

**University of South Bohemia in České Budějovice  
Faculty of Science**

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

RNDr. Thesis

**Bc. Kateřina Bílá**

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Annotation:

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.

Declaration [in Czech]: Prohlašuji, že svoji rigorózní práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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V Českých Budějovicích, dne 12. dubna 2017

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## **Declaration of co-authors**

All co-authors agree with presentation of following paper in RNDr. thesis and simultaneously they confirm participation of Kateřina Bílá on its creation.

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Responses of urban crows to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures. *Animal Cognition*, 20: 43-51.

Kateřina Bílá performed most of experiments and importantly participated on the data analyses and preparation of the manuscript.

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## Paper

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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).

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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 Mabe 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  $55 \pm 23$  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 m<sup>2</sup>) 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 m<sup>2</sup>) 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 m<sup>2</sup>) 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 m<sup>2</sup>) 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.

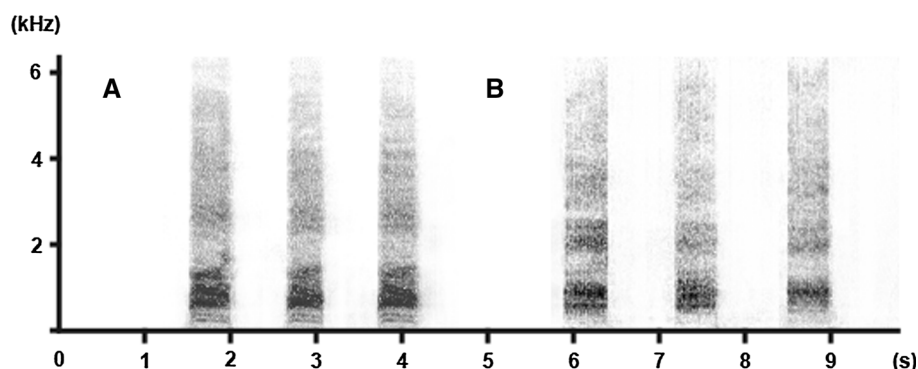
### Experimental conditions and stimuli

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

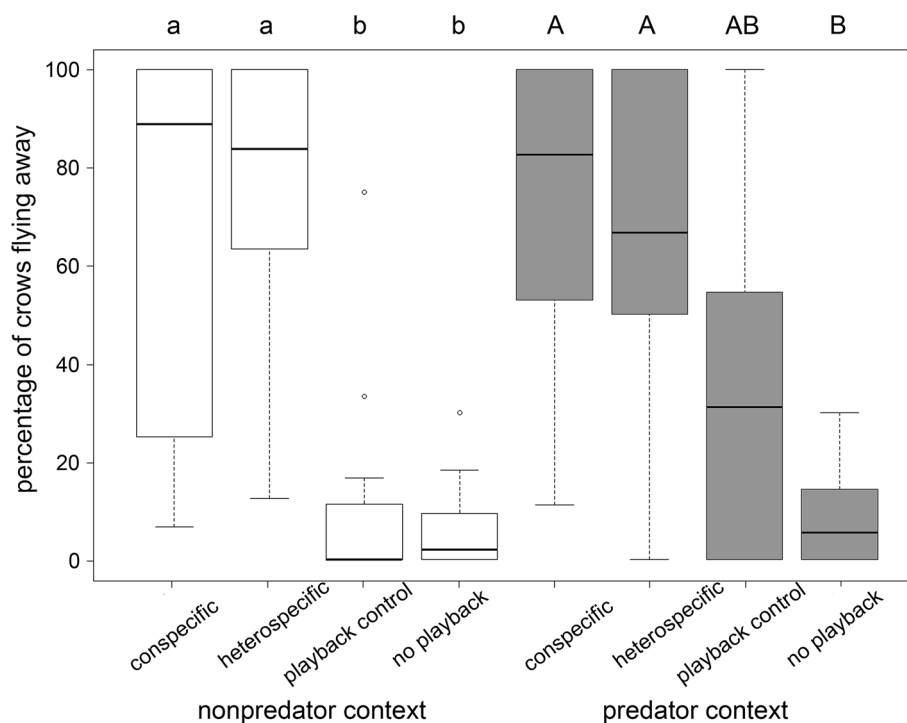
The number of calls performed by crows after the playback (ranging from 0 to 65, mean = 4.15) was not significantly

**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	<b>53.211</b>	<b>3</b>	<b><math>\ll 0.001</math></b>
	Context	0.258	1	0.631
	Condition $\times$ context interaction	<b>61.225</b>	<b>7</b>	<b><math>\ll 0.001</math></b>
Vocalizations	Condition	0.625	3	0.358
	Context	0.211	1	0.823
	Condition $\times$ 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 km<sup>2</sup>). 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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