

Subordinate ravens (*Corvus corax*) increase alarm calling when temporarily separated from group members

Christian R. Blum (✉ c.blum0@gmail.com)

University of Vienna Faculty of Life Sciences: Universitat Wien Fakultat fur Lebenswissenschaften
<https://orcid.org/0000-0003-4941-7475>

W. Tecumseh Fitch

University of Vienna Faculty of Life Sciences: Universitat Wien Fakultat fur Lebenswissenschaften

Thomas Bugnyar

University of Vienna Faculty of Life Sciences: Universitat Wien Fakultat fur Lebenswissenschaften

Research Article

Keywords: predator recognition, corvid, raven (*Corvus corax*), alarm call, status signalling, group dynamics

Posted Date: May 20th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1662378/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Background

Although predator avoidance can have immense impacts on fitness, individual variation in anti-predator behaviour remains largely unexplained. Existing studies investigating predator responses and learning have occurred in individual or group settings, but not both. Solely testing individuals allows for evaluations of only individual variations in learning or personality, while testing only in groups makes it impossible to distinguish individual differences from social effects. In this study, we directly compared common raven anti-predator behaviour both alone and in a social group. We trained 15 ravens to recognize and respond to a novel experimental predator, and then tested them in both group and isolation settings across 1.5 years.

Results

We found that dominant individuals spent more time alarm calling than subordinates, but only subordinates call more when separated whereas dominants do not. Dominants also scolded sooner than subordinates in the group trials.

Conclusions

We speculate that subordinate ravens are suppressed from, or are less capable of, performing intense anti-predator behaviour while in the group, while dominant individuals use their anti-predator responses to signal status in the group. This suggests that, in addition to its recruitment or predator-deterrent effects, alarm calling may serve as a marker of individual quality to conspecifics.

Background

Successfully recognizing and avoiding predators can have immense fitness consequences (1), but individual variation in anti-predator behaviour remains poorly understood. One well-studied factor is learning to identify predators, which is important to effectively focus anti-predator behaviour on potentially novel threats and to decrease costs of wasted defensive behaviours (2, 3). Learning can occur at an individual level, providing accurate information at a high risk to oneself, or in a social context from others, providing potentially less accurate information at a lower risk (4). Differences in the recognition of and response to predators are further amplified by individual variations in learning accuracy and personality (5, 6). Considering the importance of predation-avoidance, such individual differences may have considerable fitness impacts (2).

A less-studied contributor to individual variation in anti-predator behaviour concerns social dynamics. Social factors such as sex or dominance might heavily influence individual motivation to participate in anti-predator behaviour (7). A better understanding of the importance of social dynamics on motivational variation is interesting in its own right, and would also allow better control for motivation when studying

variation in learning accuracy. Studies on predator learning to date were either conducted at an individual or a group level (8–12). In the absence of social partners, individual testing may provide similar levels of experienced threat, and therefore similar motivation to engage in anti-predator behaviour, for all subjects. On the other hand, group testing can examine social dynamics and their impact on motivational levels, but they cannot distinguish whether an individual has not learned to recognise a predator, or is simply unmotivated to respond to it. Studies conducted in the wild also face additional difficulties in recognizing individual study subjects (e.g. (13); but see (14, 15)). Only by combining both group and individual setups for the same clearly identified individuals can we tease out the specific role of social dynamics on the motivation to engage in anti-predator behaviour.

The current study examined an important anti-predator behaviour – alarm calling – in common ravens (*Corvus corax*), a member of the corvid family. When confronted with potential predators, corvids produce harsh alarm vocalisations directed at the predator (“scolding”), presumably to harass the predator into leaving, but also to recruit conspecifics for social support (2). Such group mobbing can provide learning opportunities for inexperienced individuals (16), and has been shown to showcase alarm callers’ status in several corvid species (white-throated magpie-jays (17); hooded crows (18); black-billed magpies (19)). While for common ravens this has yet to be shown, we know they encode individual information in other call types (20–22) and respond stronger to alarm calls of adults than those of juveniles (23).

In a series of elegant studies on wild American crows (*Corvus brachyrhynchos*), Marzluff and colleagues demonstrated social learning about the potential threat of particular humans, the spread of this information within the local population, and its vertical transmission across generations (13, 24). In those studies, human experimenters could be distinguished via facial masks and their threat level was manipulated via their initial participation, or absence, at catching and banding of crows. Using a similar design, we could previously show that two captive groups of ravens can remember a ‘dangerous’ human for multiple years (25). Interestingly, individuals showed a large variation in scolding response, and dominance status was a strong predictor for their behaviour. Indeed, dominant individuals took the lead in most scolding bouts together with their closest affiliates, indicating strong social dynamics effects (25).

But why should dominant ravens differ from subordinates in scolding? A recent study on jackdaws found that the more individuals give an anti-predator response, the more attractive the display becomes to others to join (26) and, presumably, the more likely the predator is to leave. Given that ravens would profit from conspecifics participating in anti-predator defence in similar ways, the described variation in scolding seems puzzling. One possibility is that in our previous study not all of the ravens were knowledgeable about the predator stimulus, and that subordinates in particular had not yet learned that the masked human represents a risk. Another possibility is that all ravens knew about the predator, but some individuals were “free-loading” on the anti-predation efforts of others, typically dominants (27). Furthermore, it is possible that dominant individuals could afford to show more scolding than subordinates, simply because they were in a better physical condition (see (7)). The ravens’ anti-predator behaviour would thus serve as an honest signal, indicating the callers’ quality (see (28)). Finally, it is

possible that dominants actively suppress calling in subordinates to show-off or exaggerate their own quality. In fact, hindering others from calling is both energetically costly and takes time away from engaging in the actual anti-predator response, thus counteracting the effects of group mobbing. Hence, such a costly behaviour should occur only in low to moderately risky situations and/or when potential mates are in the audience. Similar status-signalling effects have also been hypothesized for raven recruitment calls at rich but defended food sources (29), where high-status individuals within the non-breeders tend to produce more calls.

In the current study, we experimentally investigated the effect of social dynamics on individual variation in ravens' scolding behaviour. We followed up on our previous study, in which we trained two groups of eight ravens each to recognize a human wearing a particular mask (Fig. 1) as a potential novel "predator" (25). During training, the masked person carried a dead raven in the hand, simulating the result of a predation event (30), but all tests were carried out with the masked person only, without any dead raven. We tested each bird in both group and individual settings, and compared scolding responses during group trials, where motivational levels might be heavily impacted by social dynamics, to the responses in the separation trials, where any direct social interactions are absent. We based our hypotheses on the considerations mentioned above, specifying effects due to individual learning (or not) and social influences (or their absence). Specifically, our two main hypotheses are:

- **Hypothesis 1** Low scolding durations by some individuals while in the group are based on a failure to learn, resulting in some individuals simply not perceiving the artificial predator as a threat.
- **Hypothesis 2** Individuals with low scolding durations in the group learned to recognize the artificial predator as a threat, but their scolding expression is decreased due to social dynamics, specifically:
 - 2a) non-scolding individuals free-load on already scolding individuals (e.g. to conserve energy or minimize risk).
 - 2b) scolding individuals showcase their quality by participating in risky behaviour, which low-quality individuals cannot afford (to the same extent).
 - 2c) scolding individuals showcase their quality by actively preventing others from scolding.

If hypothesis 1 is correct, we predict no differences in individual scolding intensity between group and separation trials. If hypothesis 2 is correct, we predict individuals with low scolding intensity in the group should increase their scolding intensity when tested in separation. Within hypothesis 2, all three sub-hypotheses would predict an effect of dominance. Notably, dominant individuals should invest more in scolding (status show-off hypotheses 2b, 2c), whereas subordinate individuals might free-load on the dominant's anti-predator behaviour (hypothesis 2a). If dominant individuals even suppress the participation of subordinates (hypothesis 2c), we would expect to see aggression towards subordinates when they engage in scolding and/or a fine-tuning of subordinates in when to call.

Methods

Subjects and housing

Study subjects were 15 captive, non-breeding ravens, housed as two groups (Group A: 5 females and 3 males, all hatched in 2010; Group B: 3 females and 4 males, one female hatched in 2010, all others in 2011). The subjects were housed in large, neighbouring outdoor aviaries with walls of wire mesh, netted ceilings and a substrate of wood chips and sand. Branches and plants were provided for perching and enrichment. Smaller, visually isolated compartments made of wood were attached to the aviaries to provide shelter and opportunities for retreat. Food was provided twice a day and consisted of meat, fruits, grain products and vegetables; water was provided *ad libitum*. All ravens were marked with coloured leg-bands for visual identification. The separation aviary was next to (allowing audiovocal contact, but visually blocked from) the two main aviaries, and constructed in the same way (Fig. 2).

Experimental Procedure

A human presenter wearing standardised clothing, consisting of an olive-grey rain poncho, rubber boots, white gloves and a plastic face-mask, walked to both main aviaries and remained still for two minutes at two fixed presentation locations per group, then left the area the same way they came. Different humans were chosen for every group presentation, but separation presentations were carried out by the same human (the animal trainer, who also presented in some group trials).

During four initial “training” trials in October 2011, the presenter wore a specific “dangerous” mask, and carried a dead raven in their hand, eliciting a scolding response and forming a strong negative association between the potential predation outcome (the dead raven) and the human wearing this particular mask (vs. a “control” mask). All subsequent group and separation trials were carried out empty-handed. Group trials were conducted approximately every 20 days until May 2012, then every 35 days until June 2013. Within group trials, which have previously been analysed and described, the “dangerous” mask condition elicited significantly longer scolding durations than the control mask condition (25).

Separation trials, where a single individual was moved from the group to the nearby separation aviary, were carried out every 20 days from December 2011 to May 2012 for group A, and from December 2012 to April 2013 for group B. The separated individual and the remaining group could not see, but still hear each other due to the aviary layout. During the separation trials we again presented the “dangerous” mask, but used an unmasked condition as control, to counteract any potential generalisation towards the control mask across 1.5 years. The data used for analysis consisted of the single separation trial and the 6 group trials closest to it, spanning on average 138 days per subject (SD = 36 days).

For all trials we video-recorded the birds’ behaviour the entire time the masked presenter was in view of the ravens (Canon Legria HF S10, Canon Legria HF S30) and regularly called out the locations and ID of all group members during filming, to allow individual recognition of all subjects throughout the video. Afterwards CRB coded the durations and latencies of the alarm calling behaviour using the software

“Solomon Coder” (31) with a precision of 0.2 seconds. While the ID of the subjects was identifiable throughout the videos, the mask type was tracked separately and not mentioned or visible on the videos.

Statistics

The analysis was carried out in R version 3.6.1 (*R Core Team (2020)*) using a generalized linear mixed model (function “glmmTMB” from the same-named package) (33) using a beta-distribution and logit link. As response we included transformed scolding duration as proportion of total duration of predator presentation (which varied slightly across group trials due to different walking speeds of different presenters). As test predictor we included presentation type (group vs. separation) and dominance (whether an individual was the dominant male or female of the group) as a factor with four levels titled “condition”; as control predictors we included factors for each subject’s rearing history (hand-raised vs. parent-raised) and sex (male vs. female), as well as a covariate for days since training. A random effect was included for subject ID. We included weights for the number of trials, as they differed per presentation type (one for separation, six for group). The four-level factor was dummy coded, the covariate centred. Sample size consisted of 15 individuals with 6 group trials and 1 separation trial per individual.

We compared this full-model to a reduced-model, lacking the test predictor for condition, but otherwise identical to the full model, using a chi squared test. We also tested for collinearity of predictors using variance inflation factors (VIF; using the function “vif” of the package “car”; version 3.0.8) (34). Overdispersion was calculated using a custom function kindly provided by Roger Mundry. To compare different levels of our test predictor “condition” we conducted post-hoc testing by re-running the model with a different reference level.

We also analysed the individual scolding order of the group trials following a similar approach: our full model was again formulated in the glmmTMB package, this time using a poisson distribution with identity link. The response was order to scold after the mask was in view of the ravens, split between the two groups. As test predictor we included dominance, as control predictors rearing history, sex, and days since training. We again included a random effect for subject ID. We then compared this full model to a reduced model lacking the test predictor for dominance, but being otherwise identical.

Results

The model comparison on the scolding duration was significant ($\chi^2 = 29.56$, $df = 3$, $p < 0.001$), indicating that the full model including the test predictor “condition” explains the data significantly better than the reduced model lacking it. Collinearity (maximal VIF = 1.47), and overdispersion (dispersion parameter = 0.92) were within acceptable limits.

Subordinate individuals increased their scolding when separated (Table 1, Fig. 3), but dominant individuals did not (post-hoc: $E = 0.22$ (95% CI[-0.62; 1.07]); $p = 0.61$). Furthermore, dominant individuals scold longer than subordinates in the group (Table 1) and in separation (post-hoc: $E = 1.37$ (95% CI[0.24;

2.51]); $p = 0.02$). Looking at the control predictors we found that scolding durations were not significantly affected by rearing type or sex, but significantly decreased over time (Table 1).

Table 1
Output from full model on scolding duration

Fixed Effects	Estimate (CI 95%)	SE	z value	p value	
(Intercept)	-2.39 (-2.95; -1.83)	0.29	-8.31	< 0.001	***
Condition group-dominant	2.04 (1.5; 2.58)	0.27	7.46	< 0.001	***
Condition separation-dominant	2.26 (1.28; 3.25)	0.50	4.52	< 0.001	***
Condition separation-subordinate	0.89 (0.29; 1.49)	0.31	2.93	< 0.01	**
Raising Parent	-0.23 (-0.87; 0.42)	0.33	-0.70	0.49	
Sex male	-0.01 (-0.48; 0.47)	0.24	-0.03	0.98	
Days since Training	-0.47 (-0.74; -0.2)	0.14	-3.36	< 0.001	***
General linear mixed model (GLMM) output showing fixed effects with response as proportion of scolding. Reference categories are "group-subordinate" for "Condition", "Hand" for "Raising" and "female" for "Sex". "Days since Training" was centred. N(individuals) = 15, N(trials) = 105. Significance codes: .<0.1; * < 0.05; ** < 0.01; *** < 0.001.					

Model comparison on the birds' scolding order was also significant ($\chi^2 = 10.37$, $df = 1$, $p < 0.001$). Collinearity was acceptable (maximal VIF = 1.21), but the dispersion parameter of 0.42 indicates underdispersion, leading to a potentially conservative test.

Across all group trials, dominant individuals produced alarm calls earlier than subordinates (Table 2, Fig. 4). We found no significant effects of sex, raising or days since training.

Table 2
Output from full model on scolding order

Fixed Effects	Estimate (CI 95%)	SE	z value	p value	
(Intercept)	2.81 (1.57; 4.05)	0.63	4.44	< 0.001	***
Dominance yes	-1.19 (-1.8; -0.58)	0.31	-3.84	< 0.001	***
Sex male	0.03 (-0.55; 0.60)	0.29	0.09	0.93	
Raising Parent	-0.12 (-1.22; 0.98)	0.56	-0.22	0.83	
Days since Training	0.01 (0.01; 0.01)	0.01	-0.46	0.64	
General linear mixed model (GLMM) output showing fixed effects with response of scolding order. Reference categories are "no" for Dominance, "female" for "Sex" and "Hand" for "Raising". "Days since Training" was centred. N(individuals) = 15, N(trials) = 98. Significance codes: .<0.1; * < 0.05; ** < 0.01; *** < 0.001.					

No analysis was carried out on the unmasked control trials, as they did not elicit a single alarm call.

Discussion

To our knowledge, this is the first study in which multiple individuals learned to recognize a novel predator in a group setting and which then evaluated anti-predator reactions in both group and separation settings. Subordinate individuals increased their scolding response when tested in separation, but dominant individuals did not. The fact that most subordinates both called, and increased their calling, in the separation trials indicates that they had indeed learned to recognize the artificial predator. These findings thus speak against hypothesis 1 (failure to learn about the predator), but are consistent with the main prediction of hypothesis 2 that social dynamics affect scolding behaviour. Furthermore, the control trials (with unmasked presenter) did not elicit a single alarm call throughout all separation trials, indicating that the birds responded to the presence of the “dangerous” mask and not the unfamiliar solitary setting or the absence of conspecifics. We can therefore also exclude any effects of idiosyncrasies of the presenter, such as stature, gait or walking speed.

Taking a closer look at the social dynamics hypothesis, our results are in principle compatible with all three sub-hypotheses: that subordinates free-load on already scolding dominants (hypothesis 2a), and that dominants use the anti-predator context for showing off (hypothesis 2b), and thereby may actively suppress subordinates from scolding (hypothesis 2c). Disentangling these hypotheses is difficult and not entirely possible in the framework of this study. However, we can find little support for the former and tentative support for the two latter hypotheses. Note that our experimental set-up allowed the individually separated ravens to remain in auditory contact with their group members. During individual tests with the masked human experimenter, group members could thus join the separated birds in scolding, which they regularly did. This observation speaks against the free-loading argument, as in the separation trials scolding conspecifics were also close by. However, the distance to the nearest scolding conspecific was larger in separation trials than in group trials and the visibility to the conspecifics was obstructed, possibly favouring free-loading in one condition more than in the other.

Turning to the show-off interpretation, we found that dominant individuals were also the first to scold in a group setting, while subordinate birds scolded later, if at all. This pattern is in line with the assumption of dominants using scolding to showcase their individual quality, not only by scolding longer but also by scolding earlier than individuals of lower rank. What does not entirely fit this interpretation is that some subordinate individuals, like the female Skadi in Group B, do repeatedly engage in scolding (Fig. 4). Finally, we occasionally observed dominant individuals attacking subordinates when those engaged in intense scolding, hinting towards active suppression of subordinate’s anti-predator behaviour. Although it seems difficult to explain why dominants should do so, our experiment might have favoured costly status-signalling, as it provided a context where predators posed a low risk and potential mates were present in the groups. Generally, our show-off interpretations are in line with previous publications on corvids suggesting alarm calling to be linked to dominance (7, 28) and social rank and recent mating

success ((35, 36); but see (37)). Considering that all our subjects were non-breeders, we can exclude prior mating success contributing to scolding, supporting the importance of rank.

Given that our attempts to differentiate between the free-loading and the two types of status-signalling hypotheses are based on fragile evidence, follow-up studies are required to clearly disentangle those hypotheses. For instance, future studies could investigate individuals' scolding responses in the group when the dominant male and female are removed, or use sound-isolated separation aviaries. Being kept in captivity and with regular contact to humans, a human-shaped predator might also pose a rather low threat level and elicit a weaker alarm response by the group (38–40). Repeating these experiments with a different predator stimulus of higher perceived threat level, and comparing the results might shed additional light on the social aspects of scolding behaviour.

Taken together, our results indicate that subordinate individuals increase their scolding response towards a learned threat (an experimentally induced “predator”) when they are separated from their group, but dominant individuals scold equally in both contexts. We conclude that low scolding in the group setting by subordinates is unlikely to be caused by lack of learning, but primarily constrained by social dynamics. This interpretation adds a new possibility to the main functions of scolding, i) for predator deterrence, e.g. to harass and deter the predator by alerting it of its detection (1, 2), ii) for social learning opportunities, e.g. transmit information about predators to inexperienced conspecifics (24, 30), and iii) for recruiting social support (41–43). Regarding all of these well-studied aspects of predator defence, we would not expect any changes in scolding behaviour between group and separation trials for subordinates only, as observed here, because the exposure to and risk from the artificial predator were the same for all ravens. We therefore suggest that social dynamics within the group influence scolding by subordinates, possibly because dominant individuals employ their intense scolding displays as a signal of high social status, and suppress calling by subordinates. Alternatively, low-status individuals cannot afford intense scolding due to energetic constraints and freeloading on those that do. Either way, the current data suggest that, in addition to its direct deterrence effects on the predator, or its recruitment effects on conspecifics, alarm calling in social contexts might play an important signalling role indicating individual quality.

Conclusions

In this study, we compared the scolding durations of 15 common ravens (*Corvus corax*) towards a learned threat, both in group and isolation settings. We found that scolding varied strongly between individuals in the group setting, with dominant individuals scolding significantly longer than subordinates. However, when separated the scolding duration of subordinates increased significantly while those of dominants stayed the same. We argue that the low scolding participation in some individuals in the group setting was not caused by a lack of learning about the potential threat, but by social dynamics which were absent in the separation trials. This raises the possibility of scolding behaviour serving as marker for individual status in addition to its established functions of recruitment, predator deterrence and facilitator for social learning.

Declarations

Ethics approval

Data collection was non-invasive and carried out under the license number 18-01, approved by the animal ethics and experimentation board of the University of Vienna.

Consent for publication

Not applicable.

Availability of data and materials

All data generated or analysed during this study and the R script are included in this published article [and its supplementary information files].

Competing interests

The authors declare that they have no competing interests.

Funding

This project was funded by the Austrian Science Fund (FWF) grants W1262-B29, W1234-B17 and Y366-B17 which included funds for open access publication fees. CRB was funded via the uni:docs stipend of the University of Vienna and a final fellowship of the Vienna Doctoral School in Cognition, Behavior and Neuroscience.

Authors' contributions

TB and CRB designed the study. CRB collected and analysed the data and drafted the manuscript under the supervision of the other authors. TB and WTF provided critical revisions to the manuscript. All authors approved the final version of the manuscript for submission.

Acknowledgements:

We thank the entire team of the Haidlhof Research Station for their help with presenting and filming, especially Sarah Deventer, Barbara Haidn, Martina Schiestl and Stephan Reber. We also thank Palmyre Boucherie for statistical support.

References

1. Caro T. Antipredator Defenses in Birds and Mammals. Chicago: University of Chicago Press; 2005.
2. Curio E. The Adaptive Significance of Avian Mobbing. *Z Tierpsychol* [Internet]. 1978 [cited 2013 Jan 15];48(2):175–183. Available from: <http://onlinelibrary.wiley.com/doi/10.1111/j.1439->

0310.1978.tb00254.x/abstract.

3. Lima SL, Dill LM. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool.* 1990 Apr;68(4):619–40.
4. Griffin A. Social learning about predators: A review and prospectus. *Learn Behav* [Internet]. 2004 [cited 2018 Feb 18];32(1):131–40. Available from: <https://link.springer.com/content/pdf/10.3758/BF03196014.pdf>.
5. Mazza V, Jacob J, Dammhahn M, Zaccaroni M, Eccard JA. Individual variation in cognitive style reflects foraging and anti-predator strategies in a small mammal. *Sci Rep* [Internet]. 2019;9(1):1–9. Available from: <http://dx.doi.org/10.1038/s41598-019-46582-1>.
6. Mumma MA, Gillingham MP, Johnson CJ, Parker KL. Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecol Evol.* 2017;7(23):10266–77.
7. Griesser M, Ekman J. Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Anim Behav.* 2004 May 1;67(5):933–9.
8. Ferrari MCO, Trowell JJ, Brown GE, Chivers DP. The role of learning in the development of threat-sensitive predator avoidance by fathead minnows. *Anim Behav.* 2005;70(4):777–84.
9. Keen SC, Cole EF, Sheehan MJ, Sheldon BC. Social learning of acoustic anti-predator cues occurs between wild bird species. *Proc R Soc B Biol Sci.* 2020;287(1920).
10. Marcellini DL, Jenssen TA. Society for the Study of Amphibians and Reptiles Avoidance Learning by the Curly-Tailed Lizard, *Leiocephalus schreibersi*: Implications for. *J Herpetol.* 1991;25(2):238–41.
11. Turner AM, Turner SE, Lappi HM. Learning, memory and predator avoidance by freshwater snails: effects of experience on predator recognition and defensive strategy. *Anim Behav.* 2006;72(6):1443–50.
12. West R, Letnic M, Blumstein DT, Moseby KE. Predator exposure improves anti-predator responses in a threatened mammal. *J Appl Ecol.* 2018;55(1):147–56.
13. Marzluff JM, Walls J, Cornell HN, Withey JC, Craig DP. Lasting recognition of threatening people by wild American crows. *Anim Behav* [Internet]. 2010 [cited 2018 Feb 25];79:699–707. Available from: <http://roslyndakin.com/wp-content/uploads/private/2010Marzluffetal.pdf>.
14. Bell MBV, Radford AN, Smith RA, Thompson AM, Ridley AR. Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proc R Soc B Biol Sci* [Internet]. 2010 Nov 7 [cited 2022 Apr 5];277(1698):3223–8. Available from: <https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2010.0643>.
15. Kern JM, Sumner S, Radford AN. Sentinel dominance status influences forager use of social information. *Behav Ecol* [Internet]. 2016 Jan 1 [cited 2022 Apr 5];27(4):1053–60. Available from: <https://academic.oup.com/beheco/article/27/4/1053/1741859>.
16. Curio E, Ernst U, Vieth W. Cultural transmission of enemy recognition: One function of mobbing. *Sci* (80-). 1978;202(4370):899–901.

17. Ellis JMS. Anti-Predator signals as advertisements: Evidence in White-Throated magpie-Jays. *Ethology*. 2009;115(6):522–32.
18. Slagsvold T. The mobbing behaviour of the hooded crow *Corvus corone cornix*: Anti-predator defense or self-advertisement? *Fauna Nor Ser C Cinclus* [Internet]. 1984 [cited 2013 Oct 5];7(2):127–31. Available from: http://apps.webofknowledge.com/full_record.do?product=UA&search_mode=GeneralSearch&qid=17&SID=P2cJXzTCpnwZcKvl8pJ&page=1&doc=1.
19. Tanager B. Self-advertisement: Relations to Dominance in Black-billed Magpies Members. *Anim Behav*. 2011;1079–88.
20. Szípl G, Boeckle M, Wascher C, Spreafico M, Bugnyar T. With whom to dine? Ravens' responses to food-associated calls depend on individual characteristics of the caller. *Anim Behav* [Internet]. 2015 [cited 2015 May 26]; Available from: <http://www.sciencedirect.com/science/article/pii/S0003347214004011>.
21. Boeckle M, Szípl G, Bugnyar T. Who wants food? Individual characteristics in raven yells. *Anim Behav* [Internet]. 2012 Sep [cited 2012 Sep 19];84(5):1123–30. Available from: <http://linkinghub.elsevier.com/retrieve/pii/S0003347212003600>.
22. Boeckle M, Szípl G, Bugnyar T. Raven food calls indicate sender's age and sex. *Front Zool* [Internet]. 2018 Mar 13 [cited 2022 Apr 5];15(1):1–9. Available from: <https://frontiersinzoology.biomedcentral.com/articles/10.1186/s12983-018-0255-z>.
23. Gallego-Abenza M, Blum CR, Bugnyar T. Who is crying wolf? Seasonal effect on antipredator response to age-specific alarm calls in common ravens, *Corvus corax*. *Learn Behav*. 2021;49(1):159–67.
24. Cornell HN, Marzluff JM, Pecoraro S. Social learning spreads knowledge about dangerous humans among American crows. *Proc R Soc B Biol Sci* [Internet]. 2012 Feb 7 [cited 2020 Apr 28];279(1728):499–508. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2011.0957>.
25. Blum CR, Fitch WT, Bugnyar T. Rapid Learning and Long-Term Memory for Dangerous Humans in Ravens (*Corvus corax*). *Front Psychol* [Internet]. 2020 Oct 21 [cited 2020 Oct 22];11:2843. Available from: <https://www.frontiersin.org/articles/10.3389/fpsyg.2020.581794/full>.
26. Coomes JR, McIvor GE, Thornton A. Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (*Corvus monedula*) (*Biology Letters* (2019) 15 (20190380) DOI: 10.1098/rsbl.2019.0380). *Biol Lett*. 2019;15(11).
27. Ale SB, Brown JS. The contingencies of group size and vigilance. 2007.
28. Wilson DR, Bayly KL, Nelson XJ, Gillings M, Evans CS. Alarm calling best predicts mating and reproductive success in ornamented male fowl, *Gallus gallus*. *Anim Behav*. 2008;76(3):543–54.
29. Heinrich B, Marzluff JM. Do common ravens yell because they want to attract others? *Behav Ecol Sociobiol* [Internet]. 1991 Jan;28(1):13–21. Available from: <http://link.springer.com/10.1007/BF00172134>.

30. Swift KN, Marzluff JM. Wild American crows gather around their dead to learn about danger. *Anim Behav* [Internet]. 2015 Nov 1 [cited 2018 Nov 21];109:187–97. Available from: <https://www.sciencedirect.com/science/article/pii/S0003347215003188>.
31. Péter A. Solomon Coder (Version: beta 15.03.15): a simple solution for behavior coding. [Internet]. 2011 [cited 2015 May 26]. Available from: <http://solomoncoder.com/>.
32. R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
33. Brooks M, Kristensen K, van Benthem K, Magnusson A, Berg C, Nielsen A, et al. (glmmTMB) Balances Speed and Flexibility Among Packages for Generalized Linear Mixed Modeling. [Internet]. *The R Journal*; 2017. p. 378–400. Available from: <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>.
34. Weisberg S, Fox J. *An R Companion to Applied Regression* [Internet]. Thousand Oaks: Sage; 2011 [cited 2020 Aug 28]. Available from: <https://experts.umn.edu/en/publications/an-r-companion-to-applied-regression>.
35. Kokolakis A, Smith CL, Evans CS. Aerial alarm calling by male fowl (*Gallus gallus*) reveals subtle new mechanisms of risk management. *Anim Behav*. 2010 Jun;79(6)(1):1373–80.
36. Wilson DR, Evans CS. Female fowl (*Gallus gallus*) do not prefer alarm-calling males. *Behaviour* [Internet]. 2010 Jan 1 [cited 2021 Dec 13];147(4):525–52. Available from: https://brill-com.uaccess.univie.ac.at/view/journals/beh/147/4/article-p525_6.xml.
37. Wilson DR, McDonald PG, Evans CS. Mechanisms of Mate Investment in the Polygamous Fowl, *Gallus gallus*. *Ethology* [Internet]. 2010 Aug 1 [cited 2021 Dec 13];116(8):755–62. Available from: <https://onlinelibrary-wiley-com.uaccess.univie.ac.at/doi/full/10.1111/j.1439-0310.2010.01800.x>.
38. Soard CM, Ritchison G. ‘Chick-a-dee’ calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Anim Behav*. 2009 Dec;78(6)(1):1447–53.
39. Courter JR, Ritchison G. Alarm calls of tufted titmice convey information about predator size and threat. *Behav Ecol*. 2010;21(5):936–42.
40. Templeton CN, Greene E, Davis K. Behavior: Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science (80-)* [Internet]. 2005 Jun 24 [cited 2015 Nov 22];308(5730):1934–7. Available from: <http://www.sciencemag.org/content/308/5730/1934.full>.
41. Dutour M, Léna JP, Lengagne T. Mobbing calls: a signal transcending species boundaries. *Anim Behav*. 2017 Sep;1:131:3–11.
42. Randler C, Vollmer C. Asymmetries in commitment in an avian communication network. *Naturwissenschaften* [Internet]. 2013 Feb 17 [cited 2021 Dec 14];100(2):199–203. Available from: <https://link-springer-com.uaccess.univie.ac.at/article/10.1007/s00114-013-1009-6>.
43. Suzuki TN. Referential calls coordinate multi-species mobbing in a forest bird community. *J Ethol* [Internet]. 2016 Jan 1 [cited 2021 Dec 14];34(1):79–84. Available from: <https://link.springer.com/article/10.1007/s10164-015-0449-1>.

Figures

Figure 1

Masks worn during the presentations. The predator mask is on the left, the control mask on the right.

Figure 2

Layout of the aviaries. Group aviaries are depicted on the left, the separation aviary on the right. Presentations were conducted either for both complete groups, or for a single separated raven. The presenter walked along the horizontal line, following the direction indicated by the arrows, and stopped at two locations per aviary (indicated by numbered circles), where they faced the ravens while remaining still for two minutes. The vertical bar represents a visual, but not acoustic barrier between the group and separation aviaries.

Figure 3

Boxplots of Scolding duration (as proportion of total presentation duration) for dominant and subordinate individuals in group and separation trials. Black diamonds show group means, coloured dots depict individual datapoints. Connecting lines are drawn for each individual between the mean scolding duration of six group trials (not depicted) to the single separation trial.

Figure 4

Order of scolding per group, based on the individual latencies to respond. Dot size indicates number of trials that elicited an alarm calling response. Subjects are sorted by group, with the top ranked male and female listed first and represented by triangles.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS1.xlsx](#)
- [TableS2.xlsx](#)
- [TableS3.xlsx](#)
- [Rscript.r](#)