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Ravens respond to unfamiliar corvid alarm calls

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ANNOTATION:

The following work encompasses a research in the behaviour of the common raven (*Corvus corax*). I tested the responses of the common raven to heterospecific alarm calls of various bird species that differ in familiarity and taxonomical relatedness to ravens. Two other corvid species (jays) and two non-corvids (gulls) were presented. The ravens were given stimuli from one jay and one gull – one of which was always familiar to the tested ravens (European) and one unfamiliar (American). The results suggest that familiarity is not as important as the membership to the Corvidae family.

DECLARATION:

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

České Budějovice, 13.4.2022

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Marika Davídková

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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.

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ORIGINAL ARTICLE

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

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(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.

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 alarm calls 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 m^2, 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 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

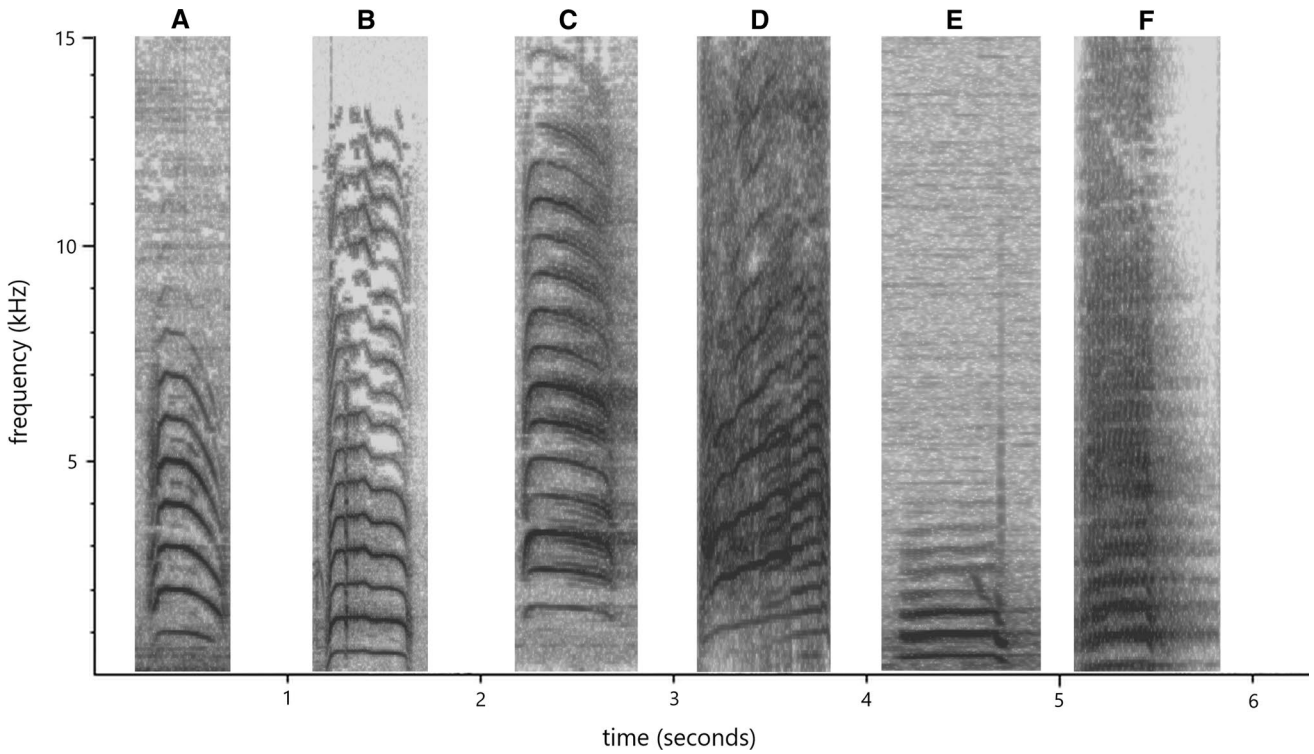

Fig. 1 Sonograms of representatives of all six presented playbacks. **a** Laughing gull (*Leucophaeus atricilla*)—alarm call, **b** black-headed gull (*Chroicocephalus ridibundus*)—alarm call, **c** blue jay (*Cyanocitta cristata*)—alarm call, **d** Eurasian jay (*Garrulus glandarius*)—alarm call, **e**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

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).

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).

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

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

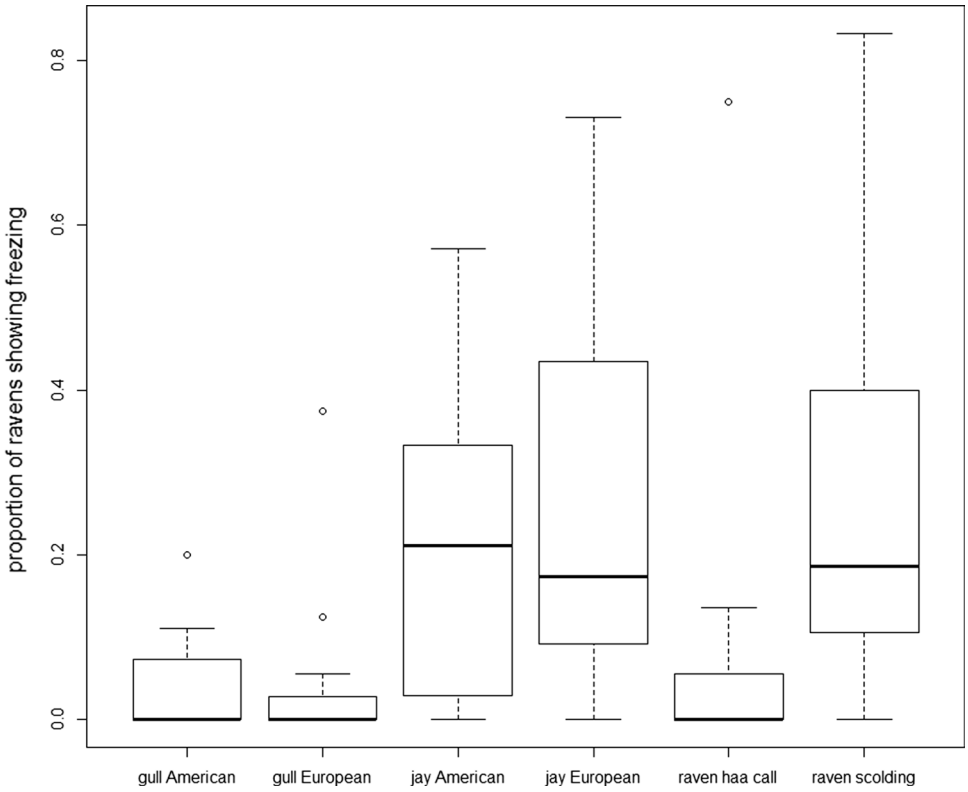

Fig. 2 The effect of particular playbacks on the proportion of ravens showing freezing, out of those present before the playback

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

(*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.

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).

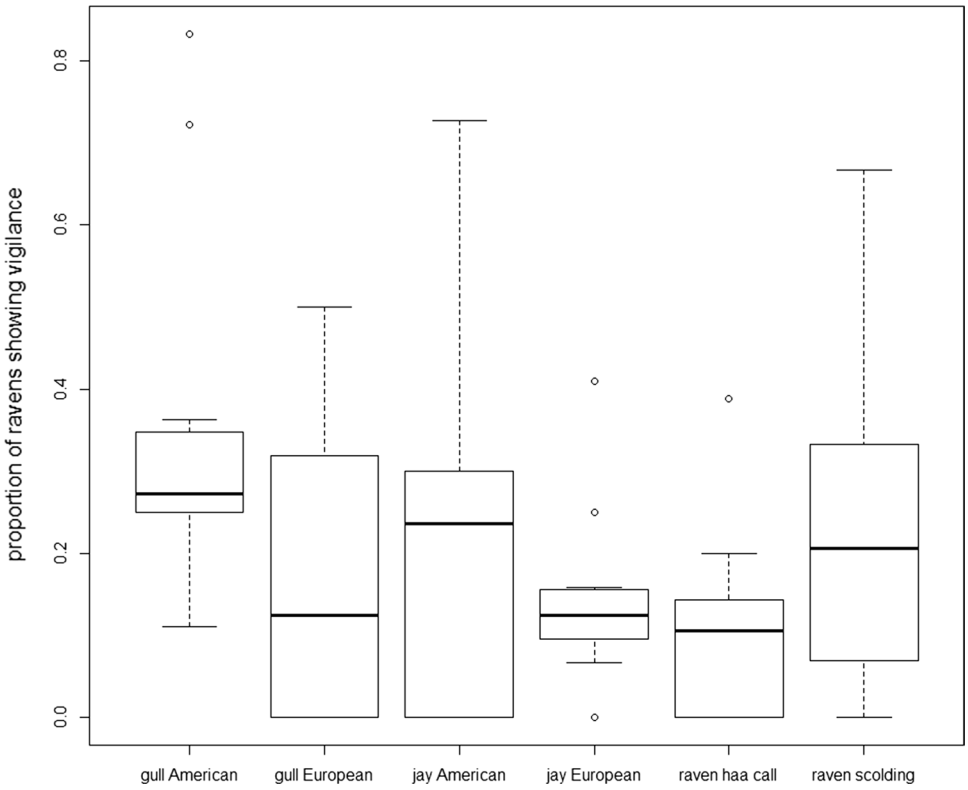

Fig. 3 The effect of particular playbacks on the proportion of ravens showing vigilance, out of those present before the playback

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

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

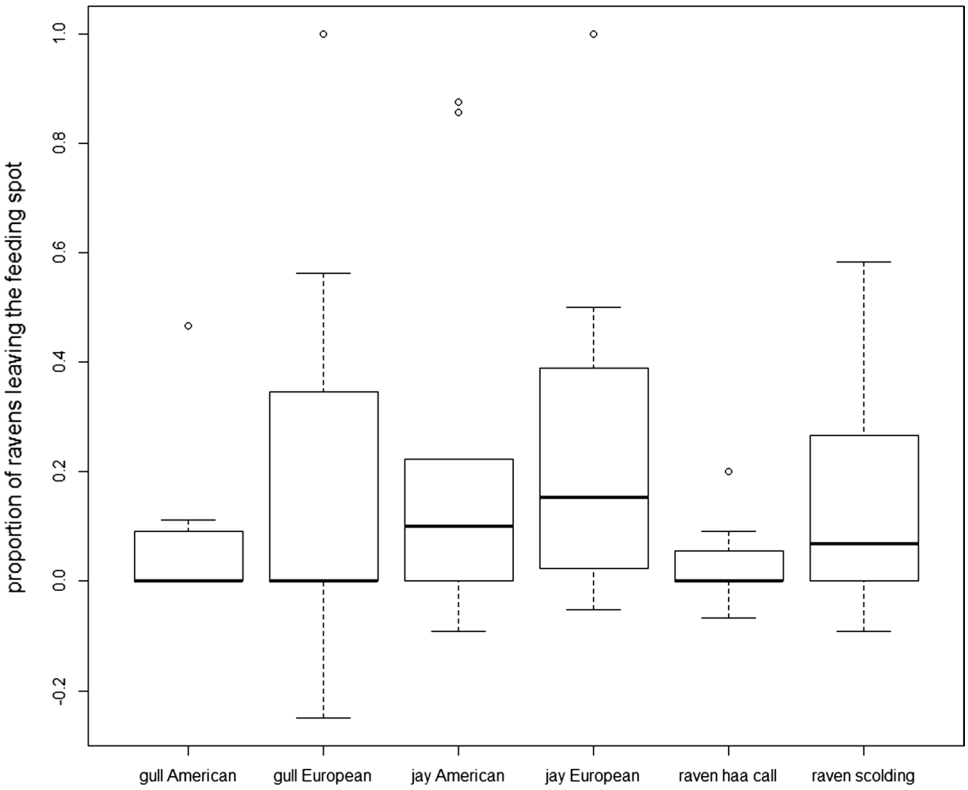

Fig. 4 The effect of particular playbacks on the proportion of ravens flying away, out of those present before the playback

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.

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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.

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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-66.006/0016-WF/II/3b/2014).

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