



Fussing over food: factors affecting the vocalizations American crows utter around food



LomaJohn T. Pendergraft*, John M. Marzluff

School of Environmental and Forest Sciences, University of Washington, Seattle, WA, U.S.A.

ARTICLE INFO

Article history:

Received 6 August 2018

Initial acceptance 1 October 2018

Final acceptance 17 December 2018

MS. number: A18-00548R

Keywords:

aggression
American crow
Corvus brachyrhynchos
food-associated call
food discovery
playback response
recruitment
vocalization

American crows, *Corvus brachyrhynchos*, often loudly vocalize when gathered around a food source. Because doing so would attract unwanted attention from predators and competitors, animals that have congregated around food are only expected to vocalize if the benefits (e.g. recruiting or announcing themselves to allies, deterring competitors, warning of danger, begging for a meal, appeasing a dominant) outweigh these costs. Here we demonstrate that wild crows change the quality of their calls depending on the amount of food present. The crows near a large food windfall gave shorter calls compared to their vocalizations in food's absence, and playback of these short calls only prompted a mild aggressive response from listening crows. In contrast, the calls given before the appearance of food were longer, and their playback elicited behaviours from the listening crows associated with aggression and territory defence. These findings suggest that crows avoid giving territorial calls near an exploitable food resource and vocalize for other reasons. Taken together, this study provides insights on how the caller's current context can shift the costs and benefits of vocalizing.

© 2019 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals that loudly broadcast their messages benefit from clear communication over a wide area but suffer potential costs. Around rich food resources, for example, wide-area communication may enable social animals to recruit unaware allies to the food or announce themselves to allies already present (Heinrich & Marzluff, 1991; Judd & Sherman, 1996). Additionally, during the fray of feeding, vigilant animals can spread alarm of nearby danger (Zuberbühler, 2009) and dominant individuals can claim ownership or deter competitors without resorting to risky physical aggression (Siracusa et al., 2017), while young or subordinate individuals might beg for food or advertise their submission (Heinrich, Marzluff, & Marzluff, 1993; Roush & Snowdon, 2001). Conversely, increased conspicuousness and potential signal interception by unintended receivers, aka eavesdropping, can be costly to a communicator (Peake, 2005). For this reason, the relative cost of loud vocalizations increases when the caller is near an exploitable resource, such as food (Searcy & Nowicki, 2005). Therefore, species that vocalize around such resources are expected to gain benefits that outweigh the cost of increased competitive or

predatory attention towards the resource. Food recruitment is particularly costly, as it explicitly informs the listener that food is present; therefore the benefits to the caller must be correspondingly high, such as increased foraging efficiency (Brown, Brown, & Shaffer, 1991; D'Vincent, Nilson, & Hanna, 1985), reduced predation risk (Elgar, 1986), increased social status (Clay, Smith, & Blumstein, 2012; Eberhard, 1975; Stevens & Gilby, 2004), access to a defended food source or increased protection of the food source against others (East & Hofer, 1991; Heinrich & Marzluff, 1991).

American crows, *Corvus brachyrhynchos*, are human-commensal, territorial corvids that occasionally vocalize in the presence of food (Mates, Tarter, Ha, Clark, & McGowan, 2015; Tarter, 2008). While crows will share food between mates and related helpers on their territory (Kilham, 1990), it is unclear whether they actively recruit family members to a food source, or simply tolerate one another's presence after they independently arrive at the same food patch. This ambiguity is due to the difficulty of classifying typical crow vocalizations (known as 'caws'), which vary significantly in duration and cadence alongside rapid oscillations in pitch (frequency) and amplitude (Laiolo & Rolando, 2003). Despite this uncertainty, American crows use caws with varying acoustic properties to signal the presence of a dangerous or novel predator (Marzluff, Walls, Cornell, Withey, & Craig, 2010; Richards &

* Correspondence: L. T. Pendergraft, School of Environmental and Forest Sciences, Box 352100, University of Washington, Seattle, WA 98195, U.S.A.

E-mail address: pendel@uw.edu (L. T. Pendergraft).

Thompson, 1978), the presence of a dead conspecific (Swift & Marzluff, 2015), their ownership and the boundaries of a territory (Parr, 1997) and to beg for food (Chamberlain & Cornwell, 1971).

What benefits could American crows gain from food vocalization? Crows recruit conspecifics to participate in antipredator harassment behaviour known as mobbing (Richards & Thompson, 1978), so they may be calling at food in response to a perceived threat. The caller would incur a cost from increased attention to both itself (via predator) and the food (via competitors), and all mobbing crows would incur costs in time, energy and risk (predators sometimes capture and kill crows during a mob). Despite these costs, we expect all listening crows, regardless of their relationship to the caller, to aid in mobbing a predator because all crows would benefit from reduced predation risk after driving the predator out of the area. Another benefit might be increased foraging efficiency: dominant territory owners that discover food within their territory would maximize the amount they and their mate are able to obtain if they keep rival territory owners and vagrants from discovering it, or alternatively keep them at bay by threatening physical confrontation, both of which might be accomplished by uttering territorial calls. Territorial calls would also attract the caller's family members to the area without alerting eavesdroppers to the presence of food (although crows in our study area rarely have helpers, so the caller would most likely only attract their mate), thus benefiting the caller via improved pair bond and kin selection. Conversely, knowledgeable rival and vagrant crows might gain access to a protected food source if they recruit others to overwhelm the dominant birds' defence, as in common ravens, *Corvus corax* (Bugnyar, Kijne, & Kotrschal, 2001; Heinrich & Marzluff, 1991). This tactic is likely to attract many listening crows, regardless of their social ties to the caller, as all recruited crows would benefit from gaining access to the food source.

In this study, we conducted three experiments on wild American crows to determine why they vocalize around food. In experiment 1, we asked (1) what types of calls do crows give in response to finding food and (2) does the size of the food bonanza, which shifts the costs and benefits of calling, affect the vocalizations given by the feeding crows? If crows recruit conspecifics to a food source, we hypothesized that they would do so when the cost of increased competition is relatively low, as would occur when they encounter a food source too large/conspicuous for a single crow to monopolize, or when the food is inaccessible to the caller. After sorting the recorded calls into categories, we determined what they meant to the crows in experiment 2 by measuring the response of wild crows to playback of selected calls from experiment 1. We compared our observations with a set of predictions built around three possible benefits to the caller: (1) ally recruitment; (2) territorial defence; and (3) danger warning. We hypothesized that if crows utilize a specific vocalization to recruit allies, then listening crows would respond to playback of that call by moving to the area and searching for food while displaying very little aggression or agitation. If the stimulus call is normally used for territorial defence or to signify dominance, then we hypothesized that the listening territory holders would interpret the playback as a challenge and respond with aggressive displays, type-matching vocalizations (Burt, Campbell, & Beecher, 2001; Searcy & Beecher, 2009; Vehrencamp, 2001) and attempts to locate the speaker. If the stimulus call is associated with danger, we predicted that the listening crows would gather in large numbers, vocalize frequently, move often and display signs of agitation without aggression. Finally, to better test whether crows are actively recruiting allies to a food source, for experiment 3 we measured the effect that different stimulus calls had on the probability of food discovery. We hypothesized that crows would be more likely to discover the food, find it more quickly and gather in greater numbers at the food if the stimulus call is associated with ally recruitment.

METHODS

Experiment 1: Behavioural Response to Food

Field procedure

We tested how unmarked wild crows responded to differing amounts of food from late April to early July 2015 at 41 locations in Washington, U.S.A. (in and around the cities of Seattle and Shoreline; 47°62'93"–47°74'54"N, 122°24'76"–122°38'21"W), with additional data collected at eight locations during January 2016 and six locations from April to May 2016 (Fig. 1). We chose a location to be a field site if we witnessed regular crow activity at that location. The sites consisted of public parks, residential neighbourhoods and parking lots. Every site was at least 150 m from any nearby sites, sufficient to limit travel between sites by crows in response to highly attractive scold calls (Swift, 2015). A single observer (L.T.P.) arrived at a site between 0530 and 1200 hours wearing one of six face-concealing disguises to prevent facial recognition by the crows along with a clipboard-mounted sign which read 'UW CROW STUDY' to limit interference by pedestrians. We minimized unwanted attention from the focal crows by remaining >10 m from nearby birds and avoiding direct gaze (Clucas, Marzluff, Mackovjak, & Palmquist, 2013). Because young crows depend on their parents for food and rarely participate in territorial aggression or mobbing behaviour (Marzluff & Angell, 2005), we omitted juvenile birds from data collection and identified them in the field using plumage and 'begging' vocalizations. If we could not locate any crows upon arrival, or if we had to abort a trial, we moved on to another site and returned later in the day.

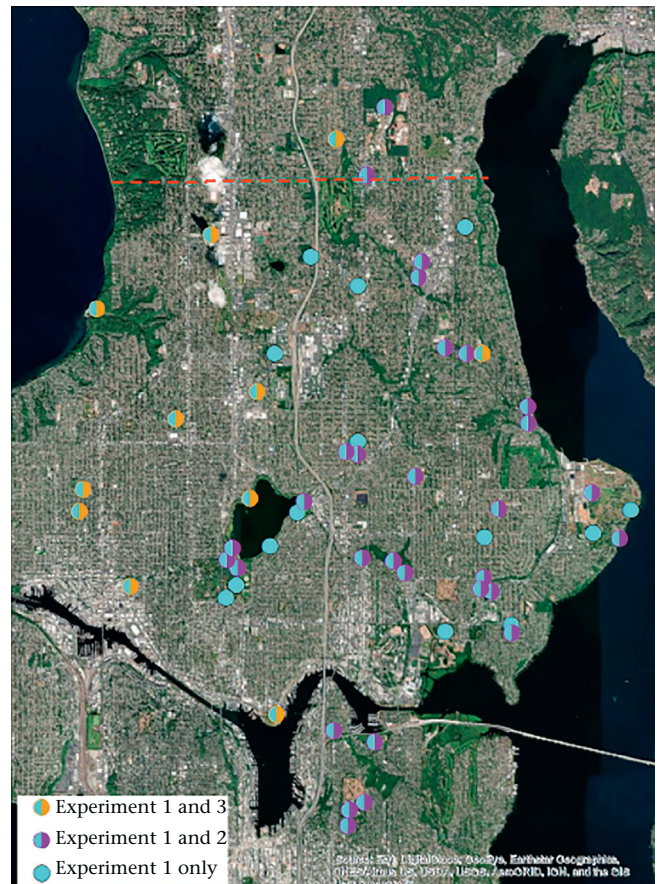


Figure 1. Map of study areas for all three experiments in Seattle (south of dashed red line) and Shoreline (north of dashed red line).

During experiment 1, crows received either 1, 5 or 25 unshelled peanuts as a stimulus. Every site received all three food treatments, with treatment order balanced across all sites and >2 days separating each treatment. Each trial consisted of three phases: prestimulus, stimulus and poststimulus (see Fig. A1 in Appendix 1 for illustration of experiment 1 phases). Prior to feeding (prestimulus phase) we observed the crows for 180 s. If the crows left the site during this time, we aborted the trial and started over after relocating them. Once we had tossed the predetermined peanut amount on the ground in full view of the crows (stimulus phase), we observed until the crows had consumed all the peanuts. If all the crows left the site during this time, we waited for them to return. If no crow had returned after 300 s, or if the crows had consumed all the peanuts at the site, we removed any remaining peanuts and observed the site for an additional 300 s (poststimulus phase), regardless of whether the crows were present. Along with recording the vocalizations given by the crows at the site, we recorded the number of crows present throughout the trial. The duration of the stimulus phase ranged from 10 s to 1350 s; to avoid biasing our data in favour of the longer trial durations, we converted total vocalizations to vocalizations/min, and total crow visits to average and maximum numbers of crows present during each phase.

During experiment 1, we also examined whether human presence altered the vocalizations given around food; at 18 of the 55 sites we surreptitiously placed the food on the ground and retreated >20 m away rather than conspicuously tossing the peanuts in full view of the crows. Because we found no significant differences between having a human provide the food and the crows finding it themselves (see Appendix 2), we pooled these treatments during analysis.

Acoustic recording and analysis

We recorded all audio in MP3 format using a Marantz PMD-671 solid-state recorder and a Sennheiser MKH 20-P48 microphone contained within a Telinga Universal Parabolic Dish MK2 housing. We mounted a GoPro Hero 3 to the microphone, which recorded an MP4 video of the microphone's current target, which we used for verification purposes. We recorded crow presence and activity on a clipboard. If there was too much activity to accurately capture on paper, we narrated what was happening in a soft voice, and transcribed the comments onto paper later in the day.

Experiment 2: Behavioural Response to Call Playback

Selecting stimulus calls

Using the vocalizations recorded during experiment 1, we first converted the MP3 audio files to WAV format with AudioDirector 5 (CyberLink Corp, 2014), then used Raven 1.5 (Bioacoustics Research Program, 2014) to create spectrograms of the recordings (DFT size: 4096 samples; window type: Hann; 50% overlap; 124 Hz bandwidth; 512 samples per frame; grid spacing: 10.8 Hz). Within Raven 1.5, we measured the vocalization microstructure by creating a selection around every individual call on the spectrogram; each selection was bounded by the start and stop times of a call, with a set lower and upper boundary of 1000–6000 Hz (see Fig. A7 in Appendix 3). We removed every selection with excessive background noise or any overlap with an adjacent selection (e.g. multiple crows calling simultaneously). From the remaining selections, we obtained various measures of each call's microstructure (see Table A1 in Appendix 3 for full list), including the duration (ms) and the frequency of maximum energy (hereafter 'peak frequency'; Hz) of each individual call, along with the number of calls given in the series (defined as the number of sequential calls uttered by a single crow, with <1 s separating each call).

After first attempting to use linear discriminant analysis to detect distinct groupings of call characteristics (see Appendix 3), we selected vocalizations based on individual call duration and series structure (structured calls are uttered in ordered groupings called series, whereas unstructured calls lack organization); previous studies have used these qualities to sort calls (Parr, 1997; Tarter, 2008). For our primary stimulus calls, we used (1) structured calls with a duration of 75–200 ms ($\bar{X} \pm SE = 190.7 \pm 3.0$ ms), which we named 'short calls', and (2) structured calls with a duration of 300–425 ms (359.2 ± 9.2 ms), which we called 'medium calls'. While the peak frequency for both are similar (short calls: 1536 ± 29 Hz; medium calls: 1528 ± 10 Hz), short calls had more vocalizations per call series than did medium calls (short calls: 4.62 ± 0.11 calls/series; medium calls: 2.57 ± 0.08 calls/series). Short calls share many similarities with the vocalization alternatively labelled inflected alarm calls (Brown, 1985; Yorzinski, Vehrencamp, McGowan, & Clark, 2006) or ko calls (Parr, 1997). The mean duration of our short calls, for example, overlapped slightly with the duration of ko calls (162 ± 34.3 ms), and substantially with that reported for short calls (152 ± 18.1 ms) described by Parr (1997). However, alarm calls can be distinguished by their higher overall frequency (Parr, 1997; inflection peak frequency: 1548 ± 61.8 Hz) compared to short calls (Parr, 1997; inflection peak frequency: 1428 ± 171 Hz).

In addition to our two primary stimulus calls, we included a heterospecific control (to ensure the crows were only responding to conspecific vocalizations) and a conspecific control (to ensure the crows were responding appropriately to a stimulus of known meaning). We used a black-capped chickadee, *Poecile atricapillus*, vocalization (each playback track used a single type of vocalization: song, $N = 22$; contact calls, $N = 3$; or alarm calls, $N = 5$) for our heterospecific control, and scold calls (alternatively referred to as mobbing calls, see Yorzinski & Vehrencamp, 2009) as our conspecific control. Specifically, scold calls signify danger (Parr, 1997), and crows predictably respond by gathering around the source of the calls, giving their own scold calls, and divebombing any predator they find at the location (Swift & Marzluff, 2015; Yorzinski & Vehrencamp, 2009; Yorzinski et al., 2006). We defined scold calls as unstructured crow calls with a peak frequency >1500 Hz ($\bar{X} \pm SE = 1628 \pm 8.5$ Hz). From the experiment 1 audio recordings, we selected exemplars of calls uttered by a single individual crow and edited them into a 10 s audio track. The short and medium call stimulus audio tracks contained at least two full sets of structured calls, while the scold control tracks contained at least eight individual vocalizations (short: 13.50 ± 0.67 vocalizations; medium: 8.24 ± 0.93 ; scold: 13.10 ± 0.90 ; see Fig. 2 for examples). Because crows increase their call rate to indicate the level of urgency when warning about danger (Yorzinski & Vehrencamp, 2009), we analysed a subset of our data using stimulus calls containing the same number of vocalizations to determine whether the crows' response was primarily due to the call duration or calling rate of the stimulus (see Appendix 5 for details). To control for crows responding with aggression because they do not recognize the caller and to increase the number of exemplars tested, we only used stimulus tracks at the site where they were recorded (although see Caveats in the Discussion).

Field procedure

We tested how crows responded to hearing conspecific calls from early June to late July 2016 at 30 sites previously used in experiment 1 (Fig. 1). We arrived at a site, observed crows and recorded as in experiment 1. For audio playback, we used a Pignose 7-100 Legendary portable amplifier connected to a wrist-mounted MP3 player via a 33 m audio cable. Upon arriving at a site, we placed the speaker at a tree or shrub within 33 m of the nearest

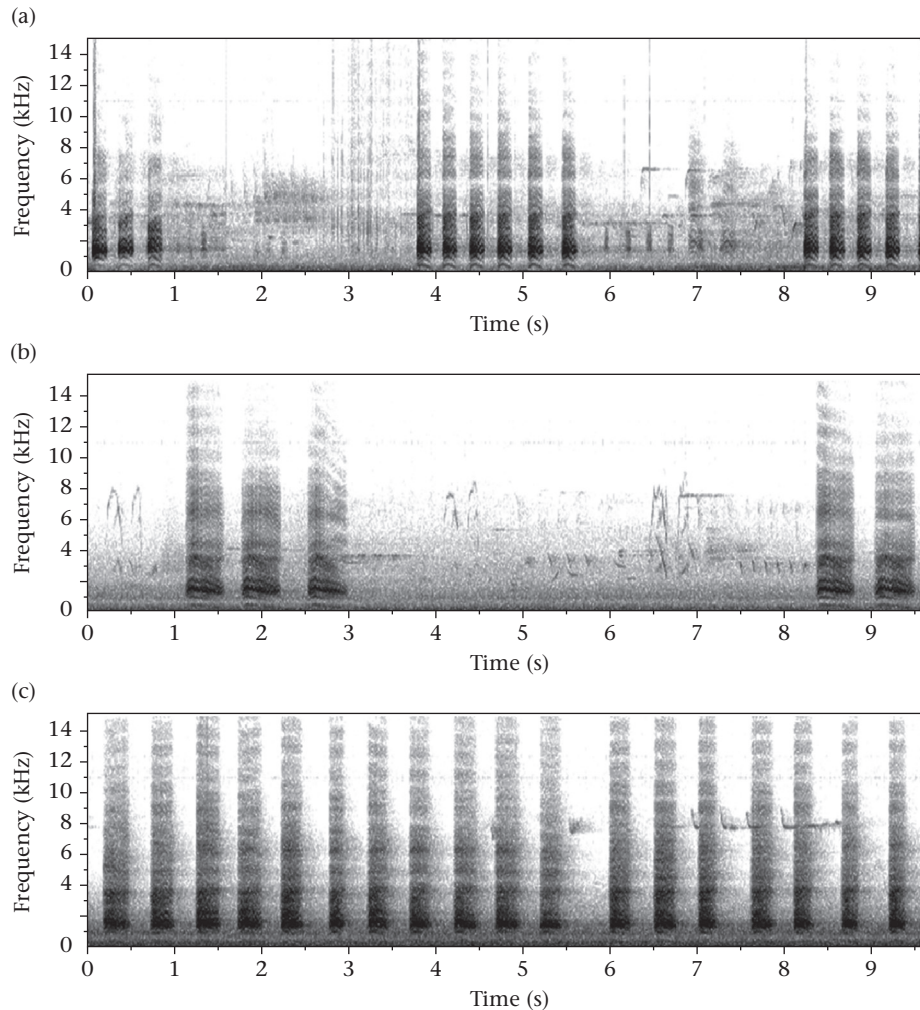


Figure 2. Spectrogram examples of (a) short, (b) medium and (c) scold stimulus calls.

crow, ideally so it would appear to the focal crow that the stimulus calls were coming from a perched bird hidden by foliage. After placing the speaker, we retreated 15–25 m away, verified that crows were still present within 33 m of the speaker, then began the trial. If the crows had moved away during set-up, we packed up the speaker, relocated the birds and set up again nearby. For each trial, we collected behavioural and vocal data across two 300 s phases, which were subdivided into 30 intervals of 10 s (see Fig. A2 in [Appendix 1](#) for illustration of experiment 2 phases). We set a watch to emit a quiet ‘beep’ every 10 s to keep track of intervals in the field. The first interval of every minute was the stimulus interval, during which we either did nothing (prestimulus phase) or played the assigned stimulus call through the speaker (stimulus phase). The remaining five intervals of every minute were observation intervals, during which we performed a focal follow on whichever crow was closest to the speaker (the focal crow) and recorded the presence or absence of the following behaviours from that crow: flight; proximity (<7 m) to speaker; dominance posturing; and wing/tail flicking ([Table 1](#)). Because our goal was to use the change in prevalence of these behaviours to discern the meaning behind different stimulus calls, we treated each behaviour as an ‘event’, rather than a ‘state’ ([Altmann, 1974](#)). In addition to those four behaviours, we recorded the total vocalizations given by the focal crow and the number of adult crows within 33 m of the speaker during each observation interval.

Experiment 3: Food Discovery Response to Call Playback

We examined the effect that different stimulus calls had on the probability of food discovery from late June to early August 2017 at 11 sites previously visited during experiment 1, but not used during experiment 2 ([Fig. 1](#)). We arrived at a site, recorded data and selected stimulus calls as in experiment 2, with the exception that we did not use scold stimulus calls. At each site, we arranged the speaker as in experiment 2 before discreetly placing a pile of 25 peanuts 7 m from the speaker. After setting up the food and speaker, we retreated 15–25 m away, verified that crows were still present within 33 m of the speaker, then began the trial. We aborted if any crows discovered the food pile prior to starting the trial, or if there were no crows within 33 m of the speaker for 300 s. As in experiment 2, we played the stimulus call every 60 s; however, unlike experiment 2, we continued to observe the food pile during the stimulus intervals (see [Fig. A3](#) in [Appendix 1](#) for illustration of experiment 3). We recorded the time when crows initially discovered the food pile and the maximum number of crows within 1 m of the food pile for all intervals after food discovery.

Statistical Analysis

We conducted all statistical analysis using RStudio version 1.0.136 ([RStudio Team, 2016](#)). As individual crows varied, for

Table 1
The behaviours recorded in experiment 2

Measure	Definition	Significance of behaviour	Prediction if stimulus call signifies:		
			Ally recruitment	Territorial advertisement	Danger warning
Average no. of adults present	The total number of adult crows within 33 m of the speaker	This measure tests whether the stimulus call attracts crows to the site	Increase	No change	Increase
Vocalization	The number of vocalizations given by the focal crow	The focal crow is sending a signal to other crows in a large area	No change	Increase	Increase
Flight	The focal crow enters flight	The focal crow desires to move to a new location, either to avoid a threat or locate an object of interest	Increase	Increase	Increase
Proximity to speaker	The focal crow is <7 m from the speaker	The focal crow is attempting to locate the source of the stimulus calls	No change	Increase	Increase
Dominance posturing	The focal crow fluffs out the feathers around its back and feet, and stands/walks in an erect posture (Marzluff & Angell, 2013)	The focal crow is attempting to intimidate other crows, often correlated with displacement attempts (Kilham, 1990)	No change	Increase	No change
Wing/tail flicking	The focal crow rapidly fans and closes its rectrices and simultaneously flicks the closed wingtips slightly upwards and down again with very little lateral movement (Kilham, 1990)	The focal crow is emotionally aroused, agitated or apprehensive (Kilham, 1990; Marzluff et al., 2010)	No change	Increase	Increase

Apart from average no. of adults present and vocalizations given, we only counted a behaviour as present/absent for each 10 s focal follow interval, then summed all the intervals where the behaviour was observed for that phase. For the average no. of adults present, we averaged the number of adults present across all 25 intervals for that phase.

experiments 1 and 2 we compared the effect that a stimulus treatment had on behaviour and call microstructure using a linear mixed model with each site (as a proxy for the crows that live there) as a random effect (we used Satterthwaite approximations to estimate degrees of freedom). The linear mixed models were computed by R package lme4 (Bates, Maechler, Bolker, & Walker, 2015), while the Satterthwaite approximations were calculated by R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015). We compared the likelihood of food discovery for the two conspecific treatments against the chickadee control in experiment 3 using Fisher's exact test. All post hoc comparisons were done using a Tukey honest significant difference test after first applying Holm corrections to the *P* value to account for the higher likelihood of committing type I error with multiple comparisons, which we accomplished using R package multcomp (Hothorn, Bretz, Westfall, & Heiberger, 2008).

Ethical Note

No animals were trapped or handled during this study. Disturbance of wild crows was limited to food provisioning (peanuts) and vocalization playback (black-capped chickadee and conspecific calls). The behaviour of crows quickly returned to normal post-stimulus. All disturbances were at least 24 h apart. All procedures were approved by the Institutional Animal Care and Use Committee of the University of Washington (IACUC; protocol number 3077-01).

RESULTS

Experiment 1: Behavioural Response to Food Presence

When we first arrived at a site and during the prestimulus phase, the crows were usually foraging on the ground or vocalizing from a perched position. Most locations had only two crows present (presumably a mated pair that controlled a territory), with additional crows temporarily visiting the site before either being chased away by the existing crows or leaving on their own (average no. of crows \pm SE = 2.31 ± 0.16 , maximum no. of crows \pm SE: 2.93 ± 0.19 ; Fig. 3a and b). During the stimulus phase, crows flew to

the food pile and either ate peanuts at the pile, cached them in the immediate vicinity or grabbed one or two peanuts and departed. During this phase, more crows visited the site and the maximum number of crows present increased (prestimulus: 2.93 ± 0.19 adults; stimulus: 3.64 ± 0.29 adults; $z = 2.54$, $P = 0.034$; Fig. 3b). The call rate also increased somewhat during this phase, albeit not significantly so (prestimulus: 4.76 ± 0.87 calls/min; stimulus: 6.69 ± 0.83 calls/min; $z = 1.79$, $P = 0.22$; Fig. 3c). The crows that were present during this phase uttered calls that were significantly shorter than the calls given prior to the food's appearance (prestimulus: 278 ± 2.1 ms; stimulus: 236 ± 1.3 ms; $z = -17.8$, $P < 0.001$; Fig. 3d). After all the peanuts were consumed (poststimulus phase), the visiting crows usually left promptly or were chased out by the residential crows, which would return to their previous activities after searching the area for peanut scraps; the call rate and average number of crows present both returned to their prestimulus levels, whereas the maximum number of crows present remained high (Fig. 3a–c). Compared to the vocalizations given while food was present, the duration of the calls uttered during the poststimulus phase increased, although not to their prestimulus state (stimulus: 236 ± 1.3 ms; poststimulus: 252 ± 1.3 ms; $z = 9.01$, $P < 0.001$; Fig. 3d); additionally, the peak frequency of the calls uttered increased slightly during each phase, to the point that the calls given poststimulus were significantly higher in pitch than the calls uttered prestimulus (prestimulus: 1544 ± 5.2 Hz; poststimulus: 1569 ± 4.0 Hz; $z = 3.25$, $P = 0.004$; Fig. 3e). The number of vocalizations per call group did not notably change between each phase (Fig. 3f).

The Effect of Food Amount on Crow Behaviour

During the stimulus phase, more crows were attracted to the site as more food became available; the maximum number of crows attracted to the 25-peanut treatment was significantly greater than in the 5-peanut treatment (5 peanuts: $\bar{X} \pm$ SE = 3.41 ± 0.49 adults; 25 peanuts: 5.04 ± 0.52 adults; $z = 3.61$, $P < 0.001$), which in turn was significantly greater than in the 1-peanut treatment (1 peanut: 2.46 ± 0.23 adults; 5 peanuts 3.41 ± 0.49 adults; $z = 2.11$, $P = 0.035$; Fig. 4b). In contrast, the average number of crows present did not significantly increase (Fig. 4a), suggesting that although many

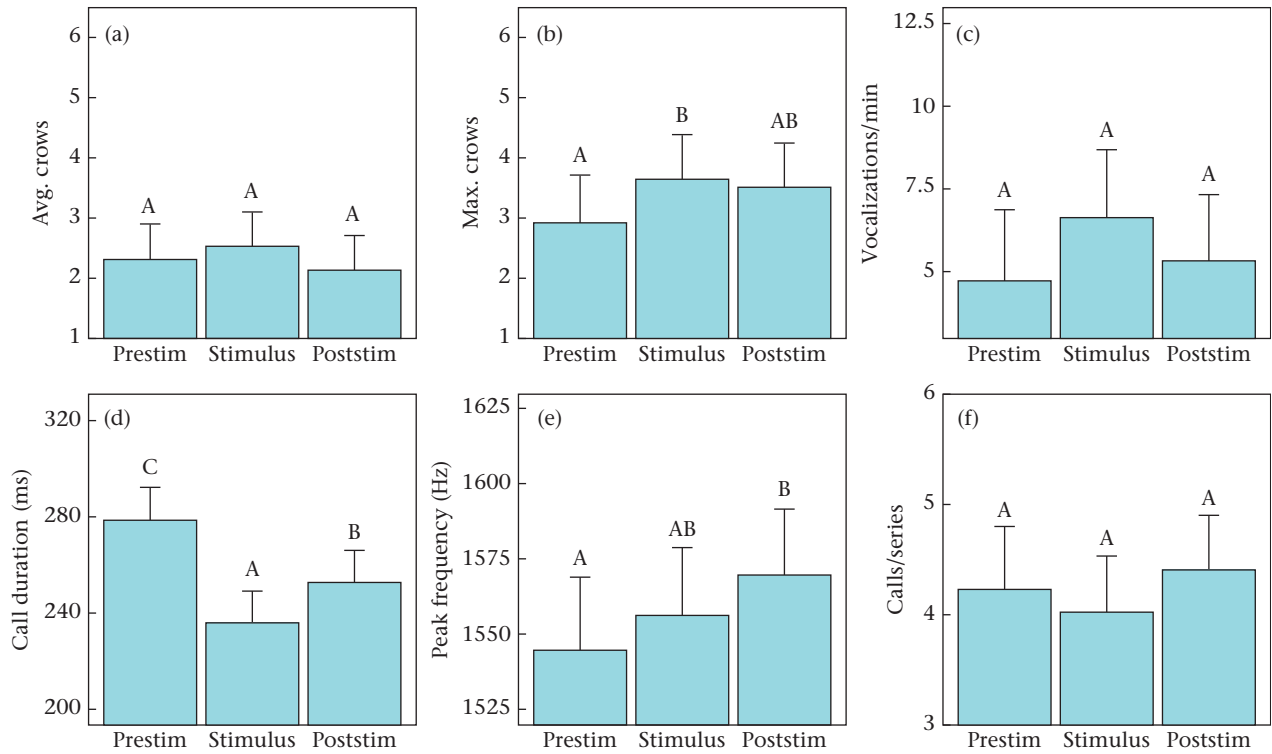


Figure 3. Mean response + 95% confidence interval for (a–c) changes in crow behaviour and (d–f) microstructure of calls uttered across the prestimulus, stimulus and poststimulus phases of experiment 1. (a) Average number of crows, (b) maximum number of crows, (c) call rate, (d) call duration, (e) peak frequency and (f) number of calls per series. Data include both feeder and nonfeeder treatments. Different letters indicate significantly distinct groups after Holm corrections to the P value.

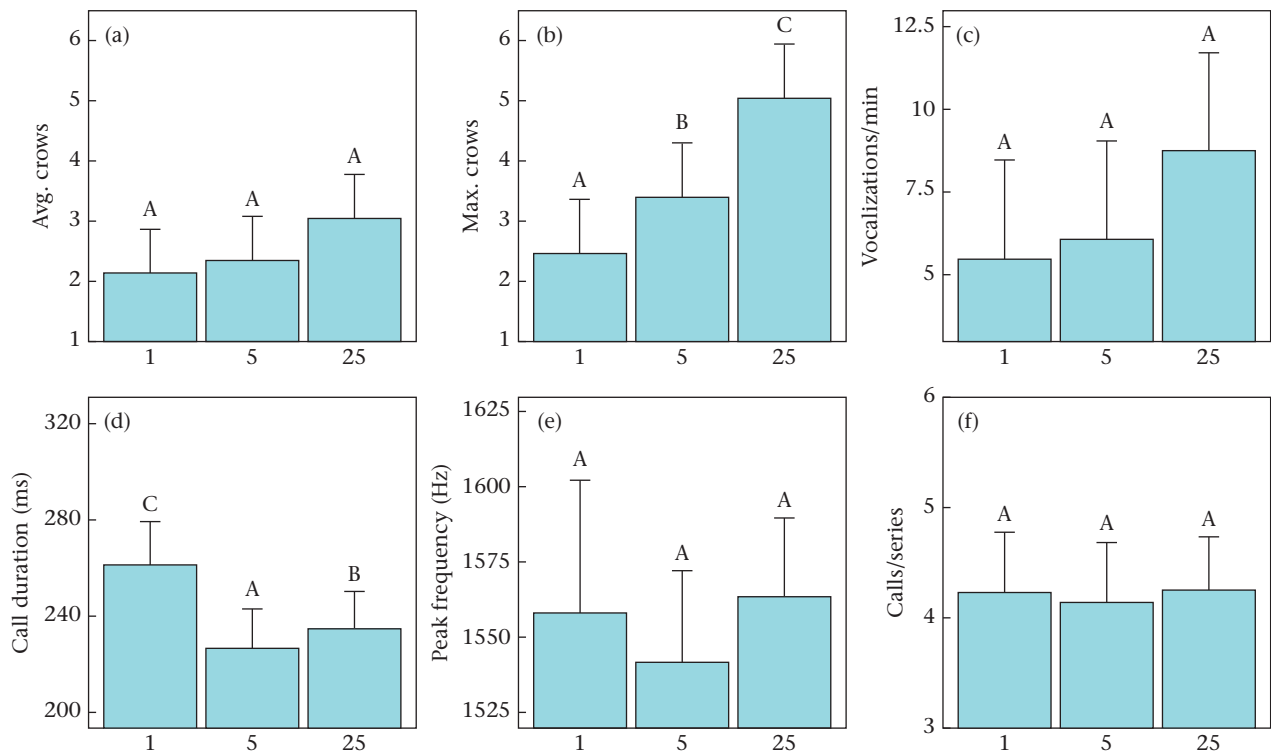


Figure 4. Mean response + 95% confidence interval for (a–c) changes in crow behaviour and (d–f) microstructure of calls during the stimulus phase for all three treatments (1, 5 and 25 peanuts) of experiment 1. (a) Average number of crows, (b) maximum number of crows, (c) call rate, (d) call duration, (e) peak frequency and (f) number of calls per series. Data include both feeder and nonfeeder treatments. Different letters indicate significantly distinct groups after Holm corrections to the P value.

crows visited the site, many did not remain for long. Their call rate also increased somewhat as more food was available, but this increase was not significant even when comparing the largest peanut treatment to the smallest (1 peanut: 5.51 ± 1.56 calls/min; 25 peanuts: 8.71 ± 1.58 calls/min; $z = 1.88$, $P = 0.18$; Fig. 4c). The calls uttered during the stimulus phase were significantly longer for the 1-peanut than the 5-peanut (1 peanut: 261.7 ± 4.7 ms; 5 peanuts: 227.2 ± 3.1 ms; $z = 5.89$, $P < 0.001$) and 25-peanut (1 peanut: 261.7 ± 4.7 ms; 25 peanuts: 235.2 ± 1.5 ms; $z = 4.70$, $P < 0.001$) treatments (Fig. 4d). Neither the peak frequency nor the number of calls uttered per call series was significantly affected by the food amount (Fig. 4e and f).

Experiment 2: Behavioural Response to Call Playback

Description of prestimulus phase behaviours

As in experiment 1, when we arrived at a site and throughout the prestimulus phase most crows foraged on the ground or vocalized from perched positions. Most locations had only one or two crows present ($\bar{X} \pm SE = 1.93 \pm 0.18$ adults <33 m of speaker), and they vocalized only occasionally (9.28 ± 3.15 vocalizations/300 s). Of the behaviours we observed during the prestimulus phase, flight was the most common (observed during 1.35 ± 0.15 intervals). The crows appeared neither afraid of nor interested in the speaker, as they occasionally walked near it but did not actively inspect it (0.89 ± 0.38 intervals). We rarely observed a dominance posture or wing/tail flick during the prestimulus phases (dominance posture: 0.13 ± 0.07 intervals; wing/tail flicking: 0.28 ± 0.07 intervals).

Behavioural response to short stimulus calls

The crows that were exposed to the short stimulus calls did not significantly change any of their observed behaviours compared to their prestimulus state, although they did slightly increase the number of vocalizations uttered and time spent in flight, dominance posturing and wing/tail flicking (Fig. 5b, c, g, i). While the duration of the calls did not change from the prestimulus to the stimulus phase, the peak frequency of the calls became significantly higher in pitch (prestimulus: $\bar{X} \pm SE = 1414 \pm 19.6$ Hz; stimulus: 1493 ± 8.0 Hz; $z = 4.81$, $P < 0.001$; Fig. 5f), as did the number of vocalizations given per call series (prestimulus: 1.94 ± 0.16 calls/series; stimulus: 4.27 ± 0.19 calls/series; $z = 3.74$, $P = 0.005$; Fig. 5h). These changes in call microstructure appear to be due to the crows responding to the short stimulus calls by uttering more of their own short calls: the vocalizations observed during the stimulus phase more closely resembled the short stimulus calls' duration (stimulus: 191 ± 3.0 ms; observed: 213 ± 3.6 ms), peak frequency (stimulus: 1536 ± 28.8 Hz; observed: 1493 ± 8.0 Hz) and call series (stimulus: 4.62 ± 0.12 calls/series; observed: 4.27 ± 0.2 calls/series) than did the vocalizations from the prestimulus phase.

Behavioural response to medium stimulus calls

Unlike the crows that were exposed to the short stimulus calls, those that heard medium stimulus calls responded with greater intensity, uttering more vocalizations (prestimulus: $\bar{X} \pm SE = 2.17 \pm 3.08$ intervals; stimulus: 64.53 ± 19.81 intervals; $z = 4.86$, $P < 0.001$; Fig. 5b) and spending more intervals in flight (prestimulus: 1.46 ± 0.30 intervals; stimulus: 4.22 ± 0.90 intervals; $z = 4.24$, $P < 0.001$; Fig. 5c), dominance posturing (prestimulus: 0.00 ± 0.00 intervals; stimulus: 1.12 ± 0.58 intervals; $z = 3.49$, $P = 0.013$; Fig. 5g) and wing/tail flicking (prestimulus: 0.29 ± 0.15 intervals; stimulus: 5.17 ± 1.57 intervals; $z = 5.40$, $P < 0.001$; Fig. 5i) compared to their prestimulus behaviour. They also spent notably more time within 7 m of the speaker although this increase was not

significant (prestimulus: 3.27 ± 1.61 intervals; stimulus: 6.38 ± 2.12 intervals; $z = 2.07$, Holm-corrected $P = 0.72$; Fig. 5e). Our analysis with the subset of stimulus calls with matching call rates returned similar results, albeit without the significant increase in dominance posturing (see Appendix 5 for details). Much as the crows responded to the short stimulus calls by giving more of their own short calls, crows that heard the medium stimulus calls uttered more medium calls: compared to the prestimulus phase, the stimulus phase vocalizations were significantly longer (prestimulus: 236 ± 6.2 ms; stimulus: 295 ± 2.3 ms; $z = 8.44$, $P < 0.001$; Fig. 5d) and somewhat lower in peak frequency (prestimulus: 1559 ± 31 Hz; stimulus: 1530 ± 3 Hz; $z = -1.77$, $P = 0.38$; Fig. 5f). These changes made the vocalizations observed during the stimulus phase more closely resemble the duration (stimulus: 359 ± 9.2 ms; observed: 295 ± 2.3 ms) and peak frequency (stimulus: 1528 ± 10.2 Hz; observed: 1530 ± 2.8 Hz) of the medium stimulus calls than did their prestimulus counterparts.

Behavioural response to scold stimulus calls

When compared to the other stimulus calls, the crows hearing scold stimulus calls responded with greater intensity than they did to the short stimulus treatment, but with less intensity than to the medium stimulus treatment. Compared to their prestimulus behaviour, the crows reacted to the scold calls by uttering more vocalizations (prestimulus: $\bar{X} \pm SE = 6.52 \pm 5.49$ intervals; stimulus: 61.97 ± 15.09 intervals; $z = 4.69$, $P < 0.001$; Fig. 5b) and taking flight more often (prestimulus: 1.33 ± 0.26 intervals; stimulus: 3.28 ± 0.53 intervals; $z = 3.25$, $P = 0.025$; Fig. 5c). The slight increases in time spent close to the speaker (prestimulus: 0.02 ± 0.00 intervals; stimulus: 2.92 ± 1.43 intervals; $z = 2.09$, $P = 0.72$; Fig. 5e) and wing/tail flicking (prestimulus: 0.39 ± 0.15 intervals; stimulus: 2.69 ± 0.93 intervals; $z = 2.76$, $P = 0.11$; Fig. 5i) were not significant. The calls uttered during the stimulus phase were significantly shorter than the prestimulus vocalizations (prestimulus: 320 ± 4.3 ms; stimulus: 296 ± 2.1 ms; $z = -4.41$, $P < 0.001$; Fig. 5d).

Behavioural response to the chickadee control calls

Crows that listened to the chickadee control stimulus did not significantly change any of their observed behaviours from the prestimulus to the stimulus phase, although there was a slight decrease in the number of crows present (Fig. 5a), suggesting that crows gradually moved away from the study site when there was no conspecific stimulus call. While the vocalizations uttered during the stimulus phase did not differ significantly from those in the prestimulus phase, calls were shorter (prestimulus: $\bar{X} \pm SE = 293 \pm 2.1$ ms; stimulus: 282 ± 3.7 ms; $z = -2.31$, $P = 0.10$; Fig. 5d) and the peak frequency slightly higher (prestimulus: 1600 ± 7 Hz; stimulus: 1628 ± 11 Hz; $z = 2.37$, $P = 0.12$, Fig. 5f) during the stimulus phase. The type of chickadee call did not affect the crows' response; the only significant difference was an elimination of dominance posturing in response to hearing chickadee contact calls (prestimulus: $\bar{X} \pm SE = 1.33 \pm 1.33$ intervals; stimulus: 0.00 ± 0.00 intervals; $z = 3.67$, $P = 0.003$).

Experiment 3: Food Discovery Response to Call Playback

When we arrived at a site the crows were usually engaged in foraging or vocalizing from a conspicuous position, as in the previous two experiments. Upon hearing the stimulus calls, the crows appeared to respond as they did during experiment 2, ignoring the chickadee control calls while reacting to the conspecific calls. Overall, the crows discovered the peanut pile in 38% of the trials ($N = 29$ tests). They had the greatest success in finding the food when we played medium stimulus calls, discovering the food in

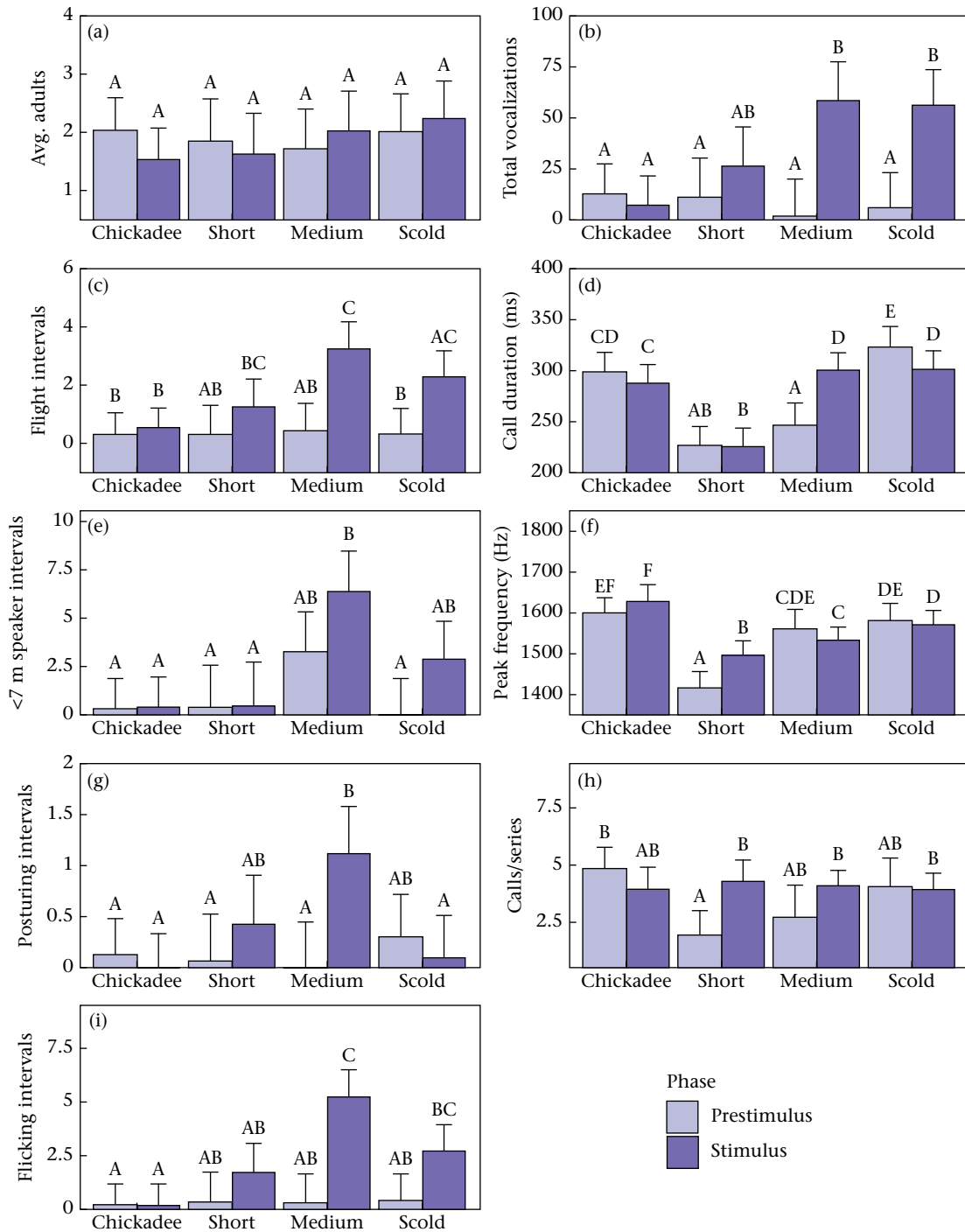


Figure 5. Mean response + 95% confidence interval for the effect each playback stimulus had on (a) the number of adults <33 m from the speaker, (c, e, g, i) the focal crow's behaviour and (b, d, f, h) the microstructure of the vocalizations uttered by the focal crow during the prestimulus and stimulus phases of experiment 2. (b) Number of calls, (c) number of flights, (d) call duration, (e) proximity to speaker, (f) peak frequency, (g) number of display postures, (h) number of calls per series and (i) number of wing/tail flicks. Different letters indicate significantly distinct groups after Holm corrections to the P value.

62.5% of trials ($N = 8$); however, this was not significantly greater than the chickadee control success rate of 18% ($N = 11$; Fisher's exact test: $P = 0.074$). Upon discovering the food source, many focal crows diverted their attention to eating and caching the food and only appeared to respond to the stimulus calls while they were being broadcast. None of the stimulus call types had a significant effect on the discovery time of the food pile or on the maximum number of adults present at the food (Fig. 6a and b).

DISCUSSION

Previous studies examining American crow vocalizations tended to focus on danger-associated calls, either from the producer's response to stimuli (Yorzinski et al., 2006; Yorzinski & Vehrencamp, 2009; but see Tarter, 2008 for additional call types) or the receiver's response to playback (Brown, 1985; Chamberlain & Cornwell, 1971; Frings & Frings, 1957; Richards & Thompson, 1978;

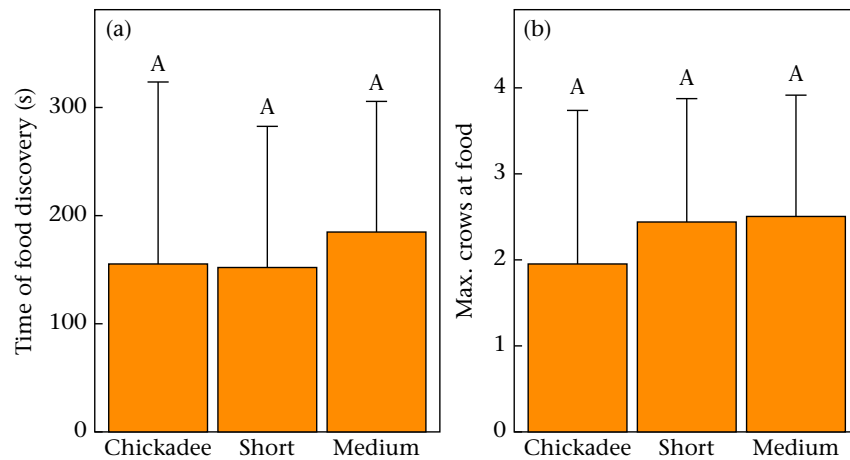


Figure 6. Mean response + 95% confidence interval for the effect each playback stimulus had on (a) the food discovery time and (b) the maximum number of crows present at the food pile. Crows discovered the food in two chickadee stimulus trials ($N = 11$), four short call stimulus trials ($N = 10$) and five medium call stimulus trials ($N = 8$). Different letters indicate significantly distinct groups after Holm corrections to the P value.

but see Parr, 1997 for additional call types). Although several studies have examined food-associated calls with other corvids (Boeckle, Szpl, & Bugnyar, 2012; Bugnyar et al., 2001; Dahlin, Balda, & Slobodchikoff, 2005; Røskaft & Espmark, 1982), to our knowledge no playback study has focused on food-associated calls with American crows.

Here, we examined why crows vocalize at food by focusing on three hypothetical reasons (ally recruitment, territorial defence and danger warning) and examined their reaction to playback to determine which hypotheses were viable. From a production standpoint, we found that American crows measurably changed the quality of their calls around food, especially if the food amount surpassed some threshold, indicating that their vocalizations were dependent on the context of the current situation. Crows avoided giving medium calls near food, and uttered scold calls in response to a perceived threat, regardless of food presence. From the receiver's side, there was minimal response from listening crows to short calls originally uttered at food, but a much stronger aggressive response to medium calls. However, we found that even aggressive crows spent time foraging at a newly discovered food source while simultaneously responding to medium call playback.

Medium Calls: Territorial Defence

Our findings support the hypothesis that medium calls are used for territorial defence and to signal aggression; the vocalizations uttered by crows during the pre- and poststimulus phases of experiment 1 tended to be longer than those given in the presence of food, and playback of these vocalizations during experiment 2 caused listening crows to react in a manner consistent with five of our six predictions for the stimulus call being associated with territorial defence (Table 1). If we consider their near-significant increase in speaker proximity to be indicative of a behaviour that we lacked the power to significantly detect, then their response would match all our conditions for territorial defence. Additionally, the crows appeared to respond to the medium stimulus calls by giving medium calls of their own: most of their vocalizations became consistently longer and lower in peak frequency compared to before the stimulus. In many songbirds, type matching during counter-singing signals aggressive escalation (Searcy & Beecher, 2009; Vehrencamp, 2001), and many avian species use vocalizations with a low frequency for aggression and intimidation, since only the largest individuals are structurally capable of producing signals with

comparatively lower pitch (Morton, 1977). This suggests that crows are using type-matched vocalizations as a challenge to the unseen caller, which is consistent with the behaviour observed in song playback experiments with other songbirds (Burt et al., 2001).

The cost of uttering medium calls appeared to change depending on the caller's current situation: the prevalence of longer calls during the prestimulus phase of experiment 1, coupled with the focal crows' vigorous response to hearing playback of medium stimulus calls during experiments 2 and 3, implies that while there is normally little cost for a caller to give medium calls within their territory, the cost is much greater should they produce them on a rival's territory. Taken together, this response is consistent with the territorial nature of crows. Despite this, crows seemed reluctant to utter medium calls around large food resources; the calls recorded during the stimulus phase of experiment 1 were much shorter if there was more than a single peanut available, which would suggest that the cost of uttering territorial calls is greater near food. During experiment 3, the only treatment that caused a near-significant increase in food discovery was the medium stimulus calls, which was probably a result of the listening crows' efforts to support their mate or to locate and expel the caller (although without individually marked crows we cannot know for certain; see Caveats below). This implies that uttering medium calls around a rich food resource increases the risk that other crows will discover it, and that the costs of additional conspecifics at the food site exceeds any benefits the territory owner might gain from their presence.

We postulated above that crows might attempt to keep rivals at bay by uttering territorial calls, but our results show that this tactic would have the opposite effect of attracting increasing conspecific attention to the area. After other crows learn of a food source, even if it is inside a rival's territory, they are often capable of obtaining some for themselves. A single bird can fly in and grab food while the owners are away caching, and a group of crows can descend en masse to overwhelm the owners' defence of the food pile. Should rivals discover the food, the cost of giving medium calls would shift from attracting competitors to wasting valuable foraging time for negligible gains; a mated pair cannot evict a flock, so rather than uttering medium calls which would be ignored, they maximize their foraging efficiency by gathering as much food as possible before the flock depletes the food source.

Despite the apparent costs, some crows did occasionally utter medium calls during the stimulus phase of experiment 1, particularly when there was only a single peanut available. We believe

these calls were uttered by unaware crows continuing an ongoing bout of medium calls from the prestimulus phase. This was especially pronounced for the single peanut stimulus as the nearest aware bird was almost always the first to reach the peanut, ending the stimulus phase before the other crows could react. Once the peanut was in a crow's possession, other crows could do little more beyond chasing the bird away; while crows will rob conspecific caches in the owner's absence (Emery & Clayton, 2004), we never witnessed a crow directly take a peanut from another.

Short Calls Associated with Food: Function Unknown

In experiment 1, we found that crows gave shorter calls while food was present, specifically when there was more than a single peanut available for consumption. Because the calls uttered in the presence of the 25-peanut pile had a slightly higher mean duration than the calls uttered around the 5-peanut pile, we do not believe that call duration is linearly correlated with food size, but rather that crows utter short calls after the food amount passes a specific threshold, perhaps the point at which there is more food than a single crow can monopolize. Additionally, these shorter calls were given in conjunction with an increase in the number of crows present near the site, which is consistent with Parr's (1997) findings that associated short structured calls with a 'call-to-arms' context, for example rallying family to expel intruding crows. Tarter (2008) and Mates et al. (2015) both linked short structured calls with food provisioning and hypothesized that they were used for familial recruitment. While our findings that short calls are associated with both a food bonanza and a large crow presence do support both hypotheses, the same could be said for short calls being used to signal aggression; perhaps the crows are vocalizing in response to the increasing number of intruders arriving at the site, rather than to recruit allies. We attempted to determine the purpose of the short calls with our playback experiments.

In experiment 2, the short stimulus calls did not elicit any significant behavioural change in listening crows, although we did observe minor increases in vocalizations, flight, dominance posturing and wing/tail flicking. These results did not closely match any of the predictions we made for how listening crows would respond to the stimulus calls (Table 1); if the short calls are used to recruit others to food, they did not attract additional crows to the site, whereas if they are used for territorial aggression, they did not elicit a strong aggressive response from the listening crows. The results seem to suggest that crows are reacting to short calls with some agitation, albeit only a mild amount compared to their response to the medium and scold stimulus calls. Additionally, the listening crows responded by uttering their own short calls, which could be a form of type-matching aggression (Searcy & Beecher, 2009), furthering the hypothesis that short calls are used to signal mild aggression. However, experiment 2 was conducted in the absence of food; perhaps crows were recruited to the area by the short stimulus calls but, finding no food in sight, departed too quickly for their arrival to statistically register as an increase.

We conducted experiment 3, which included a large food pile within 7 m of the speaker, to more closely mimic the conditions during which the short calls were uttered in experiment 1; if crows are being recruited to an area, they would now find the food they were looking for. However, while the short stimulus calls slightly increased the likelihood that the listening crows would discover the food pile, this change was not statistically significant. These results suggest that, while the benefits of giving short calls remain unknown, crows do not incur a large cost to uttering them around food. Because we were unable to recruit additional crows to the area or to food with playback, we cannot state that they are used to recruit allies to food.

What other benefits might crows gain from giving short calls around food? In a gathering that includes rival territory holders and vagrants, crows would benefit from giving appeasement calls that de-escalate tension and reduce the chance of costly fights as in common ravens (Heinrich et al., 1993). Alternatively, they might benefit from producing calls that identify themselves to better locate their mate or kin amid a large group; researchers have determined that crows may be able to identify other individuals by listening to their calls (Mates et al., 2015).

Benefits to Food Recruitment?

Most social vertebrates that recruit conspecifics to food benefit by improving their foraging efficiency, gaining access to the food source, reducing their predation risk, increasing their status among potential mates or provisioning their mates and kin (Clay et al., 2012; Eberhard, 1975; Stevens & Gilby, 2004); we postulate that crows would benefit most by gaining access to a closed food source. Vagrant common ravens can gain access to a guarded food source by recruiting conspecifics from a roost to overwhelm the territorial adults protecting it (Heinrich et al., 1993; Marzluff, Heinrich, & Marzluff, 1996), perhaps using a combination of flight displays and vocalizations (Bugnyar et al., 2001; Marzluff & Marzluff, 2011). Additionally, mated ravens cooperate with their mate and kin to alternatively distract and steal food from larger predators (Marzluff & Angell, 2005). If the closely related American crows employ any of these tactics to obtain food from a rival's territory, they would benefit from recruiting allies as in ravens.

It is not clear whether crows would benefit from food recruitment by increasing their social status, partly due to the lack of research into this topic. However, we can gain some insight by examining other members of the Corvidae family. Pinyon jays, *Gymnorhinus cyanocephalus*, live within large multifamily flocks with complex social hierarchies and vocalize to recruit group members to food; they call more often when their mate is present, suggesting that there is a social status element to these calls (Dahlin et al., 2005). There is also evidence that hooded crows, *Corvus corone*, mob dangerous predators partly for self-advertisement (Slagsvold, 1984), demonstrating that crows can gain social status by performing costly or risky behaviours. Research on common ravens has determined that they can discriminate between the calls of familiar and unfamiliar conspecifics, and that the large variation observed in raven vocalizations is partly explained by the caller's age class, sex and social status (Boeckle et al., 2012). Additional research has found that listening ravens incorporate the social information gained from the calls into their response, such as preferentially responding to the recruitment calls of familiar female callers (Szipl, Boeckle, Wascher, Spreafico, & Bugnyar, 2015), suggesting that ravens can deal with conspecifics on an individual level. Similar research has not been performed on American crows, although we do know that crow vocalizations encode information about the caller's identity, sex and behavioural context (although not age class, see Mates et al., 2015), suggesting that crows might be assessing social factors prior to responding.

The other potential benefits to recruiting conspecifics do not align with our understanding of crow behaviour. Smaller songbirds, which are more vulnerable to predation, will recruit conspecifics (and even heterospecifics) to food to reduce their predation risk via increased vigilance and risk dilution (Elgar, 1986; Sridhar, 2009). While crows will recruit to drive away predators, they do so reactively rather than proactively, and they use scold calls rather than short calls (Swift & Marzluff, 2015; Yorzinski & Vehrencamp, 2009; Yorzinski et al., 2006). Crows will also provision mates and offspring, but they do so in response to begging calls, which have been well described and are measurably different from the short

calls we recorded (Chamberlain & Cornwell, 1971; Parr, 1997; Tarter, 2008). Finally, while naïve crows may discover a rich food source from the conspicuousness of a gathered flock, the competition around the food usually prevents birds from immediately feeding; thus, recruitment would only decrease their foraging efficiency if they have already gained access to the food.

Scolds: Danger Warning

Upon perceiving a predator, American crows attempt to attract a mob of conspecifics by producing scold calls, as a mob will amplify the caller's ability to harass the predator into leaving (Swift & Marzluff, 2015; Yorzinski & Vehrencamp, 2009; Yorzinski et al., 2006). We recorded occasional scold calls throughout all phases and treatments of experiment 1, suggesting that crows are constantly vigilant for danger, even when gathered around a food source. Playback of scolds during experiment 2 caused significant increases in vocalizations and flight, and no change to dominance posturing; fulfilling three of our six predictions for how the birds would respond to danger (Table 1); if we consider the near-significant increases in wing/tail flicking and speaker proximity to be indicative of a response we lacked the power to significantly detect, then they met five of our predictions for how they would respond if the stimulus call signifies danger. However, because the number of adults did not increase significantly, their response also matches five predictions for the stimulus call signifying territorial advertisement. We believe that these calls signify danger, as the lack of dominance posturing indicates that they are not being territorial; perhaps the trial conditions impeded our ability to detect an increase in crow presence (see Caveats below). Because crows uttered scold calls during all phases and treatments of experiment 1, we believe they were primarily responding to some perceived threat, and the presence of food probably did not factor into their decision to scold. We never witnessed a predator attack a crow during any of our trials; most of the scolds we recorded were produced by crows as they flew away to join an offsite mob, or by parents agitated that their young had approached too near to the observer.

A major potential cost to alarm calling is the risk that the predator will use the call to localize and target the caller (Bayly & Evans, 2003; Sherman, 1977). Crows minimize this risk by flying into cover or gaining altitude above the predator as they vocalize; during experiment 1, crows never remained at the food once they began scolding, and immediately took flight upon hearing the scold stimulus calls during experiment 2. Scolds can play a critical role in survival; thus, while crows seem reluctant to utter territorial calls around food, ostensibly because they would attract competitors (see Medium Calls: Territorial Defence above), they will readily produce the equally attractive scold calls because the benefits of driving away a dangerous predator outweigh the cost of attracting potential competitors to a rich food source.

Caveats

As we used unmarked wild crows for our study, we could not identify individual birds. This precluded us from including social information (age class, sex, social status and territorial status) in our analysis. This might have affected the playback results; we used stimulus calls at the same location they were originally recorded, so it is likely that some of our focal birds were hearing themselves during the stimulus phase. It is not known whether crows recognize their own vocalizations during playback, but other songbird species react to hearing their own vocalizations as though they are

listening to a stranger (Beecher, Stoddard, Campbell, & Horning, 1996). Without being able to identify birds, we had no way of knowing when this was happening. During experiment 2, we were unable to detect any significant change to the average number of adults present at the site, even when we played highly attractive calls (such as scolds) for the stimulus. This could be due to three key issues. First, audio edits: during experiments 2 and 3 we standardized all stimulus calls so that the entire audio track would play within a single 10 s interval. This meant that we edited the original audio recordings of the short and medium calls so that they would play two to three call series within 10 s. Since call rate can indicate the urgency of danger-associated calls (Chamberlain & Cornwell, 1971; Richards & Thompson, 1978; Yorzinski & Vehrencamp, 2009), we may have inadvertently altered the call's meaning by increasing the rate of the call. However, as increased call urgency should also increase the number of and speed at which crows congregate in an area (whereas we were unable to detect an increase in the number of adults at the site), we do not believe this to be the case. Second, lack of visual stimuli: crows obtain important contextual information by watching the behaviour of other crows (Marzluff et al., 2010); by hiding the speaker during experiments 2 and 3, we may have deprived listening crows of cues they normally assess before responding. For example, if arriving crows were unable to locate the danger (or possibly food) that the 'caller' was signalling, then they might have got frustrated and departed before their presence could significantly affect the average over the course of a 300 s phase. Finally, family group composition: unlike eastern American crows, family groups in our study area rarely include helpers (Marzluff & Angell, 2005; Marzluff, McGowan, Donnelly, & Knight, 2001); if crows only recruit members of their family group to food, they would only be recruiting one additional adult (the mate). It would be difficult to detect the addition of a single individual at a statistically significant level without a large sample size. One final issue relates to experiment 3: the limited number of sites available kept our sample size low, which impeded our power to detect significant changes.

Conclusions

Natural selection favours individuals that successfully utilize sources of information about their environment, including eavesdropping on their competition. Because increased competition would be deleterious to an individual's fitness, counterstrategies would develop in an evolutionary arms race. When near a resource that may be exploited by listening competitors, the cost of loudly vocalizing increases, so we would not expect an animal to vocalize unless the benefit is comparatively high. In most documented cases of animals vocalizing near food, the listening animals approached the vocalizer (Clay et al., 2012), suggesting that the signal's purpose is food recruitment, although the type of benefit recruitment provides varies among species (Stevens & Gilby, 2004).

American crows make an ideal model species to study the costs and benefits of calling at food; they have lived alongside humans for hundreds of generations (Marzluff & Angell, 2005; Marzluff et al., 2001) yet many aspects of their behaviour remain enigmatic. This is partly due to their complex social structure: they will forage in large groups and gather to repel predators, yet they also maintain guarded territories with their mate and occasionally one or more helpers. This complexity offers a multitude of opportunities for researchers to study social decision making and cost–benefit analysis.

We have determined that American crows avoid giving territorial medium-duration calls at food, probably to keep competitors

naïve about the food's existence, but after other crows discover and gather around the food bonanza, they switch to short calls. We offered a list of possible benefits that the short calls could provide and postulated that the crows are calling to either recruit conspecifics to gain access to food, appease agitated birds to avoid physical confrontation or contact/locate their mate. Crow society is complex, and the cost/benefit ratio of food vocalizations is different for territory owners versus vagrants, calling on territory versus off territory, males versus females and dominant versus subordinate birds. Future research must include the contextual situation of the caller, such as its age class, sex, position relative to its territory and status to more fully understand the behaviour of these mysterious songbirds.

Acknowledgments

We thank D. Cross, D. Perkel, L. Prugh and B. Gardner for comments on experimental design. We are grateful to Thomas Bugnyar and one anonymous referee for feedback on the manuscript. This material is based upon work supported by the National Science Foundation's Graduate Research Fellowship Program, the Seattle ARCS Foundation, the University of Washington Graduate Opportunities and Minority Achievement Program and the Eastern Band of Cherokee Indians' Higher Education and Training Program.

References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3), 227–266.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bayly, K. L., & Evans, C. S. (2003). Dynamic changes in alarm call structure: A strategy for reducing conspicuousness to avian predators? *Behaviour*, 140(3), 353–369.
- Beecher, M. D., Stoddard, P. K., Campbell, E. S., & Horning, C. L. (1996). Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, 51, 917–923.
- Bioacoustics Research Program. (2014). *Raven Pro: Interactive sound analysis software (Version 1.5)*. Ithaca, NY: The Cornell Lab of Ornithology. Available from: <http://www.birds.cornell.edu/raven>.
- Boeckle, M., Szpił, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*, 84, 1123–1130.
- Brown, E. D. (1985). Functional interrelationships among the mobbing and alarm caws of common crows (*Corvus brachyrhynchos*). *Zeitschrift für Tierpsychologie*, 67(1–4), 17–33.
- Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42, 551–564.
- Bugnyar, T., Kijne, M., & Kotschal, K. (2001). Food calling in ravens: Are yells referential signals? *Animal Behaviour*, 61, 949–958.
- Burt, J. M., Campbell, S. E., & Beecher, M. D. (2001). Song type matching as threat: A test using interactive playback. *Animal Behaviour*, 62, 1163–1170.
- Chamberlain, D. R., & Cornwell, G. W. (1971). Selected vocalizations of the common crow. *Auk*, 88(3), 613–634.
- Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, 83, 323–330.
- Clucas, B., Marzluff, J. M., Mackovjak, D., & Palmquist, I. (2013). Do American crows pay attention to human gaze and facial expressions? *Ethology*, 119(4), 296–302.
- CyberLink Corp. (2014). *CyberLink AudioDirector (Version 5)*. Taipei City, Taiwan. Available from: https://www.cyberlink.com/products/audiorecorder/features_en_US.html.
- D'Vincent, C. G., Nilson, R. M., & Hanna, R. E. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Scientific Reports of the Whales Research Institute*, 36, 41–47.
- Dahlin, C. R., Balda, R. P., & Slobodkinoff, C. (2005). Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication. *Behavioural Processes*, 68(1), 25–39.
- East, M. L., & Hofer, H. (1991). Loud calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour*, 42, 651–669.
- Eberhard, M. J. W. (1975). The evolution of social behavior by kin selection. *Quarterly Review of Biology*, 50(1), 1–33.
- Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, 34, 169–174.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, 306(5703), 1903–1907.
- Frings, H., & Frings, M. (1957). Recorded calls of the eastern crow as attractants and repellents. *Journal of Wildlife Management*, 21, 91.
- Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, 28(1), 13–21.
- Heinrich, B., Marzluff, J. M., & Marzluff, C. S. (1993). Common ravens are attracted by appeasement calls of food discoverers when attacked. *Auk*, 247–254.
- Hothorn, T., Bretz, F., Westfall, P., & Heiberger, R. M. (2008). *Multcomp: Simultaneous inference in general parametric models (R package version 1.4-6)*. <https://cran.r-project.org/web/packages/multcomp/index.html>.
- Judd, T. M., & Sherman, P. W. (1996). Naked mole-rats recruit colony mates to food sources. *Animal Behaviour*, 52, 957–969.
- Kilham, L. (1990). *The American crow and the common raven*. College Station, TX: Texas A&M University Press.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). *ImerTest (R package version, 2.0-33)*. <https://cran.r-project.org/web/packages/lmerTest/index.html>.
- Laiolo, P., & Rolando, A. (2003). The evolution of vocalisations in the genus *Corvus*: Effects of phylogeny, morphology and habitat. *Evolutionary Ecology*, 17(2), 111–123.
- Marzluff, J. M., & Angell, A. (2005). *In the company of crows and ravens*. New Haven, CT: Yale University Press.
- Marzluff, J., & Angell, T. (2013). *Gifts of the crow: How perception, emotion, and thought allow smart birds to behave like humans*. New York, NY: Simon & Schuster.
- Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour*, 51, 89–103.
- Marzluff, J. M., & Marzluff, C. (2011). *Dog days, raven nights*. New Haven, CT: Yale University Press.
- Marzluff, J. M., McGowan, K. J., Donnelly, R., & Knight, R. L. (2001). Causes and consequences of expanding American crow populations. In R. Donnelly, J. Marzluff, & R. Bowman (Eds.), *Avian ecology and conservation in an urbanizing world* (pp. 331–363). Boston, MA: Springer.
- Marzluff, J. M., & Miller, M. L. (2014). Crows and crow feeders: Observations on interspecific semiotics. In G. Witzany (Ed.), *Biocommunication of animals* (pp. 191–211). Dordrecht, Netherlands: Springer. Retrieved from http://link.springer.com/chapter/10.1007/978-94-007-7414-8_11.
- Marzluff, J. M., Walls, J., Cornell, H. N., Withey, J. C., & Craig, D. P. (2010). Lasting recognition of threatening people by wild American crows. *Animal Behaviour*, 79, 699–707.
- Mates, E. A., Tarter, R. R., Ha, J. C., Clark, A. B., & McGowan, K. J. (2015). Acoustic profiling in a complexly social species, the American crow: Caws encode information on caller sex, identity and behavioural context. *Bioacoustics*, 24(1), 63–80.
- Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, 111(981), 855–869.
- Parr, C. (1997). *Social behavior and long-distance communication in eastern American crows* (Ph.D. dissertation). Ann Arbor, MI: University of Michigan. Retrieved from <http://scholar.google.com/scholar?cluster=421686267675363661&hl=en&oi=scholar>.
- Peake, T. M. (2005). Eavesdropping in communication networks. In P. McGregor (Ed.), *Animal communication networks* (pp. 13–37). Cambridge, U.K.: Cambridge University Press.
- Revelle, W. (2018). *psych: Procedures for personality and psychological research (Version 1.8.4)*. Evanston, IL: Northwestern University <https://CRAN.R-project.org/package=psych>.
- Richards, D. B., & Thompson, N. S. (1978). Critical properties of the assembly call of the common American crow. *Behaviour*, 64(3), 184–203.
- Røskoft, E., & Espmark, Y. (1982). Vocal communication by the rook *Corvus frugilegus* during the breeding season. *Ornis Scandinavica*, 13(1), 38–46.
- Roush, R. S., & Snowdon, C. T. (2001). Food transfer and development of feeding behavior and food-associated vocalizations in cotton-top tamarins. *Ethology*, 107(5), 415–429.
- RStudio Team. (2016). *RStudio: Integrated development for R*. Boston, MA: RStudio, Inc. <http://www.rstudio.com/>.
- Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour*, 78, 1281–1292.
- Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: Reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.
- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*, 197(4310), 1246–1253.
- Siracusa, E., Morandini, M., Boutin, S., Humphries, M. M., Dantzer, B., Lane, J. E., et al. (2017). Red squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour*, 154(13–15), 1259–1273.
- Slagsvold, T. (1984). The mobbing behaviour of the hooded crow *Corvus corone cornix*: Anti-predator defense or self-advertisement? *Fauna Norvegica, Series C*, 7(2), 127–131.
- Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78, 337–347.
- Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, 67, 603–614.
- Swift, K. N. (2015). *Wild American crows use funerals to learn about danger* (Ph.D. thesis). Seattle, WA: University of Washington. Retrieved from <https://digital.lib.washington.edu/443/researchworks/handle/1773/33178>.

- Swift, K. N., & Marzluff, J. M. (2015). Wild American crows gather around their dead to learn about danger. *Animal Behaviour*, 109, 187–197.
- Szipl, G., Boeckle, M., Wascher, C. A., Spreafico, M., & Bugnyar, T. (2015). With whom to dine? Ravens' responses to food-associated calls depend on individual characteristics of the caller. *Animal Behaviour*, 99, 33–42.
- Tarter, R. R. (2008). *The vocal behavior of the American crow*, *Corvus brachyrhynchos* (Master's thesis). Columbus, OH: The Ohio State University. Retrieved from https://etd.ohiolink.edu/ap/1070::NO:10:P10_ACCESSION_NUM:osu1204876597#abstract-files.
- Vehrencamp, S. L. (2001). Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society B: Biological Sciences*, 268(1476), 1637–1642.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.
- Yorzinski, J. L., & Vehrencamp, S. L. (2009). The effect of predator type and danger level on the mob calls of the American crow. *Condor*, 111(1), 159–168.
- Yorzinski, J. L., Vehrencamp, S. L., McGowan, K. J., & Clark, A. B. (2006). The inflected alarm call of the American crow: Differences in acoustic structure among individuals and sexes. *Condor*, 108(3), 518–529.
- Zuberbühler, K. (2009). Survivor signals: The biology and psychology of animal alarm calling. *Advances in the Study of Behavior*, 40, 277–322.

Appendix 1

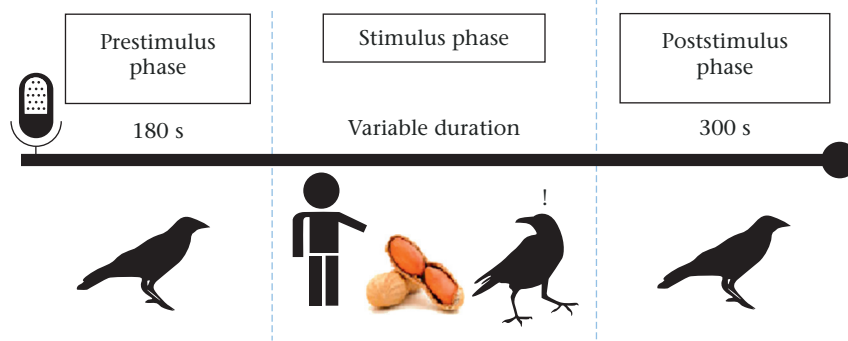


Figure A1. Illustration of the separate phases of a single trial from experiment 1 ($N = 55$).

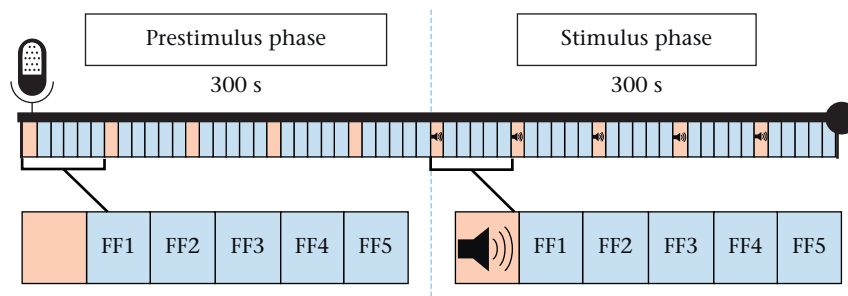


Figure A2. Illustration of the two phases of a single trial from experiment 2 ($N = 30$). Each phase contained five stimulus intervals (pink) and 25 observation intervals (blue).

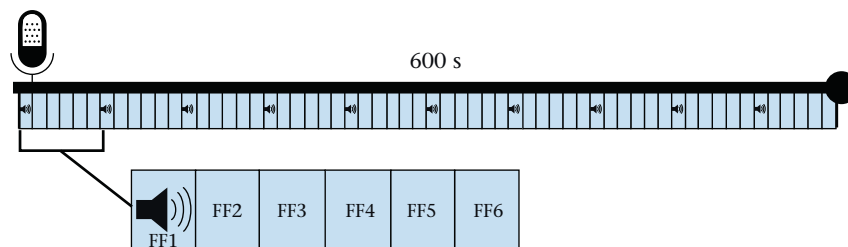


Figure A3. Illustration of a single trial from experiment 3 ($N = 11$). All 60 intervals were observation intervals.

Appendix 2

The Effect of Feeder Presence During Experiment 1

American crows are highly sensitive to human behaviour, the result of living alongside humans for hundreds of generations (Marzluff & Angell, 2005; Marzluff et al., 2001). While they are especially attentive towards dangerous people (Marzluff et al., 2010; Swift & Marzluff, 2015), crows also recognize friendly humans, forming lasting relationships with the people who feed them (Marzluff & Miller, 2014). Crows will gather in large numbers around a recognized crow feeder and follow them for some distance, occasionally ignoring the territorial boundaries of other crows as they do so (Marzluff & Miller, 2014).

During experiment 1, we examined what effect (if any) a human feeder had on the vocalizations uttered by crows in the presence of

food. For the feeder-present trials ($N = 37$ sites), we observed crows as described in the Methods. For the feeder-absent trials ($N = 18$ sites), we surreptitiously left the peanut treatment at the site while the crows were absent, then retreated >20 m away and waited for the crows to return and discover the food. Unlike in the feeder treatment trials, we could not control when the food was discovered, so the nonfeeder treatment omitted the prestimulus phase and began the trial when a crow arrived at the peanut pile at the start of the stimulus phase (Fig. A4).

During the stimulus phase, none of our measured variables were significantly affected by the presence or absence of a human feeder

(Fig. A5). When we examined both feeder presence and food amount simultaneously, the only measure significantly affected by feeder presence was the call duration during the 5-peanut treatment: crows uttered calls that were significantly shorter when a feeder was present ($z = 3.58$, $P = 0.005$; Fig. A6d). As this difference was not present for the larger 25-peanut treatment or the smaller 1-peanut treatment, we do not believe this to be indicative of any larger trend in crow behaviour. These results suggest that human presence does not significantly shift the costs or benefits to vocalizing around food.

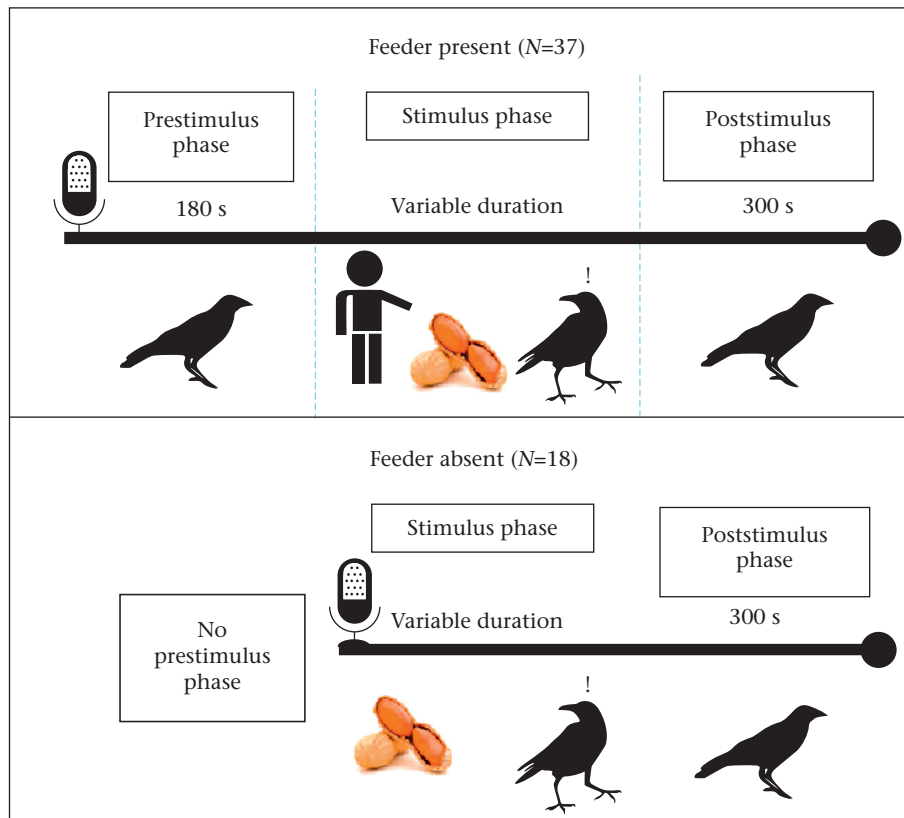


Figure A4. Illustration of the separate phases of a single trial from the feeder present treatment and feeder absent treatment of experiment 1.

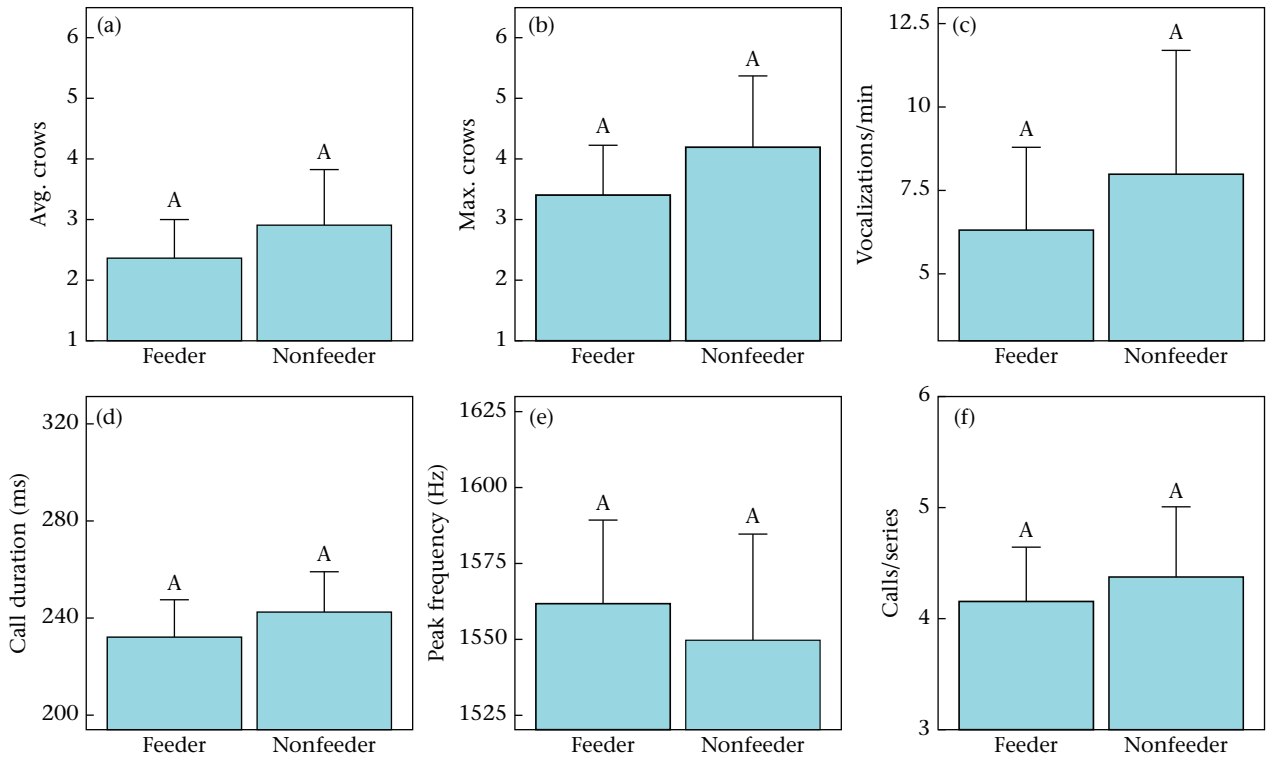


Figure A5. Mean response + 95% confidence interval for the changes in (a–c) crow behaviour and (d–f) microstructure of calls uttered during the stimulus phase for both feeder treatments of experiment 1. Data include all three peanut treatments. Different letters indicate significantly distinct groups after Holm corrections to the *P* value.

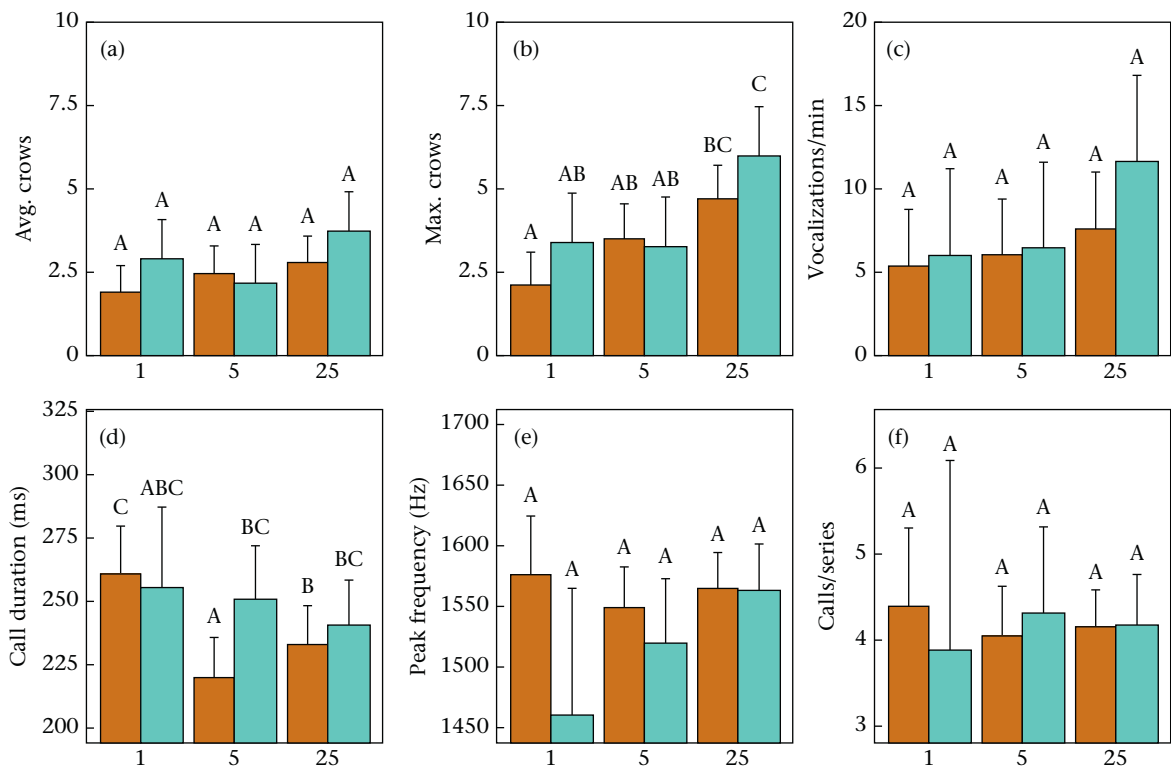


Figure A6. Mean response + 95% confidence interval for the changes in (a–c) crow behaviour and (d–f) microstructure of calls uttered for the two feeder treatments (■: feeder; ■: nonfeeder) and three peanut treatments (X axis) during the stimulus phase of experiment 1. Different letters indicate significantly distinct groups after Holm corrections to the *P* value.

Appendix 3

Identifying Group Calls Using Linear Discriminant Analysis

Prior to selecting stimulus calls for experiment 2, we attempted to use linear discriminant analysis to identify distinct call groups. From the vocalizations we recorded during experiment 1, we used Raven to obtain the following measures: call duration (ms), Q1 time (ms), centre time (ms), Q3 time (ms), peak frequency (Hz), Q1 frequency (Hz), centre frequency (Hz) and Q3 frequency (Hz) (Fig. A7). From these measurements, we calculated the following: intercall duration (ms), call group size and call group structure (see Table A1 for definitions). We calculated the linear discriminants using R package MASS (Venables & Ripley, 2002) and grouped the calls into four groups: (1) nonfeeder with 1 or 5 peanuts, (2) nonfeeder with 25 peanuts, (3) feeder with 1 or 5 peanuts and (4)

feeder with 25 peanuts. However, we found no call clusters in the linear discriminant analysis (see Table A2, Fig. A8).

Our inability to find any distinct cluster of call types for each combination of feeder/nonfeeder and big peanut pile/small peanut pile suggests that rather than being grouped into distinct call types, there is a continuous gradient in the various microstructure measures of the calls. This would allow crows to include additional information in their vocalizations (such as the ID and emotional state of the caller), albeit at the cost of lower message clarity over a long distance. Mates et al. (2015) also applied a linear discriminant analysis to a range of crow calls using additional information that we did not have access to (such as the sex and age of the calling bird) and came to the same conclusion: crow calls lie along a gradient rather than clustering into distinct categories.

Table A1

The microstructure measures obtained from the vocalizations recorded during experiment 1

Measure	Source	Description
Call duration (delta time)	Raven 1.5	Difference between the end time and begin time of the call. Units: ms
Q1 time	Raven 1.5	The point in time that divides the call into two time intervals containing 25% and 75% of the energy in the call. Units: ms
Centre time	Raven 1.5	The point in time at which the call is divided into two time intervals of equal energy. Units: ms
Q3 time	Raven 1.5	The point in time that divides the call into two time intervals containing 75% and 25% of the energy in the call. Units: ms
Peak frequency	Raven 1.5	The frequency at which maximum power occurs within the call. Units: Hz
Q1 frequency	Raven 1.5	The frequency that divides the call into two frequency intervals containing 25% and 75% of the energy in the call. Units: Hz
Centre frequency	Raven 1.5	The frequency that divides the call into two frequency intervals of equal energy. Units: Hz
Q3 frequency	Raven 1.5	The frequency that divides the call into two frequency intervals containing 75% and 25% of the energy in the call. Units: Hz
Intercall duration ^a	Calculated outside Raven 1.5	The difference between the end time of the current call and the start time of the next call in the call group. For the last call in the group, we used the difference between the start time of the current call and the end time of the last call. Not calculated for single calls. Units: ms
Calls per series ^b	Calculated outside Raven 1.5	The number of calls uttered in a series. A series was defined as every call given in sequence where the intercall duration was <1 for every call
Call group structure ^b	Calculated outside Raven 1.5	Determined if the calls in a group were part of a structured or unstructured call series. A group was considered structured if the group size was 2–9, and the crow gave no other calls within 1–3 s of the group

^a Because this measure does not include single calls that were not given as part of a group, we only used group calls when we included this measure in the analysis.

^b Because these measures repeated themselves for all calls within a group, we avoided oversampling by selecting a single call representative from each group when we included these measures in an analysis.

Table A2

List of linear discriminants for comparing the microstructure of the calls recorded during experiment 1

	LD1	LD2	LD3
Call duration	-1.296694e+01	1.365221e+01	1.108168e+01
Peak frequency	2.474165e-03	-7.973150e-04	-3.725272e-04
Q1 frequency	1.121876e-03	-1.982003e-03	9.125681e-04
Center frequency	-9.255083e-06	6.048770e-04	-4.872355e-03
Q3 frequency	-2.636972e-03	-2.956281e-04	1.642923e-03
Q1 time	-4.439718e+00	4.013079e+01	-8.727711e+01
Centre time	-2.999954e+01	-4.604220e+01	8.113566e+01
Q3 time	4.249340e+01	6.579070e 00	-3.624945e+01
Intercall duration	1.683797e+00	2.745707e-01	2.753520e+00
Group size	2.123371e-02	4.724381e-02	-1.191016e-02
Group structure	-1.970522e-01	-1.107054e+00	9.677253e-01

The groups used were (1) nonfeeder with 1 or 5 peanuts, (2) nonfeeder with 25 peanuts, (3) feeder with 1 or 5 peanuts, (4) feeder with 25 peanuts.

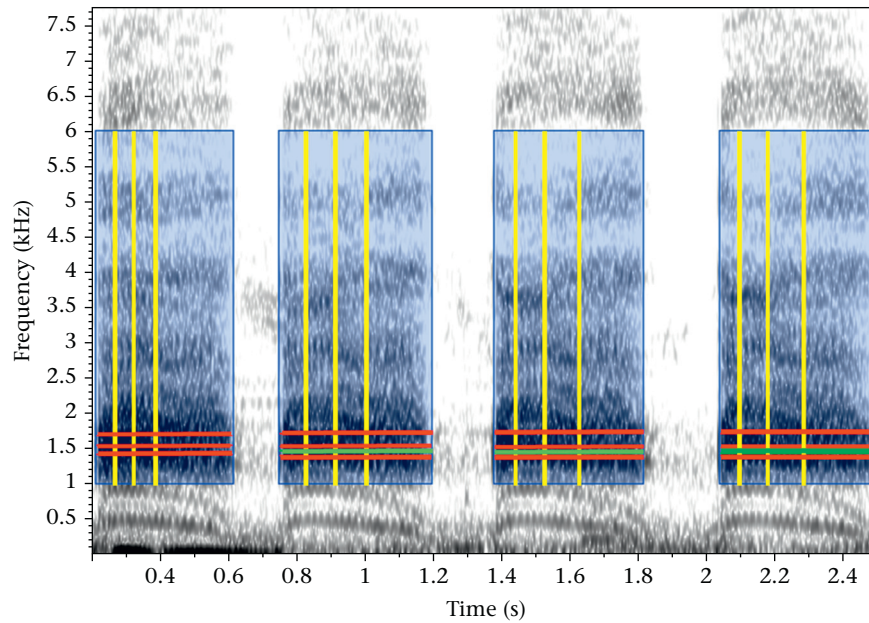


Figure A7. Example of spectrogram with selections around each valid vocalization. The calls featured here are medium stimulus calls. All the following measurements are calculated from the sound energy within the blue area (1–6 kHz and call duration): the vertical yellow lines are (from left to right) the Q1 time, centre time and Q3 time; the horizontal red lines are (from bottom to top) Q1 frequency, centre frequency and Q3 frequency; and the horizontal green line is the peak frequency (obscured by Q1 frequency in some selections). See [Table A1](#) for definitions of each measure.

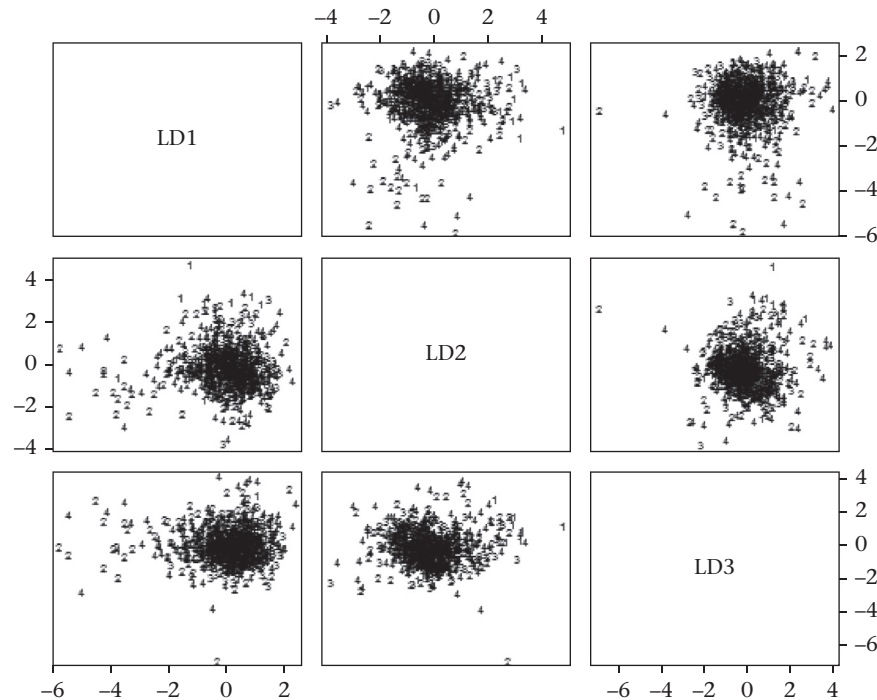


Figure A8. Plot of the clusters formed using linear discriminant analysis on the 11 microstructure measures from each vocalization recorded during experiment 1. No clusters or trends formed around any of the groups. The groups used were (1) nonfeeder with 1 or 5 peanuts, (2) nonfeeder with 25 peanuts, (3) feeder with 1 or 5 peanuts, (4) feeder with 25 peanuts.

Appendix 4

Finding Variable Correlation Using Factor Analysis

Because we compared many variables, there was a possibility that some of them may be correlated with each other. We used R package ‘psych’ (Revelle, 2018) to perform factor analyses on the tested variables for all experiments.

We measured six variables in experiment 1 (average number of crows present throughout the phase, maximum number of crows present during the phase, call rate throughout the phase, mean call duration, mean peak frequency and mean number of calls per series). However, we could not simultaneously include all six vari-

do not fit into the factors neatly. Additionally, both factors combined only accounted for 41% of the observed variability. Therefore, we must conclude that there is minimal correlation among the six behaviour variables compared in experiment 2.

We measured three variables in experiment 3 (likelihood of food discovery, time to food discovery and maximum number of crows present at the food). However, we could not directly compare likelihood of food discovery to the other two variables, as it used data from all trials ($N = 29$), whereas the other variables were pulled only from the trials where crows successfully discovered food ($N = 11$). Factor analyses failed to account for any variation ($\text{fit} = 0$) between the time to food discovery and the maximum number of crows at the food.

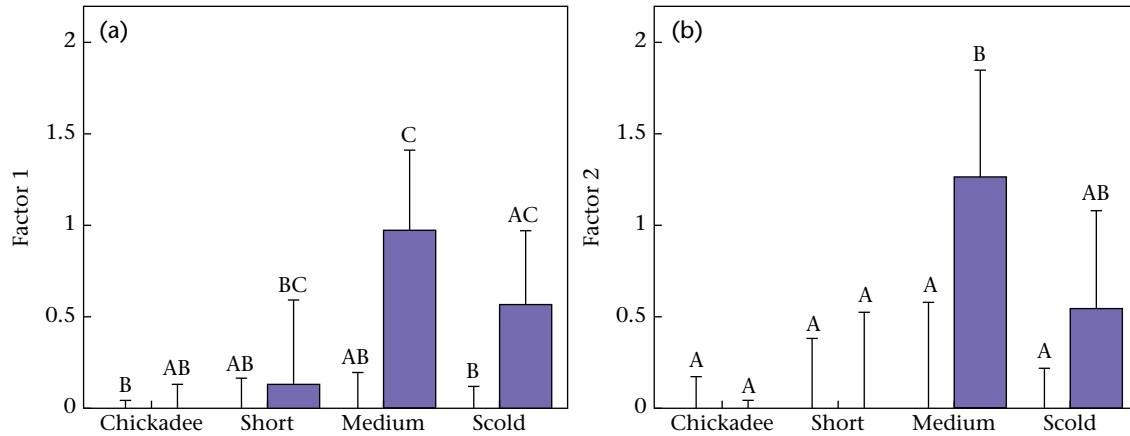


Figure A9. Mean response + 95% confidence interval for the effect each playback stimulus had on (a) factor 1 and (b) factor 2 during the prestimulus and stimulus phases of experiment 2. Different letters indicate significantly distinct groups after Holm corrections to the P value.

ables in a single factor analysis as the call microstructure variables (call duration, peak frequency and calls per series) were calculated using all the vocalizations throughout experiment 1 ($N = 2085$), while the crow behaviour variables (average and maximum number of crows and call rate) were calculated as a rate for each phase ($N = 522$). Factor analyses failed to account for any variation ($\text{fit} = 0$) for both the three call microstructure variables and the three crow behaviour variables.

We measured six behaviour variables (average number of crows present, presence of vocalizations, flight, speaker proximity, dominance posturing and wing/tail flicking) and three call microstructure variables (call duration, peak frequency and calls per series) in experiment 2. As in experiment 1, we could not directly compare the behaviour variables and the microstructure variables in a single factor analysis, as they were calculated differently (behaviour: $N = 166$; call microstructure: $N = 880$). The factor analysis failed to account for any variation ($\text{fit} = 0$) for the three call microstructure variables. We were able to account for some variation among the six behaviour variables using a factor analysis with two factors (see Table A3). However, rerunning the experiment 2 analysis using the two factors instead of the six individual variables did not reveal any additional trends compared to the six stand-alone variables (compare Fig. A9 to Fig. 5), probably because only a single variable (flight) had a uniqueness score < 0.1 while four variables had a uniqueness score > 0.5 (Table A4), suggesting they

Table A3

The factor loadings for a factor analysis combining the six behaviour variables from experiment 2 into two factors

Variable	Factor 1	Factor 2
Average no. of adults		0.115
Vocalizations	0.434	0.450
Flight	0.996	
Speaker proximity	0.248	0.613
Dominance posture	0.332	
Wing/tail flicking	0.513	0.498

Table A4

Uniqueness scores for a factor analysis combining the six behaviour variables from experiment 2 into two factors

Variable	Uniqueness
Average no. of adults	0.986
Vocalizations	0.609
Flight	0.005
Speaker proximity	0.563
Dominance posture	0.889
Wing/tail flicking	0.488

Appendix 5

Effect of Stimulus Calling Rate on Behaviour

During experiments 2 and 3 we standardized all stimulus calls so that the entire audio track would play within a single 10 s interval. To fulfil this criterion, we edited the original audio recordings of the short and medium calls so that they would play two or three call series within 10 s. However, because short call series contained more vocalizations than did medium call series (short calls: 4.62 ± 0.11 calls/series; medium calls: 2.57 ± 0.08 calls/series), the call rate of the short stimulus tracks was significantly higher than that of the medium stimulus tracks (short: $\bar{X} \pm SE = 13.50 \pm 0.67$ vocalizations/10 s; medium: 8.24 ± 0.93 ; t test: $t_{31} = -5.64$, $P < 0.001$), but not the scold stimulus tracks (short: 13.50 ± 0.67 ; scold: 13.10 ± 0.90 ; $t_{34} = -0.45$, $P = 0.658$). Since call rate can indicate the urgency of danger-associated calls

(Chamberlain & Cornwell, 1971; Richards & Thompson, 1978; Yorzinski & Vehrencamp, 2009), it is possible that the crows' response to the various stimuli was due to the call rate of the stimulus call, rather than the call duration.

We pulled a subset of the experiment 2 behaviour data where the stimulus tracks contained the same number of calls (either 9, 10 or 12 total vocalizations, see Table A5) and reran the analysis using this subset. Compared to the results we obtained using the full data set, the only change to the significant findings was that medium calls no longer caused a significant increase in dominance posturing (prestimulus: $\bar{X} \pm SE = 0.00 \pm 0.00$ intervals; stimulus: 0.33 ± 0.24 intervals; $z = 1.46$, $P = 1$; Fig. A10e). All other significant findings remained the same as those reported using the entire data set.

This demonstrates that the response by our focal crows was primarily due to the structure and duration of our stimulus calls, rather than the rate at which they were played.

Table A5

The total number of stimulus tracks containing X total vocalizations within the 10 s audio track

Total individual vocalizations present in stimulus track	5	6	7	8	9	10	11	12	13	14	15	16	17	18	22
No. of medium stimulus tracks	2	1	1	4	7	1		1							
No. of scold stimulus tracks					2	2	1	7	1	2	1	1	1	1	1
No. of short stimulus tracks					2	1		3	1	2	5				2

Each stimulus track was used only at the location where it was recorded.

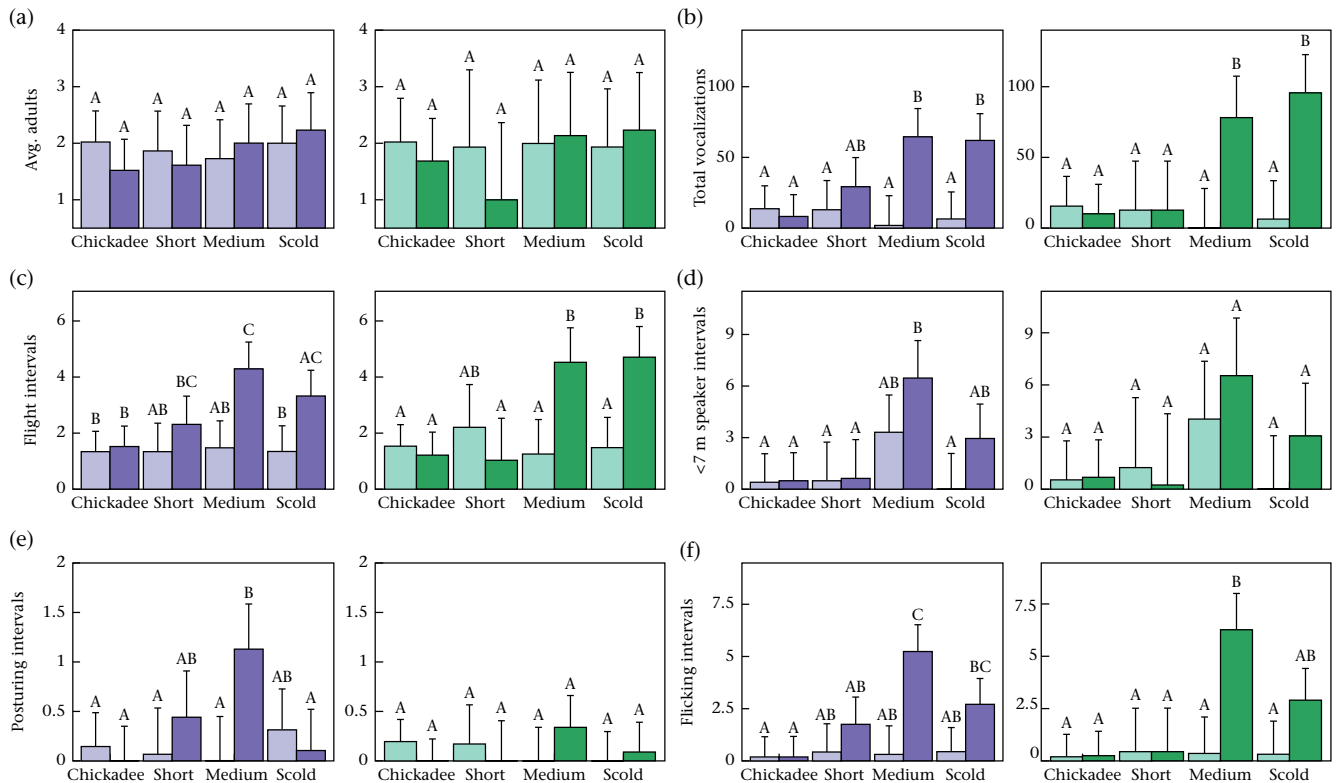


Figure A10. Mean response + 95% confidence interval for the behaviours observed during the prestimulus (light colours) and stimulus (dark colours) phases of experiment 2. The charts are paired: purple uses data from the entire data set; green uses a subset of data where the conspecific stimulus calls contained either 9, 10 or 12 vocalizations (and their accompanying chickadee control). Different letters indicate significantly distinct groups after Holm corrections to the P value.