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Přírodovědecká fakulta**

**Reakce vran na konspecifické a heterospecifické varovné
hlasy v prostředí ZOO.**

Diplomová práce

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Anotace:

I investigated if urban crows respond to con- and heterospecific alarm signals in predator and non-predator contexts in enclosures in the ZOO of Vienna. Crows responded strongly to the crow and also jackdaw alarms in both types of contexts, but also responded to the singing of great tit (control) in the predator context. This suggests that crows are aware of the danger the wolf and bear represent but are generally very cautious at the exotic Zoo animals.

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1 Úvod

1.1 Varovná vokalizace

1.1.1 Antipredační chování

Riziko predace je všudypřítomné a schopnost vyhnout se mu značně zvyšuje schopnost jedince přežít (Caro 2005). Kromě morfologických adaptací, jako například splnutí s okolím pomocí kryptise (Endler 1978; Poulton 1890; Thayer 1909) tj. změnou barvy nebo tvaru v závislosti na okolí, napodobování barvy jiného druhu (Wickler 1973), disruptivního zbarvení (Stevens & Merilaita 2009) mají zvířata také různé adaptace chování. Zvířata přizpůsobují své chování tak, aby co nejvíce snížila riziko predace (Caro 2005). Základem je výběr vhodného habitatu a správné načasování potřebných aktivit jako je krmení nebo rozmnožování. Zvířata vykazují ostražitost vůči případnému nebezpečí (Elgar 1989; Lima & Dill 1990) nebo aktivní obranu v případě kdy jsou již predátorem bezprostředně ohrožena (ex Caro 2005). V obou těchto případech jsou využívány varovné hlasy.

1.1.2 Varovné hlasy

Především u sociálních zvířat se můžeme setkat s ostražitostí (vigilancí) vůči přítomnosti predátora (Elgar 1989; Lima & Dill 1990). Jedinec může detekovat hrozbu sám, případně prostřednictvím ostatních jedinců, kteří buď vydávají varovný signál, nebo začnou rychle prchat (Davis 1975; Treherne & Foster 1981; Martin et al. 2006; Ebensperger et al. 2006). Když je hrozba detekována jedním členem skupiny, který varuje celou skupinu, mohou ostatní šetřit energii a věnovat se například sběru potravy. Ostražitost je tak velice výhodná především proto, že nemusí být na pozoru celá skupina (Pulliam 1973). Nicméně tato strategie je obecně rozšířená i u méně sociálních zvířat, kde nejsou blízké vazby mezi jedinci, například u anonymních hejn ptáků. Z toho, že každý hlídá sám sebe profitují všichni členové, protože pokud se dá hejno na útěk je pro predátora těžké identifikovat kořist (Cresswell et al. 2000).

Naopak mobbing, neboli aktivní obtěžování predátora, je strategií velmi široce rozšířenou především mezi ptáky a savci (např. Owings & Coss 1977), a je využívána v okamžiku, kdy již není možné se před predátorem schovat, nebo mu prchnout. Mobbing může pro jedince nebo jeho potomky představovat potencionální nebezpečí a je časově i energeticky náročný (Curio 1978). Například prádelník mahalský (*Plocepasser mahali*), žijící v koloniích, stráví mobbingem až 17,6 % svého času a díky tomu zanedbává i krmení mláďat (Collias & Collias 1978). Na druhou stranu se jedná se o strategii, která může být velmi účinná, protože může predátorovi způsobit i vážnější zranění, v extrémních případech dokonce smrt

(Smith & Hosking 1955). Právě proto je mobbing velice rozšířenou strategií napříč mnoha taxony obratlovců a liší se podle hrozby, kterou představují různí predátoři (Curio 1978).

Jak při mobbingu tak při vigilanci využívají savci a ptáci varovné hlasy (Caro 2005). Jejich funkce není jednoduchá a existuje několik teorií jejich evoluce (Wheeler 2008). Jejich základní funkcí je varování ostatních jedinců před nebezpečím. Může také obsahovat informaci o druhu predátora (Seyfarth et al. 1980). Některé studie se zabývají schopností zvířat rozpoznat míru nebezpečnosti predátora například podle velikosti (Templeton et al. 2005), druhu (Edelaar & Wright 2006) nebo vzdálenosti, ve které se nachází (Baker & Becker 2002, Leavesley & Magrath 2005). Varovné hlasy vypovídají o sociálních a enviromentálních kritériích (Morton 1975, Wiley & Richards 1978, Endler 1993) a také o senzorických vlastnostech příjemce (Guilford & Dawkins 1993, Bradbury & Vehrencamp 1998, Endler & Basolo 1998).

Hlavním problémem varovných hlasů je, že varující jedinec se vystavuje poměrně velkému nebezpečí (Ivins & Smith 1983). Přesto na sebe může toto riziko brát, jelikož v sociálním kontextu roste jeho prestiž a benefitují z toho jeho příbuzní (Maynard Smith 1965; Gaston 1977; Sherman 1977) nebo ostatní členové společenství (Witkens & Ficken 1979; Hogstad 1995). Navíc existují důkazy o tom, že ne každý varovný hlas je pro predátora snadno rozpoznatelný. To se děje například kvůli husté vegetaci pohlcující zvuk nebo kvůli okolnímu hluku (Marler 1955). V některých případech jsou dokonce varovné hlasy na takové frekvenci, aby je predátor špatně slyšel (Jones & Hill 2001).

Například pěvci produkují dva typy varovných hlasů – „mobbing calls“ a „seet calls“, které používají v odlišných situacích. Hlavní funkcí „mobbing calls“ je odstrašení predátora, ačkoliv toto volání také upozorňuje ostatní jedince a poskytuje informace o charakteristikách predátora. Může ho vydávat jak jednotlivec, tak celá skupina ptáků (Klump & Shalter 1984). „Seet calls“ vydává obvykle jednotlivec v případě ohrožení ze vzduchu a varuje tak ostatní, aby se vydali k úkrytu do bezpečí nebo aby znehybněli pro znesnadnění detekce (Marler 1977; Harvey & Greenwood 1978). Některé studie naznačují, že predátoři nejsou podle „seet calls“ schopni určit polohu ptáka. „Seet calls“ totiž obsahují čistější tóny na vyšších frekvencích, což znesnadňuje predátorům určení polohy na větší vzdálenost (Marten & Marler 1977).

Někdy se u zvířat můžeme setkat i s takzvanými falešnými varovnými signály. Může se jednat například o špatnou interpretaci signálu v rámci kolektivní ostražitosti (Sirot 2006), reakci na nový neznámý druh nebo situaci (Munn 1986), nebo účelné vystrašení ostatních

jedinců se sobeckým záměrem, což bylo prokázáno u mnoha druhů ptáků (Matsuoka 1980; Møller 1988, Cresswell et al. 2000; Haftorn 2000; Edelaar & Wright 2006; Rogers et al. 2006) a savců (Hare & Atkins 2001; Blumstein et al. 2004). Falešné varovné signály tvoří překvapivě velkou část varování. Ve studii, prováděné na huse velké, bylo zjištěné že více než 40 % poplašných odletů bylo způsobeno falešným varováním (Kahlert 2006) a ve studii zabývající se vodoušem rudonohým až 70 % (Cresswell et al. 2000).

Snaha o vydávání varovných hlasů, které jsou predátorem špatně lokalizovatelné způsobuje, že varovné hlasy jsou si obecně podobné co do frekvenčního rozsahu a délky trvání (Marler 1955) a může docházet ke koevoluci varovných hlasů mezi navzájem nepříbuznými druhy (Krams & Krama 2002). Obecná uniformita varovných hlasů pak umožňuje využívání těchto signálů mezidruhově.

1.1.3 Heterospecifické varovné hlasy

Jeden typ predátora většinou ohrožuje více než jeden druh kořisti, takže je výhodné rozumět i varovným hlasům ostatních druhů (Hurd 1996; Shriner 1998; Lea et al. 2008; Goodale et al. 2010). Je popsáno mnoho případů rozpoznávání heterospecifických varovných hlasů mezi různými ptáky, různými savci, ale i mezi ptáky a savci a mezi ptáky a plazy (Vitousek et al. 2007; Ito & Mori 2010; Ito et al. 2013). Heterospecifické varovné hlasy se vyskytují nejčastěji ve smíšených společenstvích a předpokládá se, že důležitým faktorem pro jejich vytváření je situace, kdy nevokalizující jedinci jsou obklopeni těmi vokalizujícími a zároveň tyto zúčastněné druhy sdílí predátory (Gaddis 1980, Greig-Smith 1981). Vokalizující druhy pak tvoří tzv. „jádro“ skupiny a ostatní druhy je následují (Sullivan 1985; Munn 1986; Ragusa-Netto 2002).

Goodale a Kotagama (2005) ukázali na timálii srílanské (*Turdoides rufescens*) a drongovi vlajkovém (*Dicrurus paradiseus*), že tyto jádrové druhy jsou velmi často sociálnější než ty, které pouze varovné hlasy odposlouchávají. Například samotářský strakapoud osikový (*Picoides pubescens*) snižuje svoji ostražitost v přítomnosti společenských a hodně varujících sýkor černohlavých (*Poecile atricapillus*) a sýkor rezavobokých (*Baeolophus bicolor*) (Sullivan 1985). „Mobbing calls“ sojky křovinné (*Aphelocoma c. coerulescens*), která je velice sociální, pak varují datla zlatého (*Colaptes auratus*), datla karolínského (*Melanerpes carolinus*), sojku chocholatou (*Cyanocitta cristata*), drozdce mnohohlasého (*Mimus polyglottos*), drozdce hnědého (*Toxostoma rufum*), ťuhýka amerického (*Lanius ludovicianus*) a pipila rudookého (*Pipilo erythrophthalmus*) (Francis et al. 1989). Ve východoafrické savaně

hrají významnou roli v heterospecifickém varování sparáci z rodu *Corythaixoides*, na které reaguje například nesociální dikdik Günterův (Lea et al. 2008) ale i další druhy africké savany (Simmons 2000). Ve smíšeném hejnu potápky západní (*Aechmophorus occidentalis*) a rybáka Forsterova (*Sterna forsteri*) pak opouští potápka svá hnízda při varovném volání koloniálně hnízdícího rybáka (Nuechterlein 1981). Nicméně, je zjevné, že i nesociální druhy mohou být věrohodnými zdroji heterospecifického varovného signálu. Např. na „seet calls“ kosa černého (*Turdus merula*) reagují hnízdící sýkory koňadry (*Parus major*) (Rydén 1978) a sociální mangusta žíhaná (*Mungos mungo*) zase umí rozpoznat varování soliterně hnízdící čejky korunkaté (*Vanellus coronatus*) (Müller & Manser 2008). Zdá se, že rozhodující je spíše ochota vydávat varovné hlasy, která je přirozeně vyšší u sociálnějších druhů.

Některé druhy na heterospecifické hlasy nejen reagují, ale dokáží v nich i rozpoznat o jaké nebezpečí se jedná. Například brhlík americký (*Sitta canadensis*) dokáže rozpoznat rozsah nebezpečí podle počtu slabik varovného zpěvu sýkory černohlavé (*Poecile atricapillus*) a adekvátně na něj reagovat (Templeton & Green 2007). Kočkodan Dianin (*Cercopithecus diana*) a kočkodan Campbellův (*C. campbelli*) dokáží nejen vzájemně reagovat na varovný hlas toho druhého, ale dokáží mezi nimi i rozlišovat, zda jde o predátora přicházejícího „ze země“ („leopard alarm call“) nebo ze vzduchu („eagle alarm call“) (Zuberbühler 2000). Na „eagle alarm call“ kočkodana Dianina reaguje i zoborožec palmový (*Ceratogymna elata*), který dokáže rozpoznat tyto dva druhy varování a vybrat jen ten, u kterého mu hrozí nebezpečí (Rainey et al. 2004). Zajímavá je také interakce mezi mangustou drobnou (*Helogale parvula*) a dvěma druhy zoborožců z rodu *Tockus*, kteří vydávají varovné hlasy i v případě predátorů ohrožujících pouze mangusty (Rasa 1983).

Některé studie naznačují mutualistické vztahy i mezi druhy, které spolu obvykle netvoří smíšená společenství. Například dva druhy australských pěvců, střízlíkovec bělobrvý (*Sericornis frontalis*) a modroplátník nádherný (*Malurus cyaneus*) dokážou vzájemně reagovat na své varovné hlasy i v době kdy netvoří společné hejno (smíšená hejna tvoří jen v zimním období) (Magrath et al. 2007). Dalším takovým případem je schopnost vrabce domácího (*Passer domesticus*) a vrabce polního (*Passer montanus*) reagovat na varovný hlas sýkory koňadry a uletět do úkrytu (Møller 1988).

1.2 Urbanizace

Městské prostředí a celkově rychlá změna přirozených habitatů v člověkem využívané prostředí přináší pro zvířata mnoho výzev. Nejčastěji se mluví o negativním dopadu (Angel et

al. 2011). Mezi nejvíce diskutované ohrožení zvířat v městském prostředí patří přímé zabíjení automobily, větrnými elektrárnami (Smallwood 2013), nárazem do skleněných ploch (Sabo et al. 2016) a drátů elektrického vedení (Tryjanowski et al. 2013). V menší míře působí negativně i nahrazení přirozené potravy např. odpadky (Schuyler et al. 2013). Významným negativním faktorem je ztráta habitatu a přeměna přirozeného stanoviště na nové, kterému se musí druhy adaptovat. Mnoho druhů toho není schopno a může dojít k jejich vymizení. Některé druhy ovšem jsou schopny urbánní prostředí osídlovat, a naopak v něm dosahují velkých denzit (Grimm et al. 2008). Přesto však nahrazování přirozených habitatů vede většinou ke snižování celkové diversity (Marzluff 2005, Chace and Walsh 2006). Neopomenutelným faktorem je pak i mezidruhovú kompetice, která může mít na diverzitu druhů v urbanizovaném prostředí také negativní vliv (např. Sedláček et al. 2004, Shochat et al. 2010).

Na druhou stranu přináší urbanizace pro zvířata i mnoho výhod, jako jsou například celoroční zdroje potravy, nové možnosti pro hnízdění a také více homogenní a předvídatelné sezónní podmínky (Shochat et al. 2010). Aby mohly tyto výhody využívat, musí se ale druhy naučit zpracovávat nové podněty, vyhýbat se novému nebezpečí, zapamatovat si ho a následně se správně rozhodovat. Možnosti genetické adaptace pro udržení tempa s lidským rozvojem mohou být v tomto směru nedostatečné. Jako hlavní mechanismus adaptace na nové urbánní prostředí se tak jeví fenotypická variabilita daného druhu ještě před tím, než čelí novým výzvám (Gross et al. 2010). Tato, původně jen částečně využívaná plasticita pak umožní danému druhu efektivně využívat antropogenním prostředí, často efektivněji než to přirozené (Hendry et al. 2008). Například bylo zjištěno, že samice sýkory koňadry z městského prostředí jsou rychlejší v řešeních nových problémů nežli ty, z prostředí lesního. Tato schopnost ovšem nijak neovlivňuje jejich hnízdní úspěšnost (Preisner et al. 2016). Některá zvířata pak vykazují menší bojácnost vůči normálně nebezpečným podnětům jako je například člověk (např. Lin et al. 2012; Møller 2008, Ducatez et al. 2016). To naznačuje důležitost učení se a přivykání novým podnětům (Shriner 1999).

Urbánní prostředí také limituje vokalizaci druhů v něm žijících, kvůli zvýšenému hluku způsobenému především dopravou (Marler & Slabbekoorn 2004; McMullen et al. 2014). Například sýkory koňadry zpívají v městském prostředí na vyšších minimálních frekvencích, aby zabránily překrytí nízkofrekvenčním hlukem vydávaným letadly, auty a ostatními zvukovými polutanty (Slabbekoorn & Peet 2003). Tento efekt by se mohl projevit i na varovných hlasech, i když pravděpodobně ne tak významně, protože varovné hlasy jsou často charakteristické vysokými frekvencemi. Nicméně Potvin et al. (2014) ukázal, že

maximální frekvence varovných hlasů je u kruhoočka austrálopacifického (*Zosterops lateralis*) v městském prostředí nižší nežli u jedinců obývajících venkov. Tato maximální frekvence dokonce lineárně klesá s narůstajícím hlukem města.

Nejednotné jsou názory na to, nakolik urbánní prostředí představuje riziko predace pro druhy, v něm žijící. Někteří autoři ukazují že urbánní prostředí má menší diverzitu predátorů a je zde proto nižší predací tlak než v prostředí přirozeném (Shochat et al. 2004). Naopak jiní vyzdvihují význam nepůvodních, domestikovaných predátorů (hlavně koček – May 1988; Fitzgerald 1990; Barratt 1997; Woods et al. 2003) a jejich velký tlak na populace urbánních druhů (hlavně ptáků – Churcher & Lawton 1987; Fitzgerald & Turner 2000). Nelze tedy usoudit, zda je z pohledu predace urbánní prostředí výhodné nebo ne, nicméně je zjevné, že i v tomto ohledu představuje pro mnohé druhy výzvu ve smyslu konfrontace s neznámými, potenciálně nebezpečnými druhy.

1.3 Krkavcovití

Pro studium schopnosti adaptovat se na urbánní prostředí je výborným příkladem čeleď krkavcovitých (Corvidae, Passeriformes). Celosvětově čeleď obsahuje kolem 120 druhů, z čehož největší rod *Corvus* zahrnuje asi 40 druhů (dos Anjos et al. 2009) a mnoho druhů opravdu silně tíhne k synantropnímu způsobu života (Maklakov et al. 2011). Je známo, že se některým krkavcovitým v antropogenním prostředí daří velmi dobře, a to zřejmě hlavně kvůli jejich inteligenci. U některých druhů krkavcovitých byly v poslední době prokázány jedny z nejpokročilejších kognitivních schopností v rámci zvířecí říše (Taylor 2014). Krkavcovití, společně s papoušky, se totiž mohou pyšnit mezi ptáky největším mozkiem v poměru k velikosti těla (Emery & Clayton 2004). Zároveň záleží i na počtu neuronů v palliu, kterých má krkavec velký (*Corvus corax*) větší počet, nežli například malpy (*Cebinae*) nebo araarauna (*Ara ararauna*) (Olkowicz et al. 2016). Mozek krkavce velkého je vůbec největší mezi všemi krkavcovitými (Mlíkovský 2003).

Další zajímavou vlastností krkavcovitých je vytváření komplexního chování jako je například schopnost vyrábět a používat nástroje (Lefebvre et al. 2002), nebo jejich dovednost vymýšlet nové způsoby, jak získat jídlo, často právě v urbánním prostředí. Například havrani (*Corvus frugilegus*) v Anglii se naučili vytahovat vnitřky popelnic, aby lépe dosáhli na jídlo, které pak vyhazují ven pro ostatní členy hejna (Clayton & Emery 2005). Vrány v některých městech se pak naučily využívat silniční provoz. V San Franciscu byly například pozorovány,

jak ženou celé hejno holubů přímo na dálnici, kde pak požíraly ty, které srazila auta (Donovan 2015). V japonském Sendai City zase vrány hází ořechy do silnice na přechodu pro chodce a čekají na červenou na semaforu, aby ty přejeté mohly posbírat a sežrat (Nikei 1995).

Zároveň jsou krkavcovití dobrým modelem pro studium antipredačního chování a používání varovných hlasů. Velká rozmanitost a využívání těchto hlasů je do velké míry způsobeno velkou mírou sociálnosti většiny krkavcovitých. Dobrým příkladem je kooperativně hnízdící sojka křovinná (*Aphelocoma coerulescens*), u které s rodičovskou péčí o mláďata pomáhá několik blízkce příbuzných ptáků (Francis et al. 1989) nebo *Gymnorhinus cyanocephalus*, žijící v stabilních hejnech čítající od 50 do 500 jedinců (Marzluff & Balda 1992). Také druhy nevyužívající helpery při hnízdění často tvoří society. Např. havrani polní hnízdí koloniálně, a i po vyhnízdění se mladí jedinci sdružují jak se svými příbuznými, tak i s nepříbuznými ptáky (Marshall & Coombs 1957). Obecně je běžné, že krkavcovití vytváří skupiny nehnízdících jedinců, které mohou být i velmi velké a vykazují složité sociální interakce (Orlaith & Bugnyar 2010).

Bylo prokázáno, že krkavcovití umí rozpoznávat a reagovat na varovné hlasy. Například krkavec velký nebo vrána americká (*Corvus brachyrhynchos*) reagují na playback varovného volání spolu s vizuálním stimulem mrtvého jedince a tomuto místu se pak vyhýbají (Avery et al. 2008; Peterson & Colwell 2014). Studie Chamberlaina & Cornwella (1971) na vráně americké ukázala, že tito ptáci používají mnoho druhů varovných hlasů, které v sociálním kontextu buď vybízejí ke shromáždění nebo k útěku. Cornell et al. (2012) pak dokázali, že jedinci vrány americké se o nebezpečí a predátorech učí od ostatních jedinců a nemusí s ním mít přímou osobní zkušenost. V dalších pokusech na vráně americké se pak zjistilo, že zatímco na playback hlasu nebezpečného výra virginského (*Bubo virginianus*) reagují ptáci útekem, na playback hlasu neškodné káně páskované (*Buteo lineatus*) nalétávají k reproduktoru a vydávají varovné hlasy, což vypovídá o jejich schopnosti rozeznávat nebezpečnost predátora pouze podle jeho hlasu (Hauser & Caffrey 1994).

Krkavcovití také mohou tvořit smíšená hejna. Např. Lockie (1956) prokázal, že havrani polní a kavky obecné tvoří při hledání potravy smíšená hejna. Smíšená hejna mohou tvořit i jedinci vrány americké a vrány rybí (*Corvus ossifragus*) (Chamberlain & Cornwell 1971). Některé druhy krkavcovitých zároveň sdílí své predátory. K významným predátorům evropských krkavcovitých pták patří hlavně výr velký (*Bubo bubo*) v jehož potravě se mimo kavky, vrány nebo straky obecné (*Pica pica*) může objevit i krkavec velký (Malafosse 1985). Ty samé druhy byly objeveny i v potravě orla královského (Chavko et al. 2007) a občasným

predátorem krkavce může být i raroh lovecký (*Falco rusticolus*). Na hejna kavek na Sicílii zase pořádá kooperativní lov raroh jižní (*Falco biarmicus*) (Leonardi 1999).

Krkavcovití ptáci jsou tedy díky jejich socialitě, velké variabilitě varovných hlasů i tvorbě smíšených mezidruhových hejn a sdílením predátorů dobrým modelem pro studium heterospecifických varovných hlasů. Přesto jsou takové studie dosud vzácné. Pouze Chamberlain & Cornwell (1971) prokázali, že na varovné hlasy vrány americké reagují i jedinci vrány rybí. Cílem mé diplomové práce tedy bylo otestovat, zda vrány obecné v městském prostředí středoevropského velkoměsta (Vídeň, Rakousko) reagují na varovné hlasy kavek obecných, které zde s nimi žijí, i když netvoří smíšená hejna, ale sdílí predátory. Studie probíhala na území Zoologické zahrady, kde vrány čelí neznámým druhům zvířat, z nichž některá pro ně mohou být nebezpečná. Proto jsem porovnávala i význam kontextu, v němž jsou varovné hlasy odposlouchávány, zda je v okolí predátor, či nikoliv.

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Manuskript

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Responses of urban crows to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures

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Abstract Urban animals and birds in particular are able to cope with diverse novel threats in a city environment such as avoiding novel, unfamiliar predators. Predator avoidance often includes alarm signals that can be used also by hetero-specifics, which is mainly the case in mixed-species flocks. It can also occur when species do not form flocks but co-occur together. In this study we tested whether urban crows use alarm calls of conspecifics and hetero-specifics (jackdaws, *Corvus monedula*) differently in a predator and a non-predator context with partly novel and unfamiliar zoo animal species. Birds were tested at the Tiergarten Schönbrunn in the city of Vienna by playing back con- and hetero-specific alarm calls and control

stimuli (great tit song and no stimuli) at predator (wolf, polar bear) and non-predator (eland antelope and cranes, peccaries) enclosures. We recorded responses of crows as the percentage of birds flying away after hearing the playback (out of those present before the playback) and as the number of vocalizations given by the present birds. A significantly higher percentage of crows flew away after hearing either con- or hetero-specific alarm calls, but it did not significantly differ between the predator and the non-predator context. Crows treated jackdaw calls just as crow calls, indicating that they make proper use of hetero-specific alarm calls. Responding similarly in both contexts may suggest that the crows were uncertain about the threat a particular zoo animal represents and were generally cautious. In the predator context, however, a high percentage of crows also flew away upon hearing the great tit control song which suggests that they may still evaluate those species which occasionally killed crows as more dangerous and respond to any conspicuous sound.

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Introduction

Urbanization is one of the greatest environmental changes of recent times (Gaston 2010). Moderate human disturbance connected with urbanization can increase the biotic diversity of an ecosystem or community (including birds—Pellissier et al. 2012; Ferenc et al. 2014). However, more intense human activities connected with dramatic changes in the environment cause an abrupt decline in species richness including birds (Jokimäki and Suhonen 1993).

Nevertheless, animals that is able to adapt to highly urbanized areas may profit from year-round availability of food (Galbraith et al. 2015) or lower number of natural predators (Gering and Blair 1999; Jokimäki and Huhta 2000) and as a result can occur in great numbers. Such an effect was observed for example in Black-billed Magpies in Poland (Jerzak 2001) showing that magpies' abundance increased three times faster in urban than rural areas between 1982 and 1996 and urban magpies had higher breeding success at the same time.

Although predation pressure by natural predators in urban areas may be lower than in rural areas (Gering and Blair 1999; Jokimäki and Huhta 2000; Lopez-Flores et al. 2009; Evans et al. 2015), there is an increased possibility to encounter non-familiar species that might potentially be dangerous (especially domestic cats—Kauhala et al. 2015). Recent studies indicate that some urban birds may develop a new defence strategy after being captured by a predator (Møller and Ibáñez-Álamo 2012). However, it might be more efficient to develop strategies that prevent the predation event in the first place (Bonnington et al. 2015; Caro 2005). Animals could be adapted to perceiving dangerous species as such, irrespective of their personal experience with them, and recognize them thanks to the ability to generalize their specific features (e.g. frontally positioned eyes or shape of teeth and beak—Griffin et al. 2001; Göth 2001; Zaccaroni et al. 2007; Ferrari et al. 2007; Binazzi et al. 2010 but see Azevedo and Young 2006 or Schetini de Azevedo et al. 2012). Alternatively, species with highly developed social cognition like corvids might learn about the possible danger of unfamiliar species indirectly via the anti-predator behaviour of other members of the society that are already experienced (Marzluff et al. 2010). Little is known about which strategy is favoured under urban conditions.

Animals show various ways of avoiding predation, among which, vigilance and the use of alarm signals are the most common, especially in social animals (Elgar 1989; Lima and Dill 1990; Beauchamp 2015). Acoustic alarm calls [especially those responding to aerial predators—see Evans and Evans (2007) for review] are usually uniform, making it difficult for the predator to locate the signaller (Marler 1955). Several examples demonstrate that it is advantageous for birds to respond not only to the alarm calls of their own species but also to those of other birds (Hurd 1996; Goodale et al. 2010), or mammals (e.g. Hauser 1988; Shriner 1998; Zuberbühler 2000; Rainey et al. 2004; Randler 2006; Flower 2011; Magrath et al. 2015). Often these species occur in mixed-species groups (Sullivan 1984; Forsman and Mönkkönen 2001; Goodale and Kotagama 2008; but see Møller 1988 for an example of birds that do not form associations). They may either use very similar alarm calls or recognize a set of different calls of

the associated species, which have the potential to encode information about specific predators (Munn 1984; Sullivan 1984; Griffin et al. 2005).

Our model species, the carrion crow (*Corvus corone*), is a widespread synanthropic species that adapts easily to human-dominated environments (Köver et al. 2015), most likely due to their highly developed cognitive and learning abilities. For example, crows in urban areas can recognize not only specific humans but also a specific car or the exact time at which zookeepers throw fishes to penguins and milk bottles are delivered to people's doorsteps, so they can catch the fishes or open and drink from the milk bottles [reviewed in Milius (2011)].

Crows are dominant over most other corvid species like jackdaws (*Corvus monedula*), magpies (*Pica pica*) or rooks (*Corvus frugilegus*) and usually do not form mixed-species flocks (Rolando and Giachello 1992). Yet, similar to other corvids, crows face medium-sized carnivores (red fox *Vulpes vulpes*, and in urban areas especially domestic dogs *Canis lupus familiaris* and cats *Felis catus*) and birds of prey (goshawk *Accipiter gentilis*) as the main predators (Randler 2008). To our knowledge, nothing is known about the role of hetero-specifics in the anti-predator behaviour of carrion crows, notably if they pay attention to, and cooperate with, other corvid species in respect of predator detection and defence.

In this study we were interested in whether carrion crows' adaptations to and perception of threat extends beyond their common set of predators: we tested wild urban birds in a predator and a non-predator context at the Tiergarten Schönbrunn, the zoo of Vienna, Austria, both of which were represented through species that crows usually do not encounter (with the exception of wolves) in their natural habitats, such as polar bears or peccaries. We further tested whether urban crows foraging in the enclosures of these zoo animals were equally responsive to conspecific alarm calls and to hetero-specific alarm calls of jackdaws with which they usually do not form mixed-species groups, but they can co-occur in the same area.

We predicted that (1) crows should respond primarily to conspecific rather than hetero-specific alarm calls, because crows and jackdaws do not live in mixed-species associations; (2) crows should respond to conspecific alarm calls more strongly in the predator than the non-predator context, based on their adaptation to their perception of species as risky or non-risky (assuming a predisposition to recognize traits shared across predators) and/or based on their experience with those species (assuming memory for previous predation events); (3) if crows, however, would respond to hetero-specific alarm calls (e.g. due to their co-occurrence with jackdaws in the area), they also should do so more strongly in the predator than in the non-predator context.

Methods

Study site and study species

Our study species was a wild population of the carrion crow (*C. corone*) inhabiting the area at and around the zoo of Vienna (Tiergarten Schönbrunn), Austria. This population comprises individuals of both subspecies recognized in Europe (*C.c. corone*, *C.c. cornix*; Cocker and Mabey 2005) together with fertile hybrids of these two forms (we refer to both subspecies and their hybrids as “crows” hereafter). Our previous research based on captures and individual marking showed that there are 20–40 territorial breeding pairs within this population depending on the year, while the rest of the birds represent non-breeders of different age classes. We ran the experiment from August to October 2014. During the time of the study, the average number of crows observed on a daily basis at the zoo was 55 ± 23 crows (mean \pm SD) (Uhl et al., unpublished).

Experimental areas

As experimental areas we chose four enclosures at the zoo of which two represented a predator and two represented a non-predator context. For the predator context, we used the zoo enclosures of polar bears (*Ursus maritimus*) and wolves (*Canis lupus*). Both species have the ability to catch and kill crows. The animal keepers at the zoo report one to two crows each year being killed by both polar bears and wolves (they have additionally been observed to catch other birds including pigeons and peacocks). Wolves are familiar to European populations of crows as predators (at least from an evolutionary point of view), as crows commonly scavenge on wolves' prey (Young et al. 2014), while polar bears are not. For the non-predator context, we chose the joint enclosure of the common eland (*Taurotragus oryx*) and African crowned crane (*Balearica regulorum*), and the enclosure of the collared peccary (*Tayassu tajacu*). None of these species have been reported to harm crows and thus were considered to pose no threat to crows.

The polar bear enclosure (area of approx. 1570 m²) was very diverse with many water surfaces and high rocks in it, the latter representing hiding and/or observing places for crows. There are no trees within the enclosure, but there are many in its immediate surroundings. Polar bears were provided with a diet consisting of meat (chicken, fish), vegetables and fruits (carrot, apples, oranges). The wolf enclosure (approx. 2410 m²) was situated in the sparse forest of the zoo, incorporating many tall and some fallen trees. The wolves' diet consisted exclusively of meat (chicken, rabbit, pork and beef). The eland and crane enclosure (approx. 1260 m²) contained a small mound and

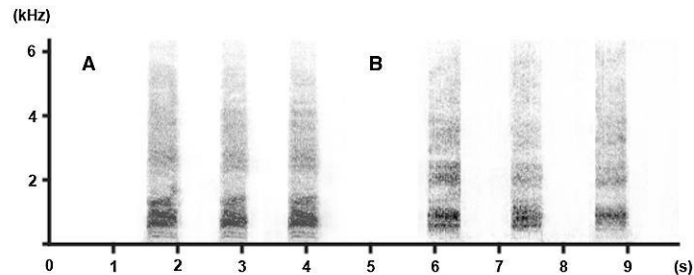
scattered trees. The food provided in this enclosure consisted of a mixture of grain and hay. The collared peccary enclosure was the smallest (approx. 550 m²) but diverse with some fallen trees, rocks and bushes. Food here consisted mainly of vegetables (carrot, cabbage) and bread. Taken together, the enclosures differed not only in respect to predation risk but also in respect to shelter, food quality and food distribution. Replicates of different enclosure types were not available for those species in the zoo. We consequently fitted enclosure as a random term in our analyses.

Experimental conditions and stimuli

We ran the experiment in four conditions: (1) in the *con-specific* condition we played back a conspecific (=crow) alarm call. (2) In the *hetero-specific* condition we played back a hetero-specific (=jackdaw) alarm call. (3) In the *playback control* condition we played back a hetero-specific (=great tit, *Parus major*) song and (4) in the *no playback* condition we did not play back any stimulus. The reasoning behind the latter two conditions was (a) to provide a general sound control (condition 3; note that instead of a great tit song we could have used any other type of non-alarm sound or noise) and (b) to have a situation in which we could score the crows' behaviour undisturbed by any playback (condition 4).

All playbacks used were derived from male birds. For the conspecific condition, we used calls from four unfamiliar, i.e. not members of the zoo population, male crows and each bird was represented with three recordings in the sample. Calls of crows were recorded between September 2011 and October 2012 in an aviary setting when birds were confronted with an unknown human intruder carrying a large object (backpack) using a Marantz PMD661 digital recorder and a Sennheiser ME65 directional microphone on a K6 module. For the hetero-specific condition, we used calls from four unfamiliar male jackdaws and each bird again was represented with three recordings in the sample. Calls of jackdaws were recorded between October 2007 and February 2008 using a Sony TCD-D100 digital audio recorder and a Sennheiser ME65 directional microphone, while the birds were foraging in the flock on the meadow near the Konrad Lorenz Research Station in Upper Austria when birds were confronted with natural enemies (mostly bird of prey flyovers). Sound files for the con- as well as hetero-specific condition were saved as.wav files with a sampling rate of 48 kHz and a 16-bit amplitude resolution. For the con- as well as hetero-specific condition, only calls with little to no background noise were used for the experiment. Figure 1 shows representatives of used alarm calls of crows (Fig. 1a) and jackdaws (Fig. 1b). For the playback control condition, we used one recording of a

Fig. 1 Spectrogram of three typical alarm calls of carrion crow (*C. corone*)—(a), and jackdaw (*C. monedula*)—(b) used in our playback experiments



singing unfamiliar male great tit purchased from a bird song database (Schulze 2003). As this was a control condition, we did not expect any variability in responses to various great tit songs; therefore, we used only one song, typical for the middle-European population. All playback stimuli were edited in Audacity 2.0.6 in a way that they consisted of three syllables with total time duration of 2 s. The volume was set to the equal level in all recordings as well as on the playback devices. For the no playback condition, we did not play any playback, and we just observed the natural behaviour of crows during feeding the zoo animals.

Experimental procedure

We ran one trial per session which reflected one of the conditions. A trial started right after the zoo animals had been fed in the respective enclosure to increase the chances that a high number of crows would attend the feeding and access the enclosure. However, we started the trial only if there were at least five crows within the respective enclosure. The mean number of crows present before the playback was 10.9 (min = 5, max = 41, SE = 6.2). A trial consisted of a 3-min baseline during which we recorded the number of crows present and assured that the presence of the experimenters did not cause the birds to fly away or trigger any other wary behaviour in the birds. Then we played back the particular stimulus for the respective condition. Each stimulus was only played back once per trial. We recorded the birds' response during the following 1 min. Stimuli were played from a loudspeaker (Mipro MA 101-C), and trials were videotaped (camcorder JVC Everio GZ-HM445BE). During each trial, there were always two experimenters present (altogether there were three experimenters: K.B., J.B., A.P.) who stood among the zoo visitors outside the enclosure and recorded the birds' responses that were outside the angle of the camera.

We recorded the number of crows present in the enclosures 10 s before and 60 s after the playback. Those birds that left the enclosure within the 1-min period

following the stimulus playback were defined as birds 'flying away'. We noted if crows that were 'flying away' landed after a short flight in close proximity to the enclosure, i.e. on the nearest trees, buildings or other elevated places, or kept flying until they were outside the experimenter's view. From those crows that stayed in the enclosure during the 1-min period after the playback, we counted the number of uttered calls. The total number of calls was then corrected by the number of crows present after the playback. In the no playback control condition, we recorded the number of crows present within the enclosure at the same time that corresponded to the time before playing back the stimulus in the other conditions, as well as the number of birds flying away and the number of vocalizations in the 1 min that otherwise followed the stimulus presentation.

We conducted one trial each in two different enclosures per day. The order of conditions was counterbalanced within and between enclosures with the restriction that we did not conduct the same condition in a given enclosure on two consecutive test days to avoid potential habituation. We conducted ten trials per condition, i.e. 40 trials, in the predator context (five trials per condition in the polar bear and five trials per condition in the wolf enclosure) and 12 trials per condition, i.e. 48 trials, in the non-predator context (six trials per condition in the eland and crane enclosure and six trials per condition in the peccary enclosure).

Statistical analysis

For both behavioural responses, we ran a generalized linear mixed effect model (GLMM).

We undertook a preliminary analysis in which we compared the percentage of crows flying away within the predator and non-predator condition by forming a generalized linear mixed effect model (GLMM) under equal settings as described below. The particular pairwise comparisons of categorical predictor zoo animal species were computed using post hoc Fisher LSD tests. We did not find any significant differences in the percentage of crows

flying away after the playback between the wolf and bear enclosures (Fisher LSD test, $Z = 0.711$, $P = 0.325$; see below for details of statistical methods) or between eland and peccary enclosures (Fisher LSD test, $Z = 0.659$, $P = 0.602$). Therefore, we pooled the data and coded them for the predator (wolf and bear) and non-predator context (eland and peccary) for subsequent analyses.

For the first model we used the percentage of birds, which flew away from the feeding place after the playback out of those which were present before the playback as response variable (counted as binomial proportion using command `cbind` in R). These data followed the gamma distribution. For the second model, we used the number of vocalizations given after the playback corrected for the number of crows present after the playback fitted as a Poisson distribution.

Both models included only two predictors, the condition (conspecific, hetero-specific, playback control, no playback) and context (non-predator and predator) and their interaction. Species of animal in each enclosure (bear, wolf, eland, and peccary) and the identity of the used playback (four crows, four jackdaws, one great tit song and one silence) were included as random factors in a random slope model. A likelihood ratio Chi-square test was used to assess the effect of the predictor. Post hoc test following the binomial distribution (Fisher LSD test) with Tukey's correction was used to compare particular values of categorical predictors. All statistical analyses were computed in R 3.2.1 (R Development Core Team 2015).

Results

Behavioural response to playbacks

The percentage of crows flying away at the respective enclosure after the playback was significantly affected by the interaction of the predictors condition and context (Table 1). Comparing conditions within contexts showed that in the non-predator context, the percentage of crows that

flew away at the enclosure both in the conspecific as well as hetero-specific condition was significantly lower than in the playback control condition (Fisher LSD test, conspecific: $Z = 4.154$, $P < 0.001$; hetero-specific: $Z = 4.821$, $P < 0.001$; Fig. 2) as well as than in the no playback condition (Fisher LSD test, conspecific: $Z = 4.825$, $P < 0.001$; hetero-specific: $Z = 5.151$, $P < 0.001$; Fig. 2). There was no difference between the conspecific and hetero-specific condition (Fisher LSD test, $Z = 0.511$, $P = 0.998$; Fig. 2). Hence, most crows flew away after hearing alarm calls, irrespective of the species producing the call. Playback control and no playback conditions did not differ significantly from each other (Fisher LSD test, $Z = 0.211$, $P = 0.999$; Fig. 2).

In the predator context, the percentage of crows that flew away from the enclosure both in the conspecific as well as hetero-specific condition was also significantly lower than in the no playback condition (Fisher LSD test, conspecific: $Z = 3.652$, $P < 0.001$; hetero-specific: $Z = 3.621$, $P < 0.001$; Fig. 2), but it did not significantly differ from the playback control condition (Fisher LSD test, conspecific: $Z = 1.801$, $P = 0.621$; hetero-specific: $Z = 1.807$, $P = 0.601$; Fig. 2). There was no difference between the conspecific and hetero-specific condition (Fisher LSD test, $Z = 0.099$, $P = 0.999$; Fig. 2). Again, the playback control and no playback condition did not significantly differ from each other (Fisher LSD test, $Z = 2.099$, $P = 0.425$; Fig. 2).

Comparing conditions between contexts showed that the percentage of crows that flew away from the enclosure did not significantly differ between the non-predator and predator context in any of the conditions (Fisher LSD tests; conspecific: $Z = 0.509$, $P = 0.999$; hetero-specific: $Z = 0.900$, $P = 0.989$; playback control: $Z = 2.111$, $P = 0.321$; no playback: $Z = 0.398$, $P = 0.997$; Fig. 2).

Vocalizations

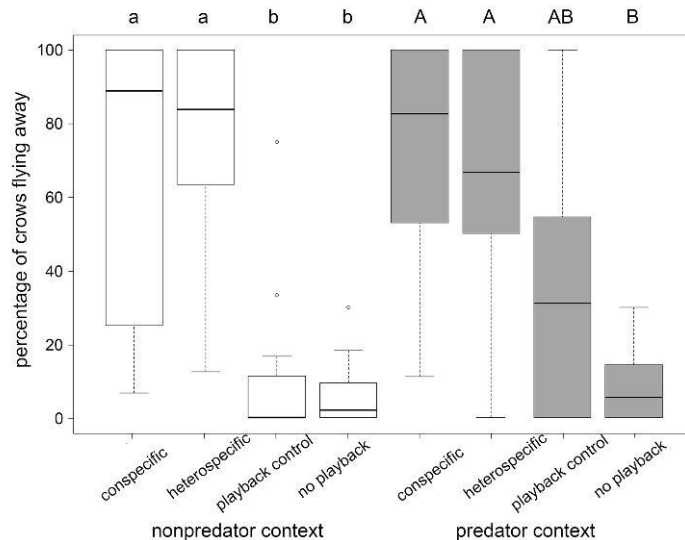
The number of calls performed by crows after the playback (ranging from 0 to 65, mean = 4.15) was not significantly

Table 1 Results of the generalized linear mixed effect models run on both response variables

Response variables	Predictor variables	Chi-square	df	P value
Proportion of crows that flew away	Condition	53.211	3	≪0.001
	Context	0.258	1	0.631
	Condition × context interaction	61.225	7	≪0.001
Vocalizations	Condition	0.625	3	0.358
	Context	0.211	1	0.823
	Condition × context interaction	0.784	7	0.901

The animal species, in which enclosure the experiment was conducted and the caller identity was included as random factors. Conditions = conspecific, hetero-specific, playback control, no playback; context = non-predator and predator. Significant effects are shown in bold

Fig. 2 Percentage of crows that flew away from the enclosure after the playback out of all crows that were present at the enclosure before the playback. Bars represent four test conditions: conspecific, hetero-specific, song control and no playback control condition. White bars represent non-predator context, i.e. eland and crane and peccary enclosure, grey bars represent predator context, i.e. polar bear and wolf enclosure. Letters above each bar refer to significant differences (*a* different from *b*, *ab* different from neither *a* nor *b*) among the non-predator context (*lower case*) and the predator context (*upper case*)



affected by condition, context or the interaction of condition and context (Table 1).

Discussion

Crows in this study clearly responded, by flying away upon the playback of the respective stimulus, in the two alarm call conditions (conspecific = crow call and hetero-specific = jackdaw call) compared to the two control conditions (playback control = great tit song, and no playback = no stimulus). However, contrary to our predictions, crows responded equally to the conspecific and hetero-specific alarm calls although crows and jackdaws differ in their feeding (Lockie 1955) and defence ecology (Röell and Bossema 1982), and crows may even represent one of jackdaws' predators (Bossema et al. 1976).

Response to hetero-specific alarm calls

One possible explanation for the use of jackdaw alarm calls by crows is that crows learned about the calls during encounters with jackdaws. Hetero-specific alarm call recognition is often learned when species encounter the same predation events [e.g. Cully and Ligon (1976) for corvids]. However, the probability of crows and jackdaws regularly encountering predatory events in Vienna is low: Vienna hosts roughly 2000–4500 crow breeding pairs but only around 40 jackdaw breeding pairs (data from BirdLife Austria, pers. information). Notably, there are hardly any

jackdaws at Vienna Zoo; although some birds may pass by from time to time, not a single jackdaw was seen during the entire period of the current study. Yet, many crows found in the Vienna Zoo roam in a much greater area in and around Vienna. Occasional experience of these crows with alarm-calling jackdaws may be enough for establishing a learned response in the local population [compare Marzluff et al. (2010)].

An alternative explanation for our results is that jackdaws' alarm calls are acoustically similar to those of crows and have convergent acoustic attributes like speed of repetition, duration and frequency (Jensen et al. 2008; Fig. 1). A similar response to hetero-specific alarm calls as found in this study has been shown by Johnson et al. (2003) on Australian mud-nesting apostlebirds (*Struthidea cinera*). These birds are able to react appropriately to the alarm calls of allopatric species, Carolina wrens, *Thryothorus ludovicianus*, which they could never hear before. Follow-up experiments revealed that apostlebirds react even to the narrow-band pulses of noise played back at the same tempo (Johnson et al. 2003). This result suggests that birds may be able to generalize their response to alarm calls to any other similar sounds.

Finally, we would like to note that we kept the number of playback conditions and trials to a minimum to avoid any potential habituation to the stimuli. We thus cannot rule out that the crows would have responded to any sound of a conspecific and hetero-specific corvid in a similar way as to the alarm calls. Future studies testing crows with other corvid calls of different meaning but of

similar valence and/or arousal level (e.g. defensive calls) may clarify whether the strong responses of crows found in this study are specific to the playback of alarm calls or not.

Response to con- and hetero-specifics in the non- and predator context

Unexpectedly, our results showed that crows responded to con- and hetero-specific alarm calls equally in the predator as well as in the non-predator context. This high caution to any alarm call despite the potential risk is in conflict with the study of Wascher et al. (2015), where crows were shown to be able to precisely evaluate the reliability of alarms and detect the cheaters.

This high level of caution is even more surprising given the fact that the crow population of this study lives in a large city (Vienna has about 1.8 mio inhabitants and an area of about 414 km²). Urban populations of corvids were shown to be generally less shy than corvids in rural habitats because they commonly encounter potentially dangerous situations and learn to cope with them (Houston 1977; Knight 1984; Knight et al. 1987). Urban species like crows must be able to adjust to novel competitors, food sources, dangers and many other factors. And crows, showing sophisticated cognitive abilities, are very successful at adapting to life in the city (McGowan 2001). Therefore, we might expect that crows would be able to assess the amount of potential threat that a particular zoo animal represents and react less to the alarm calls under the non-risky conditions.

On the other hand, the zoo environment in this study may be just the explanation of the generally high caution of the crows foraging within the zoo animal enclosures. Zoological gardens embrace a large array of exotic animals, which may represent varying threats to crows. Most of these animals are unfamiliar to them and they have no mutual evolution. Further, animals kept in captivity may represent danger to native bird populations, even when birds are usually not part of their normal diet in the wild (Stearns et al. 1988; Ross et al. 2009). Therefore, crows may not be able to precisely evaluate the potential risk they may encounter in particular enclosures. The safest strategy in such case for them may be to rather respond to any alarm call. This finding is, however, in contrast to the relatively high flexibility of corvids in learning about novel, unfamiliar predators and risks such as in Marzluff et al.'s (2010) study on American crows, which readily learned to differentiate between humans that were catching crows or not.

Another possibility could be that the crows in Vienna Zoo are well experienced with the local setting and *can* judge the degree of threat represented by different zoo

animals; yet, they keep on responding to (played back) alarm calls because these might warn from other unknown and/or hidden dangers like an approaching bird of prey, irrespective of enclosure type. Hence, the crows' flight responses do not reflect the threat perceived from a particular zoo animal, but are the result of a general arousal upon hearing alarm calls. According to this explanation, the crows' arousal level seems to be similar upon hearing con- and hetero-specific alarm calls.

Still, crows in this study seemed to be able to roughly assess potential threats by the zoo animals which is supported by the result that the crows responded equally to the playback control (song of a great tit) and a conspecific alarm when they were in polar bears or wolves enclosures, i.e. in the predator context, whereas they flew away significantly less, when the playback control was presented in the non-predator context. Although this suggests a higher wariness with predators, this interpretation has to be treated with caution as the response to the playback control did not differ significantly between predator and non-predator context. The possibility of crows being cautious with wolves is not surprising given that crows have a long co-evolution with these predators. Nevertheless, to our knowledge, crows lack any co-evolution with polar bears. It is possible that the reason for their caution with both species lies in experiencing their predatory behaviour. According to the zookeepers' personal observations crows are caught and eaten by polar bears and wolves from time to time. Crows witnessing such an event may thus lead to their very high caution towards these animals. However, it can be expected that only a few crows ever witnessed conspecifics being killed by wolves and bears, but still they may transfer their caution to other crows which do not have such a personal experience since they can quickly socially transmit knowledge about a novel artificial predator also even across generations (Cornell et al. 2012; Marzluff et al. 2010).

Predatory risk of the species kept in the enclosure is certainly only one out of several factors that could have influenced the crows' wariness and thus responsiveness to the playback of alarm calls. Unfortunately, our set-up does not allow us to experimentally test possible effects of environmental features of the enclosures like the degree of forestation or openness, as we do not have multiple forested or open enclosures with the same species available. Yet, aside of predatory risk, our data do not reveal a consistent pattern regarding these environmental features: crows showed highest vigilance at the enclosure of wolves, which is covered by a forest, and at the enclosure of polar bears, which is exactly the contrary, open but jagged. Moreover, the high readiness of crows to leave a predator enclosure is in contrast to the high-nutrition food (meat) available there.

Warning others

Contrary to the flying away behaviour, the vocalization of crows after the playback was not affected by the playback type, or the experimental condition. Crows gave few calls after the playback and very often they did not call at all. Crows rather reacted in the safest way, namely, flying away as a response and refrained from giving vocalizations themselves. This is quite surprising in such a social bird [see Warrington et al. (2015)]; nevertheless, crows responded already to an alarm call, not to a real, approaching predator. Alarm calls are usually produced after the predator encounter (Gill and Bierema 2013); therefore, the proper response to the alarm call is flying away rather than alarm calling. Moreover, the calls recorded after the playback stimulus should probably spread the alarm further. Therefore, their occurrence might also depend on the presence of eavesdroppers in the surrounding enclosures. Unfortunately, we had no possibility to check for all crows present in the larger surrounding of the enclosure, and the effect of the presence of eavesdroppers on the vocalization could not be tested.

To conclude, our study showed that crows respond strongly to conspecific and hetero-specific alarm calls regardless of the risk of predation, which may be the result of low familiarity with the zoo animals and the threat they may represent or a general wariness for unexpected events, irrespective of the enclosure type. Personal or socially transmitted experience with crows being killed may enhance crows' caution insofar that crows may fear almost any suspicious sound in the enclosures of potential crow predators. Our study further shows that studying the antipredatory behaviour in the context of zoos, where unfamiliar, exotic animals are encountered, gives us the opportunity to test animal interactions hard to observe (or even induce) in the nature.

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