents (Johnson et al. 2003; Russ et al. 2004; Fallow et al. 2011; Randler 2012).

It is particularly interesting that the responses of ravens to playbacks of the alarm calls of the Eurasian jay (this study), jackdaw (Nácarová et al. 2018), and blue jay (this study) were comparable to responses to the conspecific alarm calls. None of these species significantly share predators with ravens and one of them is unfamiliar. We may thus speculate that the alarm calls of corvids (at least of the tested species) contain acoustic features that elicit proper antipredator behaviour (freezing and vigilance) in closely related species. This interpretation is also supported by the findings that rooks (*Corvus frugilegus*) respond to artificial alarm calls simulating the natural rook alarm call in key parameters (broad frequency range, harmonic structure; Aubin 1991).

Compared to the alarm calls of other corvids, ravens generally failed to show freezing behaviour in response to the alarm calls of the gulls, but they partly responded with increased vigilance. Overall, the typical response to the playbacks of gulls was less expressive than to that of jays. The black-headed gull playback elicited only a weak response and the ravens usually continued feeding. However, after hearing the American laughing gull alarm call, ravens showed vigilant behaviour followed by cautiousness, the same as in case of the playback of the American blue jay. These findings suggest that a significant portion of ravens consider the unfamiliar alarms as communicating a potential threat, or at least to be a disturbing sound. Increased attentiveness is a typical response of ravens to unknown or unexpected stimuli (Massen et al. 2014). They probably consider the unfamiliar calls to be less reliable, and thus increase the search for the potential predator or they search for the unknown caller.

Black-headed gulls are challenged by almost the same spectrum of predators as Eurasian jays and should have been equally familiar to the tested raven population as Eurasian jays. Therefore, it is surprising that the responses of the ravens to the alarm call of the black-headed gull were so weak. This finding further supports the theory that the corvid alarm calls may include some specific features eliciting strong antipredator responses regardless of the ecological appropriateness of such a response.

Acknowledgements

We thank the Cumberland Wildpark, Grünau im Almtal for allowing us to conduct the experiments within the park and the 'Verein der Förderer der Konrad Lorenz Forschungsstelle' for permanent support. We thank Christian Blum for providing the raven playback stimuli and Alexandra Průchová and Jan Špička for the help with data collection. This research adhered to the ASAB/ABS guidelines for the use of animals in research and to the current laws of the Republic of Austria. We are thankful to Christopher Mark Steer for English editing of the manuscript.

Author contributions

MD participated in the design of experiments, collected most of the data and wrote most of the manuscript. MS participated in the design of experiments, prepared the playback stimuli, participated in the data collection and manuscript preparation. JN participated in the data collection and preparation of the manuscript. PV participated in the design of experiments, conducted the data analyses and wrote the manuscript. TB participated in the design of experiments and manuscript preparation. All authors have read the final version of the manuscript.

Funding

This study was supported by the Austrian Science Fund (FWF) project P29705 and by the Grant agency of the University of South Bohemia (048/2019/P).

Data availability

Original data are provided in the Supplement (Supplemental Material Table S1).

Compliance with ethical standards

Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permission for playback studies on wild ravens was granted by the Austrian Ministry for Science, Research and Economy (BMWFW-66.006/0016WF/II/3b/2014).

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Kapitola 6

Cowards or clever guys: an alternative nest defence strategy employed by shrikes against magpies

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Jana Nácarová, Roman Fuchs

Cowards or clever guys: an alternative nest defence strategy employed by shrikes against magpies.

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Abstract

In a multipredator situation, the antipredator response often reflects the threat particular predators represent, which is a strategy preventing energy waste or fitness loss. Red-backed shrikes (*Lanius collurio*) show a substantial variability in their nest defence behaviour, which usually follows the rules of optimal parental behaviour, vigorously attacking egg and chick predators and only passively guarding against harmless animals. Nevertheless, shrikes hesitate to attack the Eurasian magpie (*Pica pica*), which specializes in plundering passerine nests. Our previous studies have suggested that this behaviour may be the result of an alternative defence strategy, relying on nest crypsis. To test this hypothesis, at the shrike nests, we presented a magpie dummy associated with playbacks drawing the predators' attention to the presence of the nest. We predicted that the presentation of a magpie dummy associated with shrike alarm calls moves the parents to action, causing them to chase the magpie away from the nest. We showed that the presence of a magpie dummy associated with shrike alarm calls elicits a significantly more active response in shrike parents compared to a magpie dummy associated with neutral song. Parents actively moved around the dummy and produced alarm calls; nevertheless, most of the tested pairs hesitated to attack the dummy. We may conclude that the low nest defence activity of shrike parents towards magpie dummy was partly the result of an alternative strategy, which may be cancelled out by alerting the predator to the location of the nest; nevertheless, shrikes seem to be afraid of the magpie and hesitate to attack it physically.

Keywords

Nest defence, predator recognition, red-backed shrike, Eurasian magpie, multipredator conflict

Acknowledgements
We thank Christopher Mark Steer for his proof reading and two anonymous referees and editor 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.

Declarations

Funding

This study was supported by University of South Bohemia (048/2019/P).

Conflicts of interests

Authors declare no conflicts of interests.

Ethics approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permission for studies on wild red-backed shrikes was granted by the Ministry of the Environment of the Czech Republic (13842/2011-30), the license permitting experimentation with animals no. CZ01629 was offered by the Ministry of the Agriculture of the Czech Republic. This research adhered to the ASAB/ABS guidelines for the use of animals in research. Authors declare that the experiments comply with the current laws of the Czech Republic (and European union).

Consent to participate (include appropriate statements)

Not applicable

Consent for publication (include appropriate statements)

Not applicable

Availability of data and material

Original data are provided in the Supplement (Supplemental Material Table S1).

Code availability

Not applicable

Author contributions

PV participated on the design of experiments, conducted the data analyses and wrote most of the manuscript. MS participated on the design of experiments, participated on the data collection and manuscript preparation. MV participated on data collection and analyses, and manuscript preparation, JH and JN participated on the data collection and preparation of the manuscript. RF participated on the design of experiments. All authors have read the final version of the manuscript.

Introduction

In natural communities, almost all animals face a multiple predator situation (see Sih et al. 1998 for review). In contrast to this fact, many experimental studies have described prey responses to a single predator, including classical prey-predator response studies (e.g. Krebs et al. 1995). In cases where multiple predators are considered, the simple additive effect on the prey is usually supposed (Hurd and Eisenberg 1990; Martin et al. 1989; Spiller and Schoener 1994). The most often studied deviation from the additive effect of the multiple predator situation occurs when particular predators affect each other, especially when belonging to the same guild (Crowder et al. 1997; Rosenheim et al. 1993; Ferguson and Stiling 1996). Nevertheless, particular predators may substantially differ in the threat they represent to various animals, but also to their particular developmental stages (see Fuchs et al. 2019 for review).

The ability to recognise and mount an appropriate response to predators representing various levels of threat is a skill importantly increasing the fitness of the prey. There is an evident fitness loss when the dangerous predator is not recognized, but avoiding or attacking a harmless animal is also time and energy consuming (Caro 2005; Kelley and Magurran 2003). The mounting of appropriate antipredator responses during parental care presents further challenges. Multiple studies have described the conflict of risk taking during the defence of offspring (Dale et al. 1996; Listøen et al. 2000; Montgomerie and Weatherhead 1988). Parents evaluate the risk to themselves and to the offspring, as well as the value of the offspring, which results in an optimal investment in offspring defence (Dale et al. 1996).

Parents may develop several alternative antipredator strategies, where each is applicable to predators differing in the threat they represent to the parents and to the offspring. In birds, vigilance and a reliance on crypsis (of parents, chicks, and eggs) may be alternated with displays intended to distract the predator's attention from the nest (Armstrong 1952, 1956; Simmons 1951). It has been shown that this distraction behaviour may substantially increase parental fitness (Byrkjedal 1987), but on the other hand may also be fatal (Brunton 1986). In a situation where the presence of the nest is revealed, the parents may use another strategy, mobbing. This behaviour often moves the predator away from the nest vicinity (Caro 2005; Kontiainen et al. 2009; Martin 1992; Olendorf and Robinson 2000), but, again, is very energy consuming and dangerous (Andersson et al. 1980; Sordahl 1990a).

Red-backed shrikes (*Lanius collurio*) have been repeatedly shown to actively defend their nests using physical attacks to chase intruders away from the nest vicinity (Goławski and Mitrus 2008; Tryjanowski and Goławski 2004). Nevertheless, when confronted with an array of predators differing in the threat they represent to the adult shrikes and their nest's contents, they show important variability in their antipredator behaviour (Strnad et al. 2012). This study shows that shrikes are able to differentiate between relatively similar predators like the Sparrowhawk (*Accipiter nisus*) and Kestrel (*Falco tinnunculus*). Another study has shown that shrike nest defence also reflects the value of the offspring in the nest (Strnadová et al. 2018).

The most surprising result of these two studies was the zero response elicited by the Eurasian magpie (*Pica pica*). The magpie is a specialized predator of the eggs and chicks of small passerines including shrikes (Hudec 1983; Lefranc and Worfolk 1997; Roos and Pärt 2004). Shrikes confronted with a magpie dummy at their nest usually did not even approach it, staying hidden in the shrubs, and did not vocalize (Strnad, personal observation). When confronted with another similarly specialized predator, the Eurasian jay (*Garrulus glandarius*), they commonly attacked the dummy physically, even to the extent of destroying it. This difference is very marked, but hard to explain. Strnad et al. (2012) suggested that the parents may utilize an alternative strategy towards magpies, relying on nest concealment, which could be cancelled out by active mobbing by the parents.

Syrová et al. (2016) conducted an experiment simulating a multiple predator conflict where a magpie dummy was presented in association with a commonly attacked kestrel dummy (a big threat to the large chicks of shrikes). The kestrel was presented at the nest, while the magpie was presented as a bystanding dummy 10 meters from the nest, and therefore supposedly unaware of the nest's existence. The shrikes avoided attacking the kestrel in such a setup, contrary to experiments where the bystander dummy was that of an Eurasian jay, which suggested that the intention of the parents is truly not to draw the magpie's attention to the presence of the nest.

An alternative explanation of this shrike behaviour towards the magpie may simply be fear in the adults. Němec and Fuchs (2014) showed that shrikes are not willing to physically attack all dangerous intruders at their nest. They avoided attacking large-bodied species like the Common raven (*Corvus corax*), Carrion crow (*Corvus corone*), and Rook (*Corvus frugilegus*), which all represent a threat to their nest content. Shrikes only passively guarded against such dummies, producing alarm calls and showing excitement, but not attacking the dummies with the aim of chasing them away from the nest. The authors suggested that such large bodied intruders are simply beyond the mobbing skills of shrikes, therefore the parents decided not to waste energy in defending the nest. Nevertheless, this conclusion is in contrast to the results of Tryjanowski and Goławski (2004) showing that shrikes do not hesitate to attack even humans.

In the present study we decided to use another approach to uncover the intention of the shrike parents during nest defence against magpies. When we presented the stuffed dummy of a magpie at shrike nests it was always associated with playback. Playback presented at the nest may serve to cancel out the alternative strategy of parents relying on nest concealment, as some playbacks may draw attention to the location of the nest. We presented the alarm calls of shrikes as a playback supposed to be the most efficient in this respect.

We tested the following hypotheses:

- A magpie dummy associated with the playback of shrike alarm calls is attacked more often than a magpie dummy associated with both neutral playback (blackcap – *Sylvia atricapilla* song) and an empty control.
- A magpie dummy associated with the playback of shrike alarm calls is attacked equally as often as a jay dummy associated with neutral playback (blackcap song).
- A magpie dummy associated with the playback of shrike alarm calls elicits more excitement in parent shrikes than a magpie dummy associated with both neutral playback (blackcap song) and an empty control.
- A magpie dummy associated with the playback of shrike alarm calls elicits equal excitement in parent shrikes to a jay dummy associated with neutral playback (blackcap song).

Material and methods

Study population

We conducted our experiments in a population of red-backed shrikes inhabiting, in relatively high densities, the southern parts of the Doupov mountains, Western Bohemia, Czech Republic (50°10´N, 13°9´E, 400-800 m above sea level), which is a Bird area proclaimed for the protection of the Red-backed shrike population (Hora et al. 2015). Eurasian magpies, Eurasian jays as well as blackcaps are also common at this locality (AOPK ČR 2020); therefore, we suppose all tested shrikes are familiar with them. The experiments were conducted during a single breeding season between 19th June and 6th July 2017. All nests were occupied by chicks, the age of the chicks ranging from 4 to 14 days. Altogether, experiments were conducted at 17 nests.

Presented stimuli

There were four treatments at each nest: 1) an empty control with neither dummy nor playback, 2) a stuffed dummy of the Eurasian magpie accompanied by the playback of the song of a blackcap, 3) a stuffed dummy of the Eurasian magpie accompanied by the playback of the warning call of a red-backed shrike, and 4) a stuffed dummy of the Eurasian jay accompanied by the playback of the song of a blackcap. The dummies were always adult birds in an upright perching position with wings folded. The three individual dummy-playback combinations were randomly alternated in the experiments. The playback of the shrike warning call was recorded during our previous experiments presenting the stuffed dummy of a common kestrel at a shrike nest within another breeding population of shrikes (approx. 200 km distant). Three different shrike warning call playbacks were alternated randomly in the experiments. Each of them was prepared as a mixture of mobbing and alarm calls (altogether called *warning calls*) lasting 20 minutes (with 1-3 seconds of silence between them) to simulate the natural performance of the two adult shrikes defending their nest. The playback of the blackcap song was prepared from our own recording obtained at the study locality. It also encompassed three different mixtures of blackcap song (of a single male) lasting 20 minutes and separated by natural-like silence (1-2 seconds).

Experiments

During each experiment, the stuffed dummy was presented on a 1.5 m high pole situated within the very proximity (1-2 meters from the nest) and facing the nest. This simulated a direct threat to the nest, though there would still be the possibility of the nest not being discovered by the intruder. During the empty control, only the pole, with no dummy, was placed at the nest. Under the pole, on the ground, there was a loudspeaker (MIPRO MA-202B) producing the particular playbacks, or nothing in the case of the empty control. The volume of the loudspeaker was set to produce sounds with an intensity equating the natural performance of living birds. It was possible to clearly hear the playback from a distance of 100 meters away.

The dummy was brought to the nest covered by a cloth, so that the tested birds could not make a connection between the human intruder and the dummy (Strnad et al. 2012). The cloth was pulled off the dummy and the playback started. The experiment started at the moment when the first shrike appeared in the nest vicinity. A human observer with binoculars made recorded comments on the behaviour of the shrikes from approx. 50 meters (depending on the terrain), so that she/he did not affect the behaviour, but was still able to effectively monitor it. The reaction was taped on DV Camera. The behaviour of both of the parents was recorded independently, as the red-backed shrike has a significant sexual dichromatism and it is possible to distinguish between the sexes of parents even from a distance.

The presentation of each dummy lasted for 20 minutes, as did the empty control where the natural behaviour of the parents was observed. We presented all four treatments to each shrike pair within a randomized sequence during one day. The experiments were conducted between 10:00 AM and 6:00 PM. Between each 20-minute treatment, the parents were left undisturbed for at least an hour to allow them to calm down, feed themselves, and supply food to their nestlings.

Data analyses

We analysed three behaviours in the tested shrike parents. The first of these was the number of attacks performed during each 20-minute trial. Attacks were defined as flights towards the dummy with the bird decreasing its height above the ground and very often passing very closely to the dummy or even striking it physically with its bill or legs. The variability in residuals of this behaviour did not follow the gaussian distribution (it was skewed towards the low numbers); therefore, in subsequent analyses we used these data in log-transformed form.

The second type of behaviour we analysed was the number of movements performed during each trial. This was used as a measure of the excitement of the shrikes, because the changing of perches around the dummy usually enables the parents to gain a better view on the intruder and may also be understood as challenging the intruder and trying to chase it away from the nest. The variability in residuals of this behaviour also did not follow the gaussian distribution and the log-transformation of this data was used.

The third type of behaviour analysed was alarm calling. Shrikes produce three basic warning calls; one is very common and is elicited by any intruder in their territory, the other two calls are mobbing calls, produced when the intruder is attacked or chased (Lefranc and Worfolk 1997). Unfortunately, we were not able to record the vocalization of both parents during the entire trial for two reasons. Firstly, the shrikes moved fast within a large area during the trial, and it was not easy to follow them both with a shotgun microphone. Secondly, the playback produced by our loudspeaker masked many of the alarm calls produced by the parents, which biased the numbers of alarms in the shrike alarm treatment. Nevertheless, we understood that alarm vocalisation is a very important part of the antipredator response of shrikes and we did not want to omit it. Therefore, we decided to record the alarm calling behaviour in a simplified manner, as a binomial response – the occurrence of at least one alarm during an entire 20-minute trial.

We explained the variability in each of these three behaviours with the effect of four predictors: the type of treatment (with four values – empty control, magpie dummy with blackcap song, magpie dummy with shrike warning calls, jay dummy with blackcap song), sex of the parent, age of the nestling in the nest (continuous predictor), and order of the trial within the sequence (first to fourth, coded as categorical predictor). Because we conducted all four treatments at a single nest, we evaluated these effects using mixed effect models with the nest identity coded as a random factor. To evaluate the effect of predictors on the log-transformed numbers of movements and log-transformed numbers of attacks, we used Linear mixed-effect models (LMM, command lmer in R package lme4). A likelihood ratio test for gaussian distribution (F test) was used to compare particular models in the stepwise forward selection. To compare particular levels of categorical predictors, we used the Tukey HSD post hoc test (t test). To evaluate the effects of predictors on the variability in the occurrence of alarm calls in the trials (binomial response), we used a generalized linear mixed-effect model (GLMM, command glmer in R package lme4) with binomial distribution. A likelihood ratio test for binomial distribution (Chi squared test) was used to compare particular models in the stepwise forward selection. To compare particular levels of categorical predictors, we used the Fisher LSD post hoc test (z test). All computations were conducted in software R for windows (version R 3.4.4, R Core Team 2018).

Results

The number of movements was significantly affected only by the treatment, the other predictors had no effect (Table 1). The post hoc analyses showed that shrikes performed more changes of perches in the presence of the jay dummy associated with the blackcap song than in both the presence of the magpie dummy with blackcap song (Tukey HSD, t=3.989, P<0.001; Fig. 1) and the empty control (Tukey HSD, t=4.839, P<0.001; Fig. 1). Similarly, shrikes moved more in the presence of the magpie dummy associated with shrike warning calls than in both the presence of the magpie dummy with blackcap song (Tukey HSD, t=1.362, P=0.037; Fig. 1) and the empty control (Tukey HSD, t=2.213, P=0.020; Fig. 1). There was no difference between the movement rate in the presence of the jay dummy with song and magpie dummy with warning calls (Tukey HSD, t=1.026, P=0.102; Fig. 1) and between the magpie dummy with song and the empty control (Tukey HSD, t=0.851, P=0.830; Fig. 1).

Table 1 Effects of particular predictors on the variability in three observed shrike behaviours. DF – degrees of freedom. Significant effects are in bold letters.

Behaviour	Predictor	F value	DFnum/den	P
Number of movements	**Treatment**	**9.135**	**3/135**	**<0.001**
	Parent sex	0.579	1/135	0.448
	Nestlings age	2.305	1/135	0.131
	Trial order	1.203	4/135	0.313
Number of attacks	**Treatment**	**27.607**	**3/135**	**<<0.001**
	Parent sex	2.811	1/135	0.096
	Nestlings age	**6.206**	**1/135**	**0.014**
	Trial order	1.243	4/135	0.296
Behaviour	Predictor	Chi value	DF	P
Occurrence of alarm calls	**Treatment**	**26.149**	**3**	**<<0.001**
	Parent sex	1.230	1	0.255
	Nestlings age	**8.883**	**1**	**0.003**
	Trial order	4.170	4	0.384

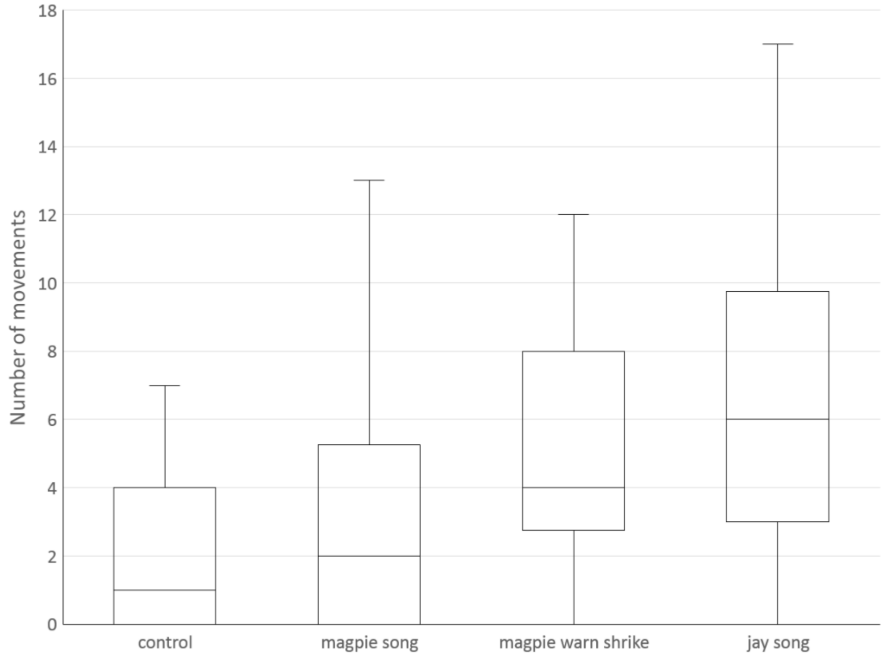

Figure 1 – Number of movements (changes in perching position) performed by 34 shrike parents in the presence of particular dummies presented at their nest.

The number of attacks performed by the shrike parents on the presented dummies was affected by the treatment and by the age of the nestlings in their nest (Table 1). Shrikes attacked the jay dummy associated with the blackcap song the most, more often than the magpie dummy with song (Tukey HSD, t=7.657, P<0.001; Fig. 2), magpie dummy with warning call (Tukey HSD, t=5.484, P<0.001; Fig. 2) and the empty control (Tukey HSD, t=8.080, P<0.001; Fig. 2). There were no attacks in the experiments with the empty control and the magpie dummy associated with the song of a blackcap, which did not mutually differ (Tukey HSD, t=0.423, P=0.974; Fig. 2). The attack rate to the magpie dummy associated with the shrike warning was significantly higher than in the empty control (Tukey HSD, t=2.596, P=0.041; Fig. 2) and slightly higher than in the presence of the magpie dummy associated with the blackcap song (Tukey HSD, t=1.773, P=0.074; Fig. 2). The number of attacks significantly increased with the increasing age of the nestlings in the nest (R=0.678, P=0.014; Fig. 3).

The occurrence of at least one alarm or mobbing call during the trial was significantly affected by the treatment and age of the nestlings in the nest (Table 1). The alarms occurred less often in the empty control than in the presence of the jay dummy with song (Fisher LSD, z=4.111, P<0.001; Fig. 4), magpie dummy with warning (Fisher LSD,

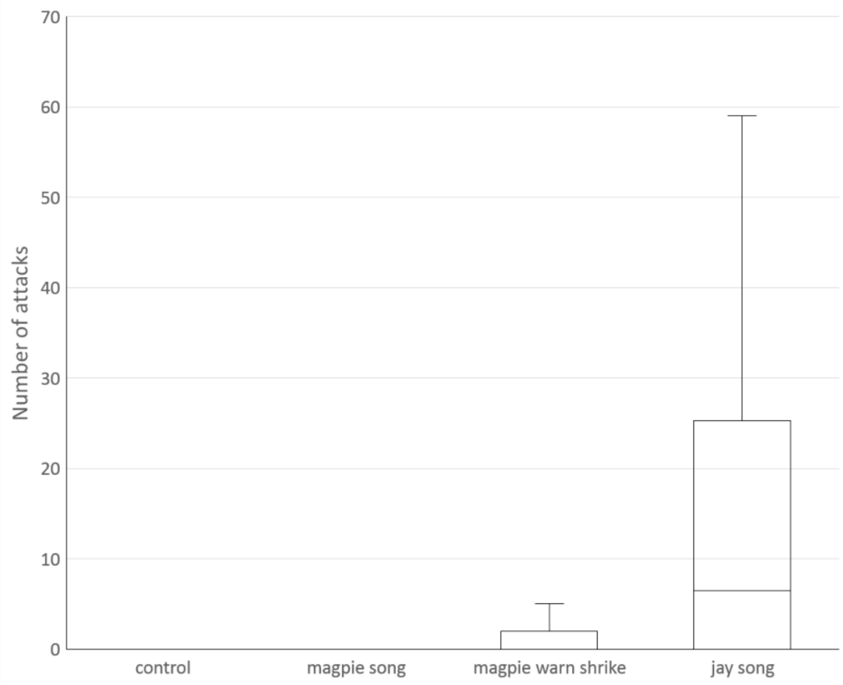

Figure 2 – Number of attacks performed by 34 shrike parents towards particular dummies presented at their nests.

z=3.451, P=0.001; Fig. 4), and slightly also than in the presence of the magpie dummy with song (Fisher LSD, z=2.223, P=0.063; Fig. 4). There was no difference in the occurrence of alarms in the presence of the jay dummy with song and the magpie dummy with song (Fisher LSD, z=1.882, P=0.189; Fig. 4), jay dummy with song and magpie dummy with warning (Fisher LSD, z=0.852, P=0.856; Fig. 4), and magpie dummy with song and warning (Fisher LSD, z=1.211, P=0.606; Fig. 4). The occurrence of warning calls elicited from shrike parents during the trial was more probable in trials at nests with older nestlings (R=0.859, P=0.003; Fig. 5).

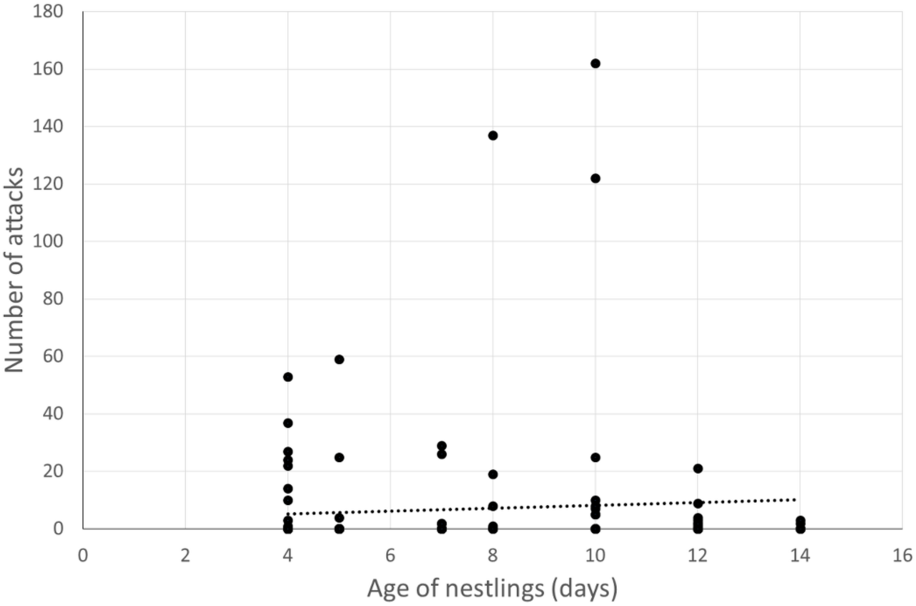

Figure 3 – The effect of the age of the nestlings on the number of attacks performed by their parents. Total number of tested shrikes is 34.

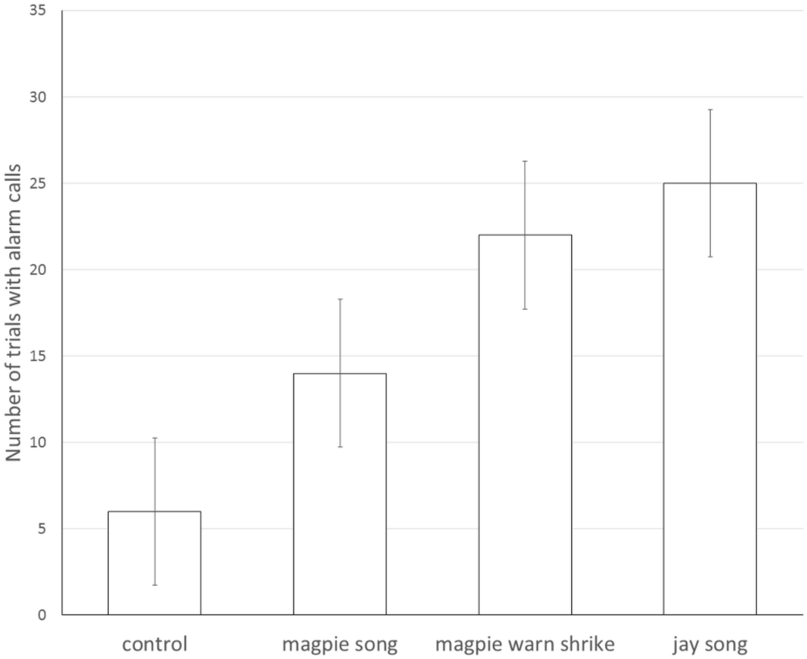

Figure 4 – The effect of the presented dummy on the number of trials, in which at least one warning (alarm or mobbing) call occurred. The total number of trials is 34.

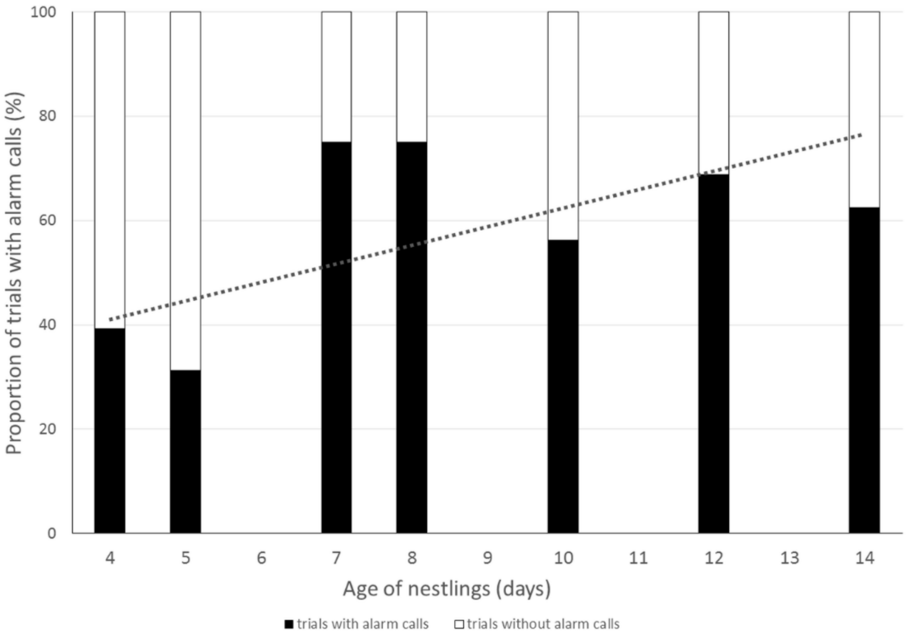

Figure 5 – The effect of the age of the nestlings on the proportion of trials, in which at least one warning call occurred. The total number of trials is 34.

Discussion

We showed that the general excitement of shrike parents in the presence of a magpie dummy associated with the warning calls of the red-backed shrike is almost equal to the excitement in the presence of a jay dummy. Shrikes were even willing to attack the magpie dummy, and they did so significantly more often than in the case of the magpie dummy associated with the blackcap song.

Our results show that the response of shrike parents to the magpie dummy associated with blackcap song being present at their nest was very similar to the empty control. Shrikes did not attack the dummy, but also showed little excitement resulting in a low number of changes of perch and relatively low warning vocalisation. The alarm calling occurred in 14 trials out of 34 where the magpie dummy with blackcap song was presented. Moreover, even during the empty control without any dummy, the alarm calling occurred in six trials. Such alarm calls represent natural behaviour in shrikes and were probably addressed to naturally occurring intruders, the experimental devices (loudspeaker on the ground), or the distant human observer. When the magpie dummy was present at the nest and associated only with the control blackcap call, the increase in shrike vocalization was only small. Some pairs simply stayed hidden in the shrubs and only passively guarded against the dummy from a distance with no signs of excitement.

These results are in full concordance with the previous research on the behaviour of shrikes during nest defence against magpies. Strnad et al. (2012) showed that the attack rate upon the magpie is zero, i.e. equal to the totally harmless pigeon (*Columba livia* f. *domestica*). Subsequently, Syrová et al. (2016) showed that shrikes are even willing to avoid attacking the regularly attacked kestrel when the magpie is bystanding. These results suggested that red-backed shrikes adopt an alternative antipredatory strategy when confronted with a magpie. This strategy includes not drawing the magpie's attention to the nest, staying hidden in the shrubs, and relying on the concealment of the nest. This strategy would be very useful whenever the magpie cannot be effectively chased away from the nest. Klvaňová et al. (2011) showed that House sparrows (*Passer domesticus*) avoid chasing magpies away from their nests. Similar results were obtained in experiments with linnets (*Linaria cannabina*, Drachmann et al. 2002).

Nevertheless, there may be two basic reasons for parents to give up active mobbing. The first resides in the actual ability of the parents to attack the intruder. Many species of small passerines do not use active mobbing with attacks towards the intruder and keep their distance from a predator as they do not want to put themselves at risk of predation (Curio et al. 1983; Kleindorfer et al. 2005) or when an active reaction will not be effective (Dale et al. 1996; Wheelwright and Dorsey 1991). The antipredator response is usually limited to vocalisation (Baker and Becker 2002; Bartmess-LeVasseur et al. 2010; Bureš and Pavel 2003; Burhans 2000; Freeberg et al. 2014; Greig-Smith 1980; Groenewoud et al. 2019), but the parents very often simply witness the depletion of their nests with no response at all (Ibáñez-Álamo et al. 2015). The red-backed shrike, on the contrary, is known for its very active and vigorous nest defence against many intruders including humans (Tryjanowski and Goławski 2004). The zero response to the magpie is thus more surprising in this case.

Němec and Fuchs (2014) showed that in response to large-bodied corvids (ravens, crows, rooks) shrikes adopted a very similar strategy as towards magpies and stayed at quite a distance from these dummies without mounting any attacks. The authors suggest that the reason for this passive behaviour may reside in the fear of these large intruders, which would be probably similar as in the case of linnets and sparrows from the above mentioned studies. Nevertheless, we cannot rule out the possibility that the parents (maybe of all these species) are aware of the well-developed nest-locating ability of corvids. Several studies have shown that predators are attracted to nests using parental antipredator behaviour as the main cue (Krams 2001; Krama and Krams 2004; Krams et al. 2007). Corvids are the most successful among those predators, probably due to their good long-term spatial memory (Clayton and Krebs 1995; Zinkivskay et al. 2009) and mental abilities such as the capacity for object permanence (Pollok et al. 2000; Zucca et al. 2007). Parents which decide to stay hidden and rely on nest concealment may profit from a higher fitness compared to those attacking the magpie, chasing it away for a while, but being depredated by the returning magpies when not present at the nest.

Our results show that once the magpie is associated with conspicuous shrike warning calls, parent shrikes start to be active, move around the dummy, vocalize and occasionally attack it. This suggests that the presence of the nest is disclosed by the alarming individual (the loudspeaker in our case) and parents decide to change their strategy. A similar ability to switch between different antipredator strategies was previously documented in birds using distraction displays. The *broken wing display* is a frequently used strategy in shorebirds, which has two phases. In the first phase, the parent behaves as if its wing is broken and moves away from the nest to attract the predator's attention. When the predator has followed the parent pretending injury far enough the second phase is initiated and the parent flies away (Gómez-Serrano and Lopéz-Lopéz 2017; Shettleworth 2010; Simmons 1951).

A more similar example to our study is Kryštofková et al. (2011) who showed that Blackbirds (*Turdus merula*) stayed hidden in vegetation when a predator dummy (magpie) was presented far from the nest. When the predator was presented nearer, blackbirds started to defend their nests. Similarly, Bureš and Pavel (2003) showed that the antipredator behaviour of flycatchers (*Ficedula hypoleuca*), blackcaps, and pipits (*Anthus pratensis*) importantly changed as the predator was presented closer to the nest. Baker and Becker (2002) showed a quicker response in Black-capped chickadees (*Poecile atricapilla*) to Prairie Falcon (*Falco mexicanus*) presented at a distance of 1m than at 6m, and they also gave more chick-a-dee calls to the stimulus presented at 1m.

Nevertheless, an alternative explanation for our results suggests that parent shrikes simply responded to the red-backed shrike alarm calls. The main response of shrikes was a significant increase in alarm calling and general excitement, which is a regular response to alarm calls in passerines (reviewed by Leavesley and Magrath 2005). The actual number of pairs that decided to attack the magpie dummy when it was associated with the alarm calls was 7 out of 17 tested, which is far less than in the case of the jay dummy (14 out of 17). Therefore, we cannot conclude that the alarm call playback completely cancelled the alternative antipredatory strategy of shrikes, and a certain degree of fear of shrikes towards magpies may still play its role in forming the antipredatory behaviour.

The question remains of why this strategy (no matter if motivated by fear or adaptive response to sophisticated predators) is triggered by the presence of a magpie (and maybe also other larger corvids) and not a jay. Magpies as well as jays are similar in size (del Hoyo et al. 2010), and cognitive abilities (see above). The diet of magpies is a little more vertebrate-biased, compared to that of jays, especially during the spring and summer (eggs, nestlings, reptiles; Krištín 1988) but also winter (carrion, small rodents; Holyoak

1968). Nonetheless, a jay also represents a threat to the nest and e.g. blackcaps adapt their parental behaviour in order not to disclose the presence of their nests as a defence against jays (Leniowski and Węgrzyn 2018). We may thus presume that jays are also able to associate the antipredatory behaviour of parents with the presence of a nest. Therefore, the question of why the red-backed shrikes attacked the jay dummy in our experiments so vigorously is rather interesting.

In our experiments, we were able to show the effect of the age of the nestlings on the number of attacks performed and in the occurrence of alarm vocalization. In both behaviours, the activity increased with increasing age of nestlings. This is in concordance with the reproductive value hypothesis (Patterson et al. 1980, Redondo 1989, Redondo and Carranza 1989) suggesting that with the increasing value of offspring (through parental investment) the intensity of their defence by parents also increases. Nevertheless, for red-backed shrikes, the Vulnerability hypothesis (Harvey and Greenwood 1978) has rather been suggested (Strnadová et al. 2018). It presumes that there is a steep increase in the antipredator activity of parents between the stage of eggs and chicks, because of the higher conspicuousness of nestlings. Our results show that even during the stage of nestling stage, parental investment in nest defence increases, probably due to the higher value of the chicks. The larger value of older nestlings to parents is generally caused by their greater chance of reaching maturity (Kleindorfer et al. 1996) and higher reproductive potential (Redondo 1989). Moreover, older nestlings are more valuable in cases when there is a low possibility of re-nesting (Andersson et al. 1980, Montgomerie and Weatherhead 1988), which also is the case for red-backed shrikes as they are a long-distance migrant (del Hoyo et al. 2010; Lefranc and Worfolk 1997).

Conclusions

Our results do not allow us to be sure whether the very low antipredator activity of shrike parents towards the magpie dummy represents an alternative defence strategy. Nevertheless, we showed that the association of the magpie dummy with alarm playback moves the parents to action. They leave their shelters and move around the dummy and produce alarm calls, though, they decide to attack the dummy only rarely. It seems that shrikes do possess an alternative strategy, which is adaptive to the extraordinary predatory skills of magpies, but some level of fear still also affects shrike behaviour.

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Publikace:

Veselý P, **Syrová M,** Voháňková M, Nácarová J, Havlíček J (submitted) Cowards or clever guys: an alternative strategy of shrikes defending nests against magpies.

Davídková M, **Syrová M**, Průchová A, Nácarová J, Veselý P, Bugnyar T (2020) Ravens respond to unfamiliar corvid alarms. Journal of Ornithology 161: 967-975. DOI: 0.1007/s10336-020-01781-w; *IF2018: 1,472; Q2.*

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Vybrané mezinárodní konference (postery; *prezentující)

Syrová M*, Hromádková T, Pavel V, Veselý P (2019): Responses of nesting Arctic terns (*Sterna paradisaea*) to disturbance by human; ASAB 2019 Summer Conference; Konstanz, Germany. August 26–28 2019; Book of abstracts, pp. 153.

Hromádková T*, **Syrová M***, Pavel V (2017): Can terns effectively adapt to human presence? Nesting behaviour and antipredation strategies of Arctic terns in two colonies on Svalbard; ASSW; Prague, Czech Republic. April 4–7 2017; Collection of abstracts, pp. 113.

Syrová M*, Pavel V (2016): "Fight or flight?" – antipredation strategies of nesting Arctic terns (*Sterna paradisasa*). Polar ecology conference, Ceske Budejovice, Czech Republic. September 19–21 2016, Collection of abstracts, pp. 115.

Syrová M*, Němec M, Strnad M, Poláková S, Fuchs R (2012): Shrikes vs. magpie: why do not shrikes expel the magpie from their territories?; The 14th International Behavioral Ecology Congress; Lund, Sweden. August 12–17 2012; Collection of abstracts, pp. 125.

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

Vybrané tuzemské konference (přednášky a postery; *prezentující)

Syrová M*, Němec M, Veselý P, Strnad M, Voháňková M, Havlíček J, Nácarová J, Landová E, Fuchs R (2019): Bojovat nebo utéct? Aneb jak ťuhýk brání své hnízdo před strakou?; 46. etologická konference; Bratislava 7. - 10. listopadu 2019; Sborník abstraktů str. 40; přednáška.

Syrová M*, Hromádková T, Pavel V, Veselý P (2019): Dokáží se rybáci efektivně přizpůsobit lidské přítomnosti?; Zoologické dny; Brno 8. - 9. únor 2019; Sborník abstraktů, str.182 – 183; přednáška

Syrová M*, Němec M, Veselý P, Landová E, Fuchs R (2018): Bojovat nebo utéct? Ťuhýk obecný jako inteligentní obránce hnízd; Zoologické dny; Praha 8. - 9. února 2018; Sborník abstraktů str. 205; přednáška.

Davídková M*, Veselý P, **Syrová M**, Průchová A, Nácarová J, Bugnyar T (2018): Reakce krkavce velkého (*Corvus corax*) na heterospecifické varovné hlasy. 45. etologická konference; Ostrava 9. - 12. listopad 2018; Sborník abstraktů, str. 49; poster.

Syrová M*, Němec M, Bendová L, Poláková S, Fuchs R (2012): Věrohodnost atrapy a intenzita mobbingu ťuhýka obecného (*Lanius collurio*); Zoologické dny, Olomouc 9. - 10. února 2012; Sborník abstraktů, str. 187; poster.

Fuchs R*, Němec M, Strnad M, **Syrová M**, Součková T (2011): Ťuhýci, dravci a krkavci: Co nám o kognitivních procesech u ptáků může prozradit antipredační chování?; 38. etologická konference, Kostelec nad Černými lesy 9 - 12. listopadu 2011; Sborník abstraktů, str. 23; přednáška.

Syrová M*, Bendová L, Poláková S, Němec M, Fuchs R (2010): Věrohodnost atrapy a intenzita mobbingu ťuhýka obecného (*Lanius collurio*); 37. Etologická konference, Smolenice 15. - 17. listopadu 2010; Sborník abstraktů, str. 86; poster.

Školitelství

Kovářová E, Varovné hlasy krkavcovitých (Corvidae), Bc. práce, zadáno 2019

Krausová L, Reakce ťuhýka obecného (*Lanius collurio*) na kukačku obecnou (*Cuculus canorus*). Bc. práce, zadáno 2019

Pilíková A, Připravenost středoškolských studentů na vysokoškolskou modulární výuku buněčné a molekulární biologie a genetiky. Mgr. práce, zadáno 2020 – školitel specialista

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2014-2018 Výzkumný ústav živočišné výroby, Praha–Uhříněves: vědecký pracovník (vedení pokusů, analýza dat, sepisování publikací)

Organizace soustředění pro studenty SŠ: Týden se současnou biologií (2016, 2017, 2018, 2019, 2020); Víkend pro řešitele Biologické olympiády (2014, 2015, 2017, 2018, 2019, 2020)

Organizace tuzemských konferencí: konference České a Slovenské etologické společnosti (2015, 2017, 2018, 2019, 2020), Zoologické dny (2016)

Organizace mezinárodních konferencí: Arctic Science Summit Week (2017); 4th European Students Congress in Behaviour and Cognition (2017)

Pedagogické zkušenosti:

Kurzy na PřF JU (cvičící: Terénní praxe 1, Terénní praxe 2, Terénní praxe 4 – zoologická část, Cvičení ze zoologie obratlovců, Praktika z etologie II, Cvičení z ekologie; garant: Mezioborová exkurze, Vertebratologická exkurze, Zoologická exkurze v rámci DVPP)

Akce pro učitele SŠ na PřF JU (Zpátky do lavic 2016, Víkend pro učitele SŠ 2016, 2017, 2018, 2019, 2020)

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Kroužkovací licence Kroužkovací stanice Národního muzea Praha (od 2013)

Osvědčení o odborné způsobilosti k navrhování pokusů a projektů pokusů (od 2014)

Členství v organizacích: Česká společnost ornitologická (ČSO) od 2015; Česká a Slovenská etologická společnost (ČSEtS) od 2016 - člen výboru (pokladník: 2016–2020); Association for the Study of Animal Behaviour (ASAB) od 2019

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Antipredační chování ptáků
Ph.D. Thesis Series, 2021, No. 7

Printed in the Czech Republic by Typodesign
Edition of 10 copies

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