Food amount affects the vocalizations around and possibly recruitment to a food source by American crows

Loma Pendergraft

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Committee:
John Marzluff
Donna Cross
David Perkel

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University of Washington

Abstract

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LomaJohn T Pendergraft

Chair of the Supervisory Committee:

Dr. John Marzluff

School of Environmental and Forest Sciences

While many non-human vertebrates share food, active recruitment to a food source is rare and limited to social species that benefit from having additional conspecifics at the food source. Here I demonstrate that wild American crows (*Corvus brachyrhynchos*) change the qualities of their calls around large food sources, but these changes did not appear to increase the number of crows present at the food bonanza. The crows near a large food windfall gave shorter calls compared to their vocalizations around a small amount of food (especially if they saw a human produce the food), and playback of those short calls did not prompt an aggressive response from listening crows. In contrast, the calls given before the appearance of food had a longer duration, and playback of those longer calls elicited behaviors from the listening crows associated with aggression and territory defense. These findings suggest that crows might be recruiting allies to food sources that are highly conspicuous, either from the large number of food items or from the visibility of the human source. Taken altogether, this study provides important insights into the importance that crows place on human behavior, possibly an adaptation from generations spent living in human-dominated landscapes.

INTRODUCTION

Food sharing is broadly defined by Stevens & Gilby (2004) as occurring when "an individual can defend a food item but allows another individual to consume part of the item" and "includes both passive (tolerated theft) and active sharing (facilitated transfer, food recruitment)." While many non-human species share food (Stevens & Gilby 2004), far fewer species (aside from eusocial insects, see Wilson 1971) actively signal the location of food to others. Such recruitment may be rare because it will only persist in a population if the benefits of recruiting additional conspecifics to a food source outweigh the cost of increased depletion of said food source. For example, cliff swallows (*Petrochelidon pyrrhonota*) only give a unique squeak call to recruit conspecifics to a newly discovered insect swarm when foraging conditions are poor, as a flock can better track the swarm's movements thus prolonging the time the caller can exploit the swarm (Brown et al. 1991). The fitness benefits to the caller are further increased if the recruited conspecifics are kin, as predicted by kin selection theory (Eberhard 1975), therefore active food recruitment is more likely to occur in social species that live in groups containing one or more family members than in solitary species or those living in groups of unrelated individuals.

Members of the Corvidae family (aka corvids: crows, ravens, magpies, and jays) are social songbirds that communicate using a wide variety of calls (Marzluff and Angell 2005). Most corvids share food among mates, both as a matter of courtship and to reinforce the pair-bond (De Kort et al. 2006, Clayton & Emery 2007, Ostojić et al. 2013). Despite the prevalence of food sharing, little is known about whether they actively utilize a signal to recruit conspecifics to food. Perhaps the most well-known case of food recruitment among corvids is the behavior of the common raven (*Corvus corax*); vagrant ravens that discover an animal carcass usually cannot approach due to the resident territorial adults, so they lead conspecifics from a roost to the food site in order to overwhelm the territorial pair's ability to defend it, although the mechanism by which they recruit others is presently unclear (Heinrich et al. 1993, Marzluff et al. 1996).

American crows (*Corvus brachyrhynchos*) are territorial corvids that share food between mates and related helpers on their territory (Kilham 1990), but it is unclear whether they actively recruit family members to a food source, or simply tolerate each other's presence after they independently arrive at the same food patch. This ambiguity is due to the difficulty of classifying the typical crow vocalizations (known as caws), which show significant variation in duration and cadence, alongside rapid oscillations in pitch (referred to as frequency for the remainder of this paper) and amplitude (Laiolo & Rolando 2003). American crows can signal the presence of a dangerous or novel predator (Richards & Thompson 1978, Marzluff et al. 2010), a dead conspecific (Swift & Marzluff 2015), their ownership / boundaries of a territory (Parr 1997), and beg for food (Chamberlain & Cornwell 1971) using caws with varying acoustic properties. Because of the difficulty distinguishing between caws, most authors who study crow communication focus on the structural parameters of the calls when sorting them, such as call duration, harmonic frequency (pitch), the number of calls given in sequential order, and whether a group of calls are given in a structured or unstructured sequence (Chamberlain & Cornwell 1971, Parr 1997, Tarter 2008).

American crows have also lived alongside humans for hundreds of generations, and have become unusually sensitive to human behavior as a result (Marzluff & Angell 2005). While they are especially attentive towards the danger that humans can pose, such as actively avoiding humans in areas where it is legal to shoot crows (Knight et al. 1987) or learning the faces of dangerous people after a single unpleasant event and remembering those individuals for long periods of time (Swift & Marzluff 2015, Marzluff et al. 2010), crows are also highly receptive towards friendly humans, and can form lasting relationships with the people who feed them (Marzluff & Miller 2014). Crows that have regularly been fed by humans will gather in large numbers around a recognized crow feeder, and will continue to follow the feeder for some distance, occasionally ignoring the territorial boundaries of other crows as they do so (Marzluff & Miller 2014). This demonstrates that crows alter their behavior to better take advantage of a human feeder, therefore any study on food recruitment must address the additional variable of human feeder presence.

To test whether American crows vocally recruit conspecifics to a food source, I conducted two experiments on wild crows. In Experiment 1, I asked: (i) what types of calls do crows give in response to finding food, and (ii) does the size of the food bonanza or the presence of a human feeder affect the calls given by the feeding crows? If crows do recruit conspecifics to a food source, I hypothesized that they will do so when they encounter a food source too large or conspicuous for a single crow to monopolize. For Experiment 2, I recorded how wild crows responded to playback of select calls from Experiment 1, and compared my observations with a set of predictions built around three possible reasons for a crow to vocalize: i) ally recruitment, ii) territory defense, or iii) danger warning. If crows utilize a specific vocalization to recruit allies, I hypothesized that they 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 defense or to signify dominance, then I hypothesized that the listening crows would interpret the playback as a challenge, and respond with aggressive displays, type-matching vocalizations, and attempts to locate the speaker. Finally, if the focal crows responded to the stimulus call by forming a mob (gathering in large numbers, vocalizing heavily, spending much time in flight, and displaying signs of agitation, but not aggression), that would match my prediction for how the crows would behave if the call is used to warn of danger.

METHODS

Experiment 1: Crow Behavioral Response to Food

I tested how crows responded to a human feeder (referred to as the Feeder Treatment in the remainder of this paper) at 36 locations in and around Seattle, Washington (47°N, -122°W) from late April to early July 2015, with additional supplemental data collected at 5 locations during January 2016 (**Fig. 1**). I arrived at a site between 0530 and 1200, and recorded the number of crows present, their vocalizations, and their arrival at/departure from the site across time. I visited each site three times and fed the crows either a small (1), moderate (5), or large (25) number of peanuts as a stimulus. Every site received all three food treatments, with treatment order balanced across all sites and >2 days separating each treatment.

The feeder treatment for Experiment 1 consisted of 3 phases (**Fig. 2A**). Prior to feeding (Phase 1) I observed for 3 minutes. If the crows left the site during this time, I aborted the trial and started over after relocating them. Once I tossed the predetermined peanut amount on the ground in full view of the crows (Phase 2), I observed until the crows had consumed all the peanuts. If all the crows left the site during this time, I waited for them to return. If no crow had returned after 5 minutes, or if the crows had consumed all the peanuts at the site, I removed any remaining peanuts and observed the site for an additional 5 minutes (Phase 3), regardless of whether the crows were present. The duration of Phase 2 ranged from 10 seconds to 1350 seconds; to avoid biasing my data in favor of the longer trial durations, I converted the total vocalizations to vocalizations per minute, and total crow visits to average crows present throughout each phase and maximum number of crows present at any one time during each phase. Because I compared 3 behavioral response variables for each treatment, my risk of committing Type I error increases to 15% if I did not compensate for the multiple comparisons, so I applied Holm-Bonferroni corrections to my post-hoc tests.

In addition to recording how crows responded to food provided by a human feeder, I also measured crow response to finding food without a human feeder present (hereby referred to as the Nonfeeder Treatment). I collected data for the nonfeeder treatment trials between 0400 and 0530 at 6 sites from late April to early July 2015, with additional supplemental data collected at 3 locations during January 2016 and 6 locations during April and May 2016 (**Fig. 1**). These trials were identical to the feeder treatment Experiment 1 trials, except instead of conspicuously presenting the peanut treatment in full view of the crows, I surreptitiously left the peanut treatment in a conspicuous place while the crows were absent from the site, then retreated at least 20 m and waited for the crows to return and discover the peanuts (**Fig. 2B**). Unlike in the feeder treatment trials, I could not control when the peanut pile was discovered, so for the nonfeeder treatment, I omitted the Pre-stimulus phase (Phase 1) and started the trial with the Stimulus Phase (Phase 2) when a crow arrived at the peanut pile.

Acoustic Sampling

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

Acoustic Analysis

I converted all MP3 audio files to WAV format with AudioDirector 5 (CyberLink Corp 2014), then used Raven 1.5 (Bioacoustics Research Program 2014) to convert the recordings into spectrograms (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, I measured the microstructure of each call by creating a selection around every individual call on a spectrogram. Every selection was bounded by the start and stop times of the call, with a set lower and upper boundary of 1000-6000 Hz (**Fig. 3**). I removed every selection with excessive background noise or any overlap with an adjacent selection (e.g. multiple crows calling simultaneously). Within every remaining selection, Raven 1.5 obtained the following measures: Call duration (msec), Q1 Time (msec), Center Time (msec), Q3 Time (msec), Peak Frequency (Hz), Q1 Frequency (Hz), Center Frequency (Hz), and Q3 Frequency (Hz). From those measurements, I calculated the following: inter-call duration (msec), call group size, and call group structure (see **Table 1** for definitions). I used those 11 microstructure measures in conjunction with linear discriminant analysis to look for distinct groupings in the vocalizations I recorded in Experiment 1.

Experiment 2: Crow Behavioral Response to Call Playback

I tested how crows responded to hearing conspecific calls from early June to late July 2016 at 32 of the sites that I used in Experiment 1 (**Fig. 4**). Because I found no distinct call types in Experiment 1 (see results), I decided to select stimulus calls that varied in call duration; previous studies have used call duration as a major component in sorting crow calls (Parr 1997, Tarter 2008). I selected 2 different call types to be used as stimulus calls: i) structured calls with a duration between 75-200 msec (Short calls), and ii) structured calls with a duration between 300-425 msec (Medium Calls); calls with those durations are on opposite ends of the call duration distribution and share the same range in duration (**Fig. 5**). In addition to the 2 stimulus calls, I included black-capped chickadee (*Poecile atricapillus*) calls to ensure crows are reacting only to conspecific vocalizations, and scold calls (unstructured crow calls with a peak frequency > 1500 Hz) as a conspecific control to ensure that the crows were reacting appropriately to a stimulus call's context. Specifically, unstructured calls signify danger (Parr 1997), and crows predictably respond by gathering around the source of the calls, giving their own unstructured scold calls, and divebombing any predator they find at the location (Swift & Marzluff 2016, Yorzinski et al. 2006). I selected exemplars of these calls from the audio recordings I obtained from Experiment 1 and edited them into 10-second segments. The Short and Medium stimulus tracks contained at least 2 full sets of structured calls, while the Scold control tracks contained at least 8 individual vocalizations (see **Fig. 6** for a comparison of the microstructural measures of the conspecific stimulus calls). To control for crows responding with aggression because they don't recognize the caller and to increase the number of exemplars tested, I used stimulus calls only at the location where they were originally recorded.

I arrived at a site between 0630 and 1300 and set up my speaker within 33 m of any crows I could locate. I tried to place the speaker near a tree or shrub, ideally so it would appear to the focal crow that the stimulus calls were coming from a perched bird hidden by foliage. Once I set up the speaker, I 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, I packed up the speaker, re-located the birds, and set up again nearby (N=12). Experiment 2 consisted of 2 phases; the pre-stimulus phase and the stimulus phase, both of which lasted for 5 minutes.

During the pre-stimulus phase, I collected baseline behavioral and vocal data without using a stimulus. During the stimulus phase, I played the 10-second stimulus track once every minute while simultaneously collecting vocal and behavioral data (**Fig. 7**). I collected data for both phases using the following schedule: 10 seconds of stimulus (during the pre-stimulus phase, nothing occurred during this time), followed by 50 seconds of focal following (divided into five 10-second intervals). I repeated this procedure for the duration of the phase. I set my watch to emit a quiet "beep" every 10 seconds to keep track of intervals in the field.

During the focal follow intervals, I focused my attention on the crow that was closest to the speaker and recorded whether the focal crow performed any of the following behaviors during each interval: flight, close proximity (<7 m) to speaker, dominance posturing, and wing/tail flicking (see **Table 2** for descriptions and significance). Because my goal was to use the change in prevalence of those behaviors to discern the meaning behind different stimulus calls, I treated each behavior as an "event", rather than a "state", and recorded the presence or absence of each behavior from the focal crow throughout each 10-second interval (Altman 1974). I defined the focal crow as whichever crow was closest to the speaker at the start of the current interval. In addition to those 4 behaviors, I also recorded the total number of adult crows within 33 m of the speaker during the interval, and the total vocalizations given by the focal crow per interval. Because I compared 6 behavioral response variables for each treatment, my risk of committing Type I error would have increased to 30% if I had used $\alpha=0.05$ as my critical value. To avoid this, I applied Bonferroni correction to my critical value (I used $\alpha=0.0083$ as the critical value for these behavioral response tests) and used Holm-Bonferroni corrections for my post-hoc tests.

Acoustic Sampling and Playback

I recorded and processed the vocal responses of crows as in Experiment 1. Additionally, I used a Pignose 7-100 Legendary portable amplifier to play the stimulus calls during the playback phase. I recorded the presence/absence of each behavior by the focal crow on a clipboard. The speaker was connected to a wrist-mounted mp3 player with a 33 m audio cable.

Selection and Categorization of Study Sites

I utilized a total of 55 sites in and around Seattle, WA, for my two experiments. I chose a location to be a field site if I witnessed regular crow and human activity at that location. The field sites consisted of public parks, residential neighborhoods, and parking lots, and every site was at least 150 m away from any nearby sites (see **Fig. 1** and **Fig. 4**). In Seattle, crows rarely travel more than 90 m in response to scolding calls which are highly attractive (Swift 2015).

When I visited a site, I wore 1 of 6 different disguises to prevent the crows from recognizing me on return visits (**Appendix 1**). I also attached a white sign to my clipboard that read “UW CROW STUDY” to deter interference by pedestrians or the police. When I located crows on a site, I approached to within 10-25 m and began the experiment. I avoided flushing the crows while collecting data by remaining at least 10 m away from the nearest bird and avoiding direct gaze (Clucas et al. 2013). If I could not locate any crows, I moved on to another site and returned later in the day.

Statistical Analysis

I conducted all statistical analysis using RStudio version 1.0.136. For both Experiment 1 and Experiment 2, I used Welch two sample t-tests (when sample size was <30) and two-sample

Z-tests (when sample size was >30) from a linear mixed model with location as a random effect to compare the effect that each treatment had on the crow behavior and call microstructure. Because I used a linear mixed model, the t-tests used Satterthwaite approximations to estimate degrees of freedom. The linear mixed models were computed by R package lme4 (Bates et al. 2015), while the Satterthwaite approximations were calculated by R package lmertest (Kuznetsova et al 2016). I used R package MASS (Venables & Ripley 2002) to calculate the linear discriminants and conduct the linear discriminant analysis on all the vocalizations' microstructures. The post-hoc comparisons were done using a Tukey Honest Significant Difference test after first applying Holm-Bonferroni corrections to account for the higher likelihood of committing type I error with multiple comparisons. Because I used a linear mixed model, I used R package multcomp (Hothorn et al 2008) to perform the Tukey HSD test and apply Holm-Bonferroni corrections.

RESULTS

Experiment 1: Crow Behavioral Response to Food

Description of Behavioral Response to Experiment Phases

When I first arrived at a site, but before I provided food (Phase 1), the crows were usually pre-occupied with ground foraging 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 (Avg. crows: mean (SE) = 2.31 (0.16), Max crows: 2.93 (0.19)). After the crows became aware that peanuts were present (Phase 2), either by seeing me toss peanuts on the ground or independently discovering the pre-planted peanut pile, they usually responded by flying to the pile and either eating peanuts at the pile, caching peanuts in the immediate vicinity, or grabbing 1-2 peanuts and departing. During this phase, more crows visited the site and the maximum number of crows present increased (z=2.54, P=0.034), as did the average crows present and the call rate, though not significantly so (**Fig. 8**). The crows that were present during this phase uttered calls that were significantly shorter in duration compared to the calls given prior to food's appearance (z = -17.8, P<0.001) (**Fig. 9**). After all the peanuts were consumed (Phase 3), the visiting crows usually left promptly or were chased out by the residential crows, that would return to their previous activities after searching the area for peanut scraps; the call rate and avg. number of crows present both returned to their pre-stimulus levels, whereas the max number of crows present remained high (**Fig. 8**). Compared to the vocalizations given while food was present, the duration of the calls uttered after all the food was consumed increased, although not to their pre-stimulus state (z =9.01, P<0.001) (**Fig. 9**). Additionally, the peak frequency of the calls uttered increased slightly during each phase, to the point that the calls given during Phase 3 were significantly higher in pitch than the calls uttered during Phase 1 (z=3.25, P=0.0035) (**Fig. 9**). The number of vocalizations per call group and proportion of calls given in a structured sequence did not notably change between each phase (**Fig. 9**).

The Effect of Peanut and Feeder Treatment on Crow Behavior

In general, the larger peanut treatments attracted more crows to a site than the smaller peanut treatments; the maximum number of crows to arrive at site with a large peanut treatment (25 peanuts) was significantly greater than the number that arrived for the small peanut treatment (1 peanut) for both the feeder (z=4.89, P<0.001) and nonfeeder (z=3.35, P=0.009) treatments (**Fig. 10**). While the vocalization rate was unaffected by peanut treatment (although it tended to be slightly higher for the nonfeeder treatment, see **Fig. 10**), the calls that were uttered had a shorter duration (Feeder treatment: z= -10.12, P<0.001; Nonfeeder treatment: z= -2.83, P=0.029) when there were many peanuts present (**Fig. 11**). The number of vocalizations given in each call group did not significantly change between treatments, and while the peak frequency and proportion of calls given in a structured sequence did, those differences followed no clear pattern with regards to increasing peanut treatment or distinct feeder effects (**Fig. 11**). While there were some minor differences between the feeder and nonfeeder treatments of the Food Response Experiment, the only significant difference between them was the duration of the calls uttered during the 25-peanut treatment: they were shorter for the feeder treatment than for the nonfeeder treatment (z=5.09, P<0.001) (**Fig. 11**). I found no call clusters in the linear discriminant analysis of the 11 microstructure measures I obtained from the Food Response Experiment vocalizations (See **Appendix 6** and **Appendix 7**).

Experiment 2: Crow Behavioral Response to Call Playback

Description of Pre-stimulus Phase Behaviors

As in the Food Response Experiment, when I arrived at a site, but before I played any stimulus calls (Pre-stimulus phase), most crows were preoccupied with ground foraging or vocalizing from perched positions. Most locations had only one or two crows present (mean (SE) = 1.93 (0.18) adults within 33 m of speaker), and they vocalized only occasionally (mean (SE) = 9.28 (3.15) vocalizations / 5 minutes). Of the behaviors I observed during each interval, flight was the most common (mean (SE) = 1.35 (0.15) flight intervals / 25 intervals total). The crows appeared neither afraid of nor interested in the speaker, as they occasionally walked near it but did not actively inspect it (mean (SE) = 0.89 (0.38) intervals <7 m from speaker / 25 intervals total). I rarely observed an occasional dominance posture and wing/tail flick during the pre-stimulus phases (Dominance Posture: mean (SE) = 0.13 (0.07) intervals/25 total; Wing/Tail Flicking: 0.28 (0.07) intervals/25 total). The crows responded to audio playback with varying degrees of intensity (see below for details), but they appeared to treat the stimulus calls as if a nearby bird was vocalizing.

Behavioral Response to Structured Short Stimulus Calls

The crows that were exposed to the short stimulus calls slightly increased the number of vocalizations uttered (z=1.27, P=1.0), time spent in flight (z=1.40, P=1.0), dominance posturing (z=1.13, P=1.0), and wing/tail flicking (z=1.41, P=1.0) compared to their pre-stimulus state (see **Fig. 12** and **Fig. 13**). Between the short call treatment and the control treatment, the change in mean from the pre-stimulus to the stimulus phase did not significantly differ for any of the six observed behaviors. (**Table 3**). While the duration of the calls did not change from the pre-stimulus to the stimulus phase, the peak frequency of the calls became significantly higher in pitch (z=4.81, P<0.001), as did the number of vocalizations given per call group (z=3.74, P=0.005) (**Fig. 14**). The crows were also slightly more likely to call in a structured sequence after hearing the short stimulus calls, though not significantly so (z=2.38, P=0.35) (**Fig. 14**). 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 resemble the stimulus calls' duration (Stimulus: mean (SE) = 191 (3.0) msec; Observed: 213 (3.6) msec), peak frequency (Stimulus: 1536 (28.8) Hz; Observed: 1493 (8.0) Hz), call group size (Stimulus: 4.62 (0.12) vocalizations/group; Observed: 4.27 (0.2) vocalizations/group), and call group structure (Stimulus: 0.91 (0.03) proportion structured; Observed: 0.82 (0.05) proportion structured) than do those vocalizations from the pre-stimulus phase (see **Appendix 2** and **Appendix 9**).

Behavioral Response to Structured Medium Stimulus Calls

Unlike the crows that were exposed to the short calls, those that received the medium call treatment responded with greater intensity. Crows that listened to the medium stimulus calls gave more vocalizations (z= 4.86, P<0.001) and spent more intervals in flight (z=4.24, P<0.001), dominance posturing (z=3.49, P=0.013), and wing/tail flicking (z=5.40, P<0.001) compared to their pre-stimulus behavior (see **Fig. 12** and **Fig. 13**). They also spent notably more time within 7 meters of the speaker, though this increase was not significant after applying Holm-Bonferroni corrections (z= 2.07, P=0.72) (**Fig. 13**). When comparing their change in behavior from the pre-stimulus phase to the stimulus phase; the crows in the medium call treatment significantly increased the number of vocalizations ($t_{64.8}$=4.19, P<0.001), time spent in flight ($t_{66.3}$=3.04, P=0.003), time spent in dominance posture ($t_{68.0}$=3.11, P=0.003), and time spent wing/tail flicking ($t_{61.6}$=4.24, P<0.001) compared to the changes observed during the chickadee control (**Table 3**). The increase in the number of crows present ($t_{56.4}$=1.88, P=0.065) and the time spent near the speaker ($t_{62.9}$=1.62, P=0.11) from the pre-stimulus to the stimulus phase for the medium call treatment were also marginally higher compared to the changes observed for the chickadee control (**Table 3**). Much as the crows responded to the short stimulus calls by giving more of their own short calls, the crows that heard the medium stimulus calls gave more medium calls: compared to the pre-stimulus phase, the stimulus phase vocalizations were significantly longer in duration (z=8.44, P<0.001) and somewhat lower in peak frequency (z= -1.77, P=0.38) (**Fig. 14**). These changes make the vocalizations observed during the stimulus phase more closely resemble the duration (Stimulus: mean (SE) = 359 (9.2) msec; Observed: 295 (2.3) msec) and peak frequency (Stimulus: 1528 (10.2) Hz; Observed: 1530 (2.8) Hz) of the medium stimulus calls than do their pre-stimulus counterparts (see **Appendix 2** and **Appendix 9**).

Behavioral Response to Unstructured (Scold) Stimulus Calls

When compared to the other stimulus calls, the crows that heard the 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 pre-stimulus behavior, the crows reacted to the scold calls by uttering more vocalizations (z=4.69, P<0.001) and flying around more often (z=3.25, P=0.025) (see **Fig. 12** and **Fig. 13**). They somewhat increased their time spent close to the speaker (z=2.09, P=0.72) and wing/tail flicking (z=2.76, P=0.11), but these increases were not significant (**Fig. 13**). When comparing their change in behavior from the pre-stimulus phase to the stimulus phase, the crows that received the scold treatment significantly increased the number of vocalizations uttered ($t_{62.4}$=3.95, P<0.001) compared to the changes observed during the control treatment; their time spent in flight ($t_{64.4}$=2.22, P=0.030) and time spent wing/tail flicking ($t_{59.2}$=2.18, P=0.033) also increased relative to the control treatment, but these changes were not considered significant at the Bonferroni adjusted critical value of 0.0083 (**Table 3**). The calls uttered during the stimulus phase had a shorter duration (x= -4.41, P<0.001) and were somewhat more likely to be given in an unstructured sequence (z=2.37, P=0.35) compared to the pre-stimulus vocalizations **(Fig. 14**).

Behavioral Response to the Chickadee Control Calls

Unlike the conspecific call treatments, when the crows listened to the chickadee control stimulus they did not significantly change any of their observed behaviors from the pre-stimulus to the stimulus phase, although there was a slight decrease in the number of crows present (see **Fig. 12** and **Fig. 13**). When testing the mean change in behavior from the pre-stimulus to the stimulus phase for the chickadee treatment against zero, the only behavior that somewhat differed from zero change was the number of crows present ($t_{67.9}$=-1.87, P=0.067) (**Table 3**). While the vocalizations given by the crows during the stimulus phase did not significantly differ from those given during the pre-stimulus phase, the call duration was somewhat lower (z= -2.31, P=0.10), the peak frequency was slightly higher (z=2.37, P=0.12), and the calls were marginally more likely to be structured (z=2.30, P=0.39) during the stimulus phase vs the pre-stimulus phase (**Fig. 14**).

DISCUSSION

Although food sharing is common among social vertebrates, especially between related individuals, active food recruitment is rarely observed because the costs of additional foragers at a food patch outweigh the benefits to the recruiting individual except in a few unique cases. In this study, I have provided evidence that American crows change the acoustic microstructure of their calls depending on aspects of a food source, but was unable to link those modified calls to the recruitment of additional allies. However, my study did demonstrate that those calls are not associated with territorial defense or fear, which would suggest that those short calls uttered around food could be contact calls between family members. My study also provided evidence that medium calls are used to advertise territories and signal aggression, unstructured calls are used to signify danger, and calls by crows are graded rather than clustered into distinct categories.

Ally Recruitment?

In the Food Response Experiment, I demonstrated that crows measurably change the quality of their calls in the presence of food, especially if there's more food than a single crow can quickly monopolize. Specifically, the duration of the individual vocalizations becomes shorter and the peak frequency rises in pitch. 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, e.g. 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 my findings that short calls are correlated with both a large food presence and an increase in the number of crows 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 intruders arriving at the site, rather than to recruit allies. I addressed this with a playback experiment.

In the Call Playback Experiment, I demonstrated that the focal crows do not behave aggressively in response to the short stimulus calls (at least when compared to the other treatments). The focal crows' change in behavior after hearing the short stimulus calls match 4 out of 6 predictions for the stimulus calls being associated with ally recruitment (no significant change in vocalizations, proximity to speaker, posturing, or flicking), whereas they met only 1 out of 6 predictions for territorial defense and 2 out of 6 predictions for danger warning (see **Table 2**). However, while the short calls did not elicit a major change to the listening crows' behavior, they did cause a marginal increase in vocalizations, flight, posturing, and flicking. This would suggest that the crows are reacting to short calls with some aggression, albeit only a mild amount when compared to their response to the medium and scold stimulus calls. Most of the vocalizations that the crows gave in response to hearing the short stimulus calls appeared to be their own short calls; their vocalizations became shorter in duration, they gave more calls per group, and they became more consistent in giving calls in structured groups compared to before the stimulus. In most songbirds, type matching during counter-singing signals aggressive escalation (Searcy & Beecher 2009), but in this case the relatively minor increase in increasing wing/tail flicking, dominance posturing, and vocalizing suggest that the listening crows were not highly threatened or agitated by the short stimulus calls. This refutes the hypothesis that short calls are used to signal aggression towards the intruding crows.

While my study was able to determine that short calls are not used to signal aggression, I was unable to demonstrate that short calls are used for recruiting allies; the mean number of crows did not increase from the pre-stimulus phase to the stimulus phase. I'm uncertain whether I would have been able to detect a significant increase in the number of crows present, even if the stimulus call was highly attractive; the mean number of adults at the site was only 2.23 for the scold treatment, and that call type is highly attractive (Yorzinski and Vehrencamp 2009). If crows use short calls to recruit family members, then in most cases the number of adults would only increase from 1 to 2, which is consistent with my observed value of 1.62 crows present during the stimulus phase of the short call treatment. Thus, while further research is still required to definitively determine if short calls are used as a contact call or to recruit allies, I have demonstrated that these calls are not used to signal danger or aggression.

Importance of Human Feeder?

Despite the evidence that crows quickly learn to recognize individual human feeders and adjust their behavior to best exploit the feeder's habits (Marzluff and Miller 2014), I observed only minor changes in behavior between the feeder and nonfeeder trials during the Food Response Experiment. The slightly higher vocalization rate and number of crows present might be due to the time of day; for many of the nonfeeder trials I arrived and set up the food pile before sunrise. While this practice ensured that none of the crows could see me place the pile and thus link me to the peanuts, it also potentially biased my data: crows (like most birds) are presumably hungriest in the early morning, meaning there would be more crows foraging and on the lookout for foraging opportunities during the nonfeeder trials. There were more noticeable differences in the microstructure of the calls uttered during the feeder and nonfeeder trials: when the feeder was present, the call duration decreased significantly for each of the peanut treatments, whereas it only significantly decreased once for the nonfeeder treatment. Marzluff and Miller

(2014) also described crows as usually giving a short staccato sequence of 3-5 calls when flying towards a recognized human feeder. If crows are using shorter calls to recruit allies in a non-dangerous setting, this would mean that crows are more likely to recruit when a person is providing food vs just finding it on their own. If true, perhaps they do this because a person is visually conspicuous to distant crows- there's little chance at keeping the food pile a secret, so the caller recruits allies to share and protect the pile from interloping crows. Additionally, if a person regularly feeds them, then that feeder is both well known to the surrounding crows (caller needs to quickly bring in allies to keep attentive neighbors away) and represents an ongoing source of food (recruiting allies might not reduce the amount of food available to the caller). By design, the disguises I wore and the fact that I visited each site only 3 times kept the crows from associating me with food, which might explain why I did not observe a major change in the crows' behavior for the feeder and nonfeeder treatments.

Territorial Advertisement

Unlike the calls given in the presence of food, the vocalizations uttered by crows during the pre- and post-stimulus phase of the Food Response Experiment tended to be of longer duration. Additionally, the calls given in the presence of food were longer for the individual peanut than they were for the large peanut piles regardless of whether a human feeder was present. Tarter (2008) and Parr (1997) both described structured calls with a medium duration (between 250-350 msec) as being used in counter-calling, which in other songbirds is associated with aggression and territorial defense (Burt et al. 2001, Vehrencamp 2001). This is supported by the results from the Call Playback Experiment; the focal crow's change in behavior after hearing the medium stimulus calls are consistent with 5 out of my 6 predictions for the stimulus call being associated with territory defense (increased vocalizations, flight, dominance posturing and wing flicking, with no change in number of crows present), whereas they met 4 out of 6 predictions for danger warning and only 2 out of 6 predictions for ally recruitment. 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 in duration and lower in peak frequency compared to before the stimulus. Most avian species use vocalizations with a low frequency to signify increased aggression and intimidation, since usually only the largest individuals are structurally capable of producing the signals with the lowest pitch (Morton 1977). The behavior I observed suggests that the crows are using type-matched vocalizations as a challenge to the unseen caller, which is consistent with the behavior observed in song playback experiments for other songbirds (Burt et al. 2001). This supports the hypothesis that medium calls are used for territory defense and to signal aggression.

Unstructured Calls and Danger

Among the various vocalizations I recorded in the Food Response Experiment, I recorded many calls given in an unstructured sequence. Playback of unstructured vocalizations elicited responses from the focal crows that were consistent with how I predicted they would behave in the presence of danger (increased vocalizations, flight, and wing/tail flicking, and no change to speaker proximity and dominance posturing). Most authors have described danger calls as being given in either fully unstructured sequences, or with a highly variable number of calls per group (Chamberlain & Cornwell 1971, Parr 1997, Tarter 2008). Since I used only unstructured calls for my scold stimulus calls, my results support this conclusion, and thus conclude that the crows were responding appropriately to the context of the stimulus calls.

Caws are Graded, not Clumped

My failure 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's 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 I did not have access to (such as the sex and age of the calling bird), and came to the same conclusion: crow caws lie along a gradient rather than clustering into distinct categories.

Overall

Those vertebrates that actively signal the location of food to others are all social species that uniquely benefit from recruiting others to a food source, either to improve their foraging efficiency, gain access to a food source, or reduce their predation risk. Humpback whales (*Megaptera novaeangliae*) recruit conspecifics to improve their foraging efficiency; by coordinating their movements to corral prey into a dense school, each whale can individually increase the amount of prey they can capture compared to hunting alone (D'Vincent et al. 1985). The spotted hyena (*Crocuta crocuta*) recruit kin to displace and defend against unrelated conspecifics and other large predators from a carcass that they would otherwise have been unable to approach (East & Hofer 1991). House sparrows (*Passer domesticus*) recruit conspecifics to reduce the risk of predation; they give recruitment calls around a food patch until a flock has formed around it, at which point they cease calling (Elgar 1986). If American crows are using short structured calls to recruit allies around large and conspicuous food sources, I posit that they would be recruiting to defend a food windfall from knowledgeable rivals as opposed to increasing their foraging efficiency or decreasing their predation risk; future studies are needed to fully determine if and why American crows recruit allies.

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FIGURES AND TABLES

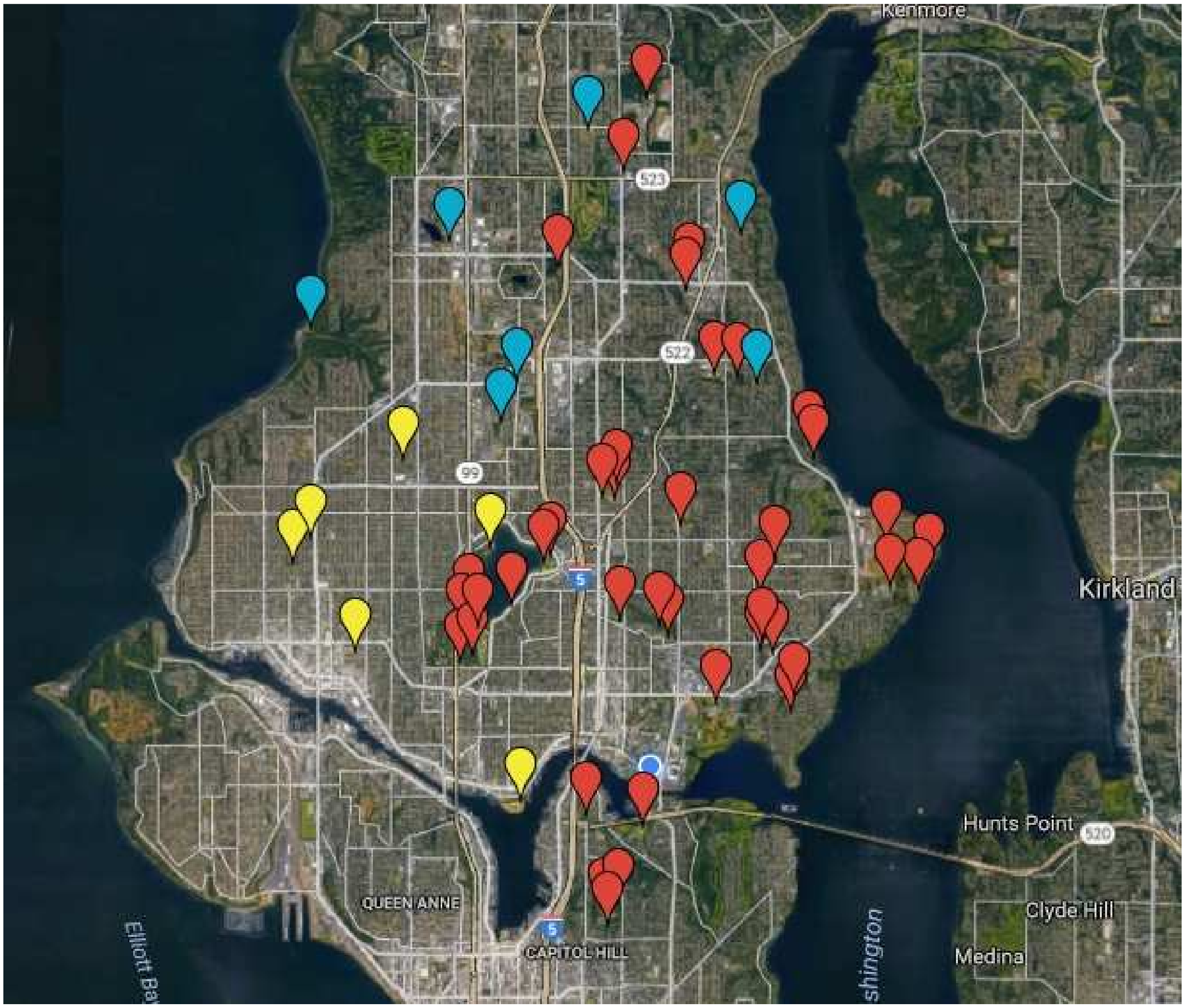


Figure 1. Map of Experiment 1 study sites in Seattle. Red points are the study sites visited from April-July 2015, blue points are the locations visited during January 2016, and yellow points are the locations visited during April-May 2016. Every site was at least 150 m from any nearby sites.

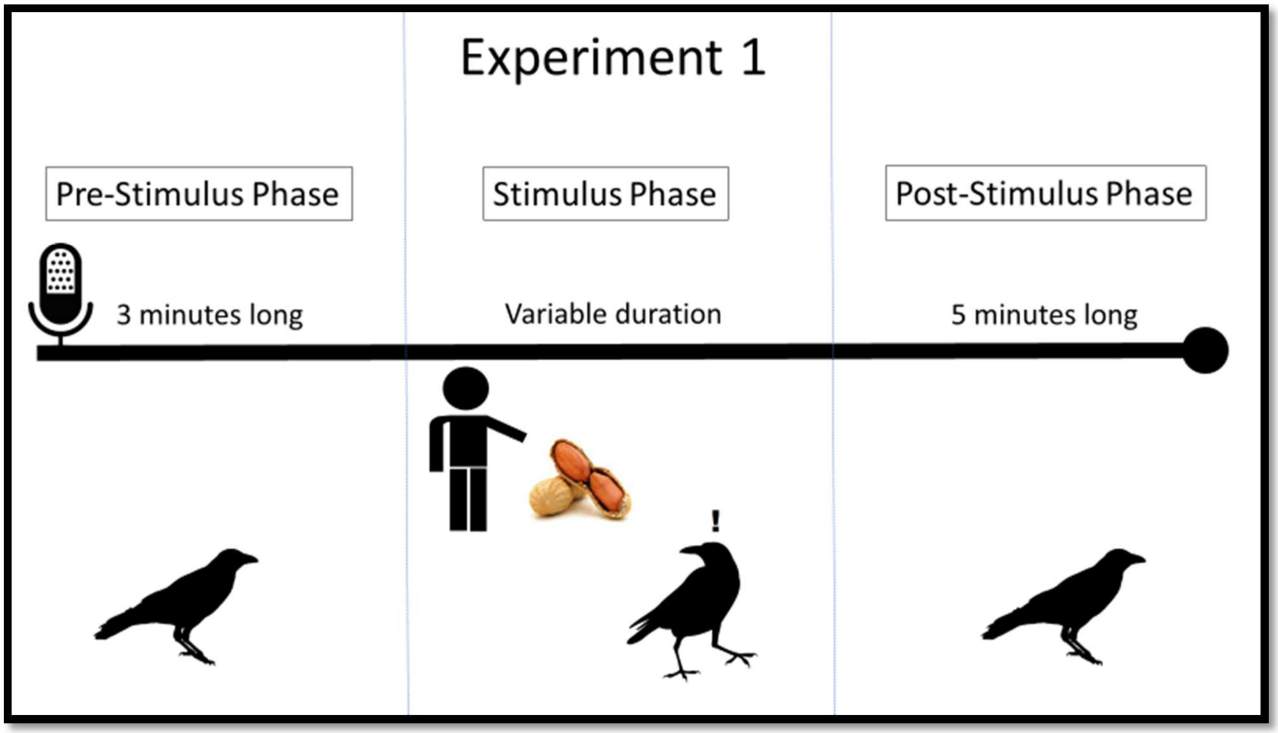


Figure 2A. Illustration of the separate phases of a single trial from the feeder treatment of Experiment 1. Phase 1 (the pre-stimulus phase) began once I started the audio/video recording and ends after 3 minutes. At the end of Phase 1, I approached the crows and tossed out a pre-determined number of peanuts, triggering the beginning of Phase 2 (the stimulus phase). Phase 2 continues until the crows had eaten all the peanuts, at which point Phase 2 ended and Phase 3 (the post-stimulus phase) began. Phase 3 ends after 5 minutes, at which point I ended audio/video recording.

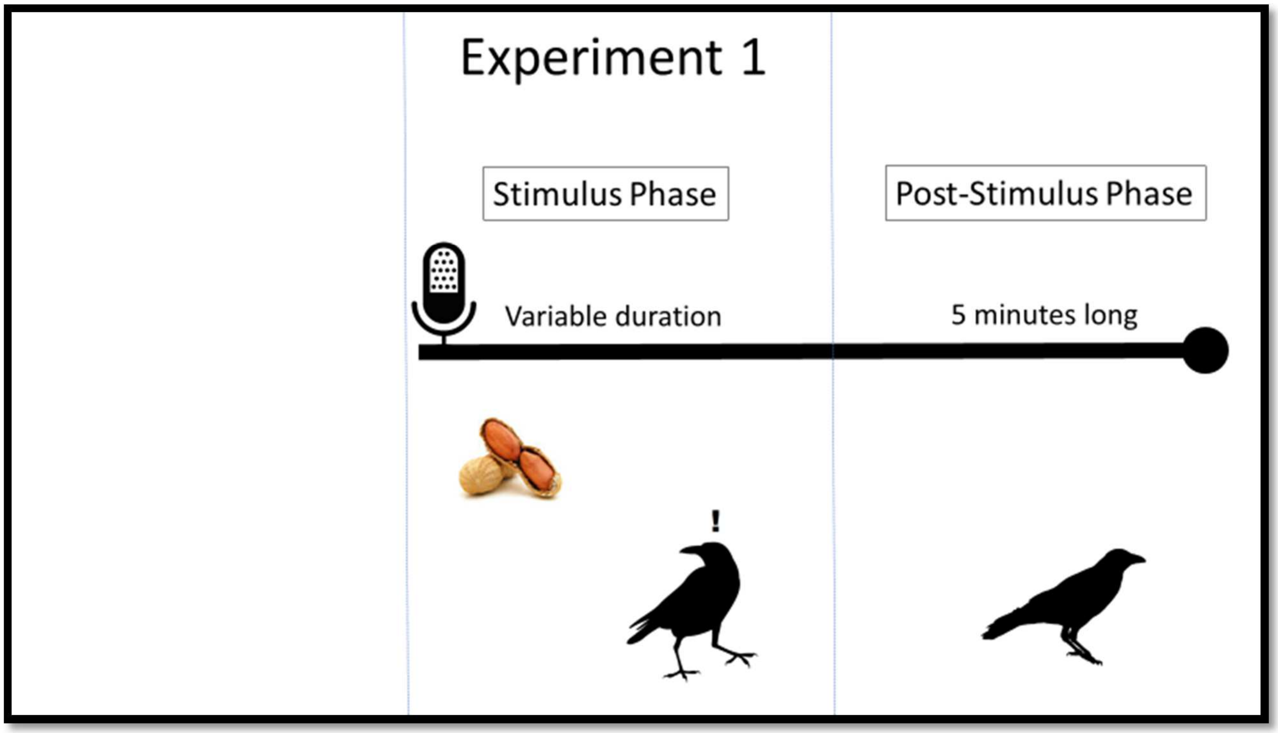


Figure 2B. Illustration of the phases of a single trial from the nonfeeder treatment of Experiment 1. The nonfeeder treatment requires that the crows find the peanut pile independent of a human feeder, so I placed the food surreptitiously in a conspicuous location, then retreated at least 20 m away. The stimulus phase began once a crow arrives at the food pile. The remainder of the trial proceeded identically to the feeder treatment version of Experiment 1.

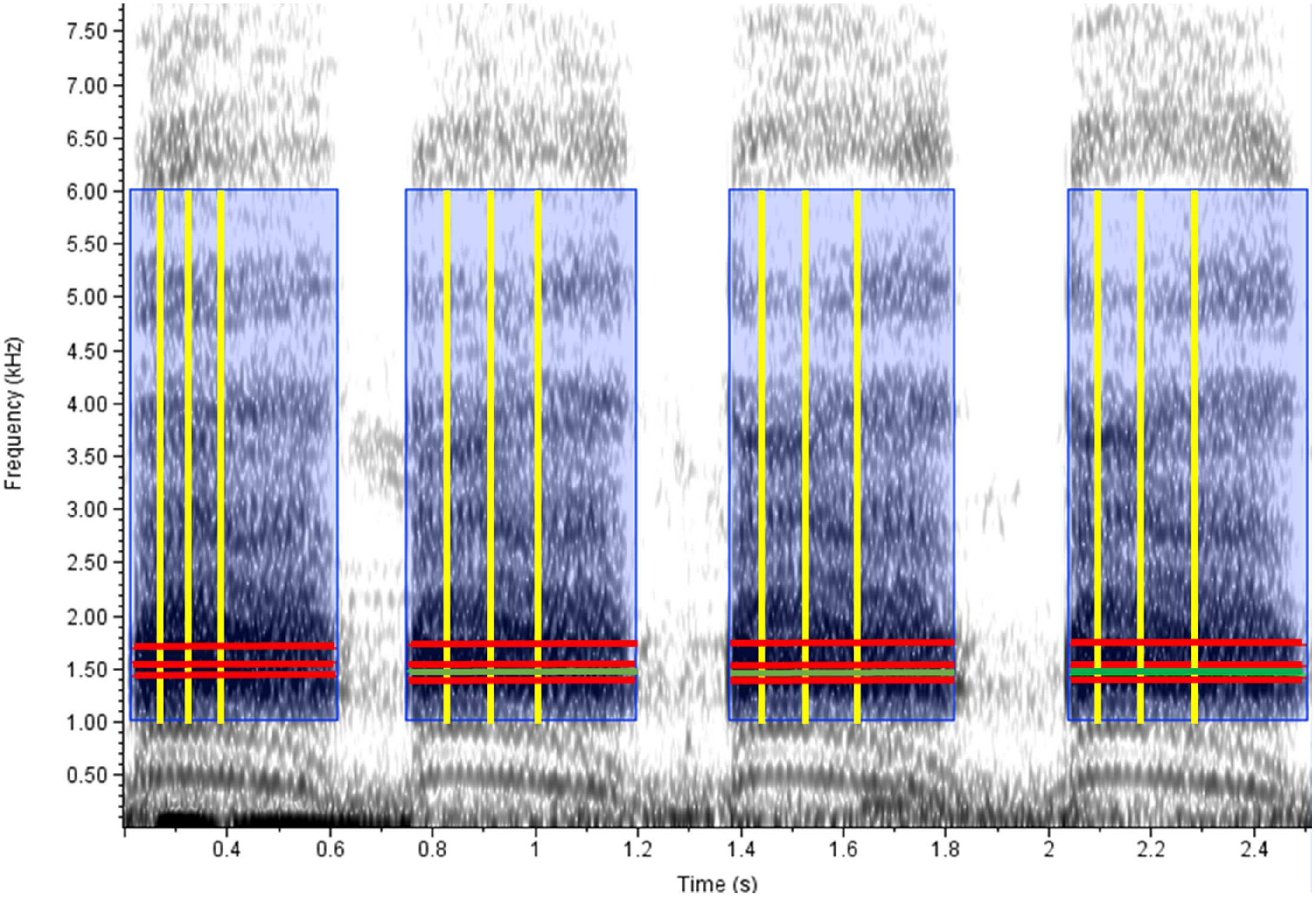


Figure 3. Example of spectrogram with selections around each valid vocalization. The calls featured here are medium stimulus calls. All the measurements calculated by raven are based on the sound energy within every selection (blue area). This image models where the Raven 1.5 measures occur within the selection; the vertical yellow lines are (from left to right) the Q1 time, center time, and Q3 time; the horizontal red lines are (from bottom to top) Q1 frequency, center frequency, and Q3 frequency; and the horizontal green line is the peak frequency (obscured by Q1 frequency in some selections). See Table 1 for definitions of each measure.

Measure	Source	Description
Call duration (Delta Time)	Raven 1.5	Difference between the end time and begin time of the call. Units: msec
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: msec
Center Time	Raven 1.5	The point in time at which the call is divided into two time intervals of equal energy. Units: msec
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: msec
Peak Frequency	Raven 1.5	The frequency at which max 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
Center 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*	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, I 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: msec
Call Group Size**	Calculated outside Raven 1.5	The number of calls uttered in a call group. A call group was defined as every call given in sequence where the intercall duration was <1 for every call.
Call Group Structure**	Calculated outside Raven 1.5	Determined if the calls in a group are 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 seconds of the group.

Table 1. The microstructure measures obtained from every vocalization

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

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

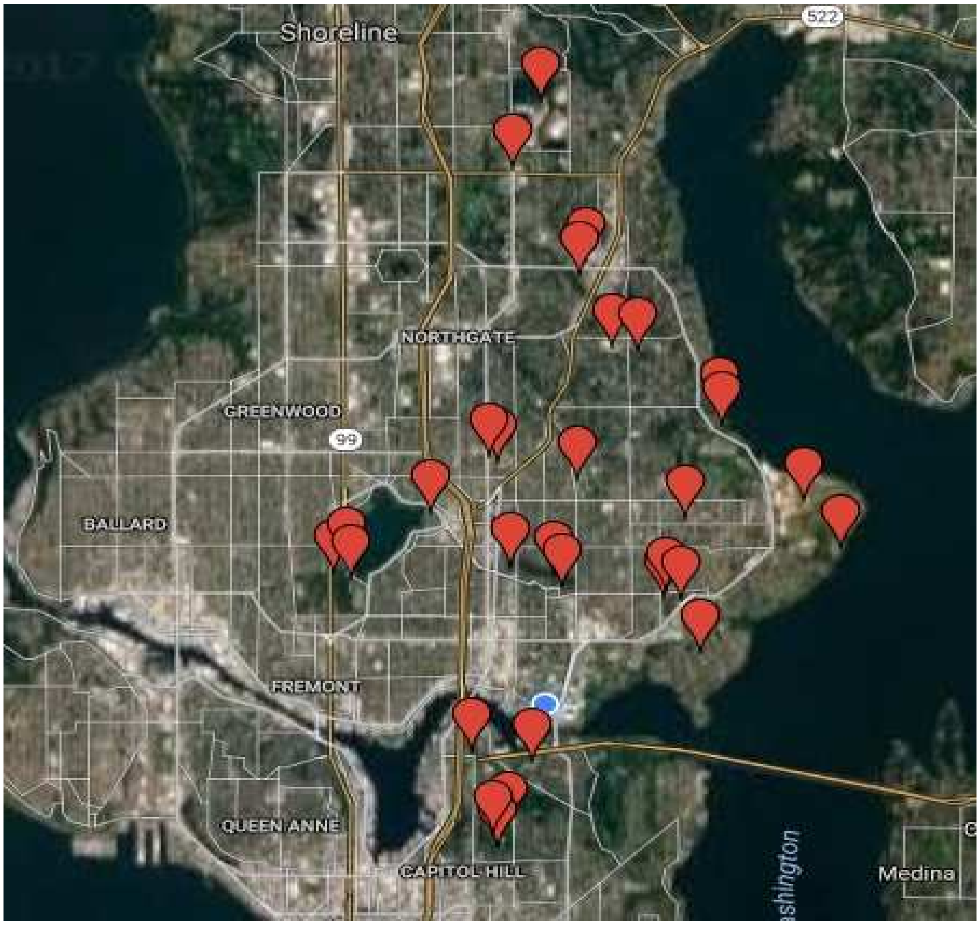


Figure 4. Map of Experiment 2 study sites. All locations were previously used in Experiment 1.

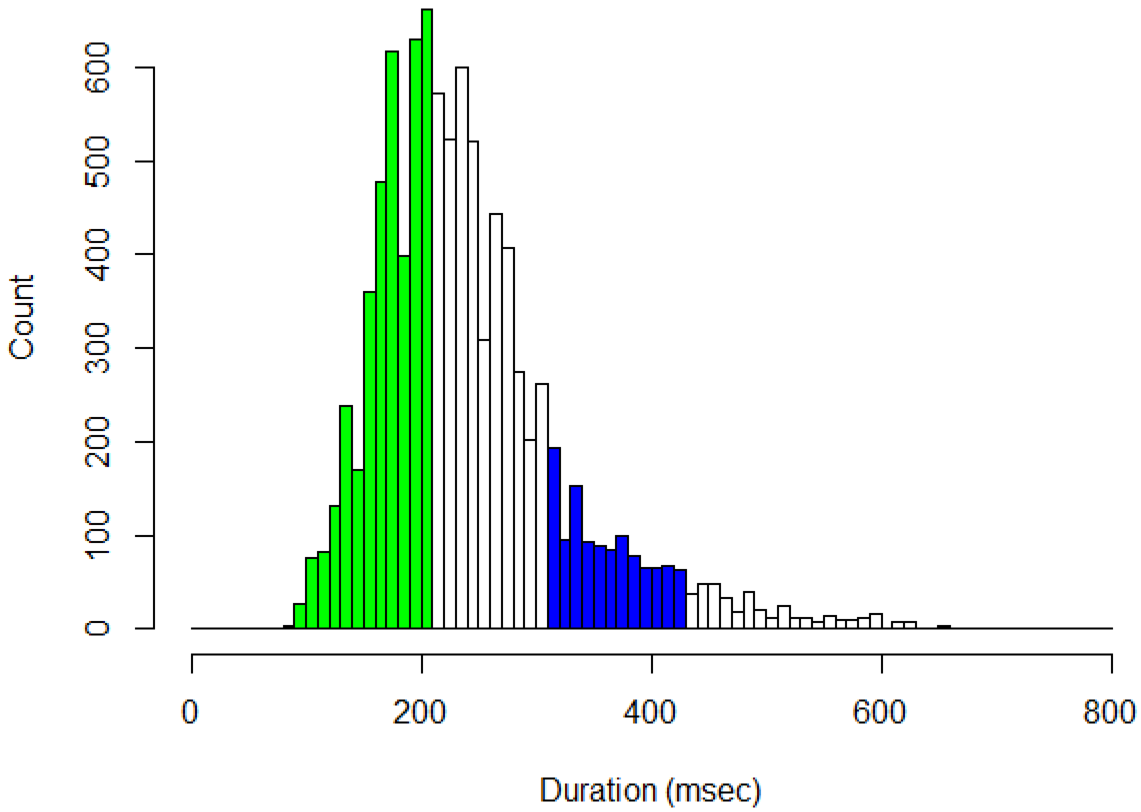


Figure 5. Histogram showing the distribution of call duration from the vocalizations recorded in Experiment 1. The green bars are calls with a duration 75-200 msec, from which I pulled exemplars for use as short stimulus calls in experiment 2. The blue bars are calls with duration 300-425 msec, from which I pulled exemplars for use as medium stimulus calls in experiment 2.

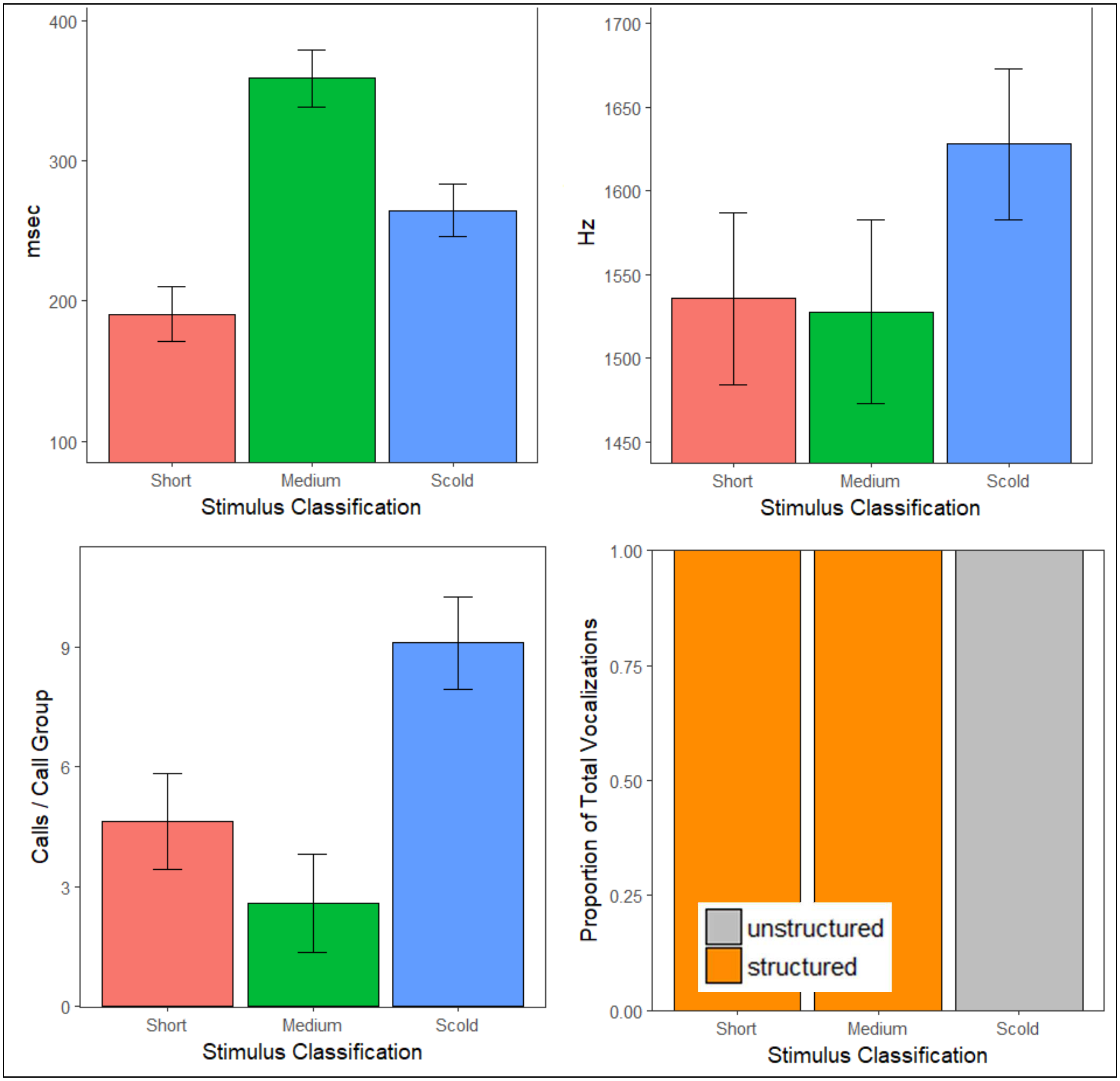


Figure 6. Comparison of the various micro-structural measures of the vocalizations used as stimulus calls during the Playback Experiment. Displays mean response for call duration (top left), peak frequency (top right), vocalizations per call group (bottom left), and proportion of structured vs unstructured call groups (bottom right). The values used in this table can be found in **Appendix 2**.

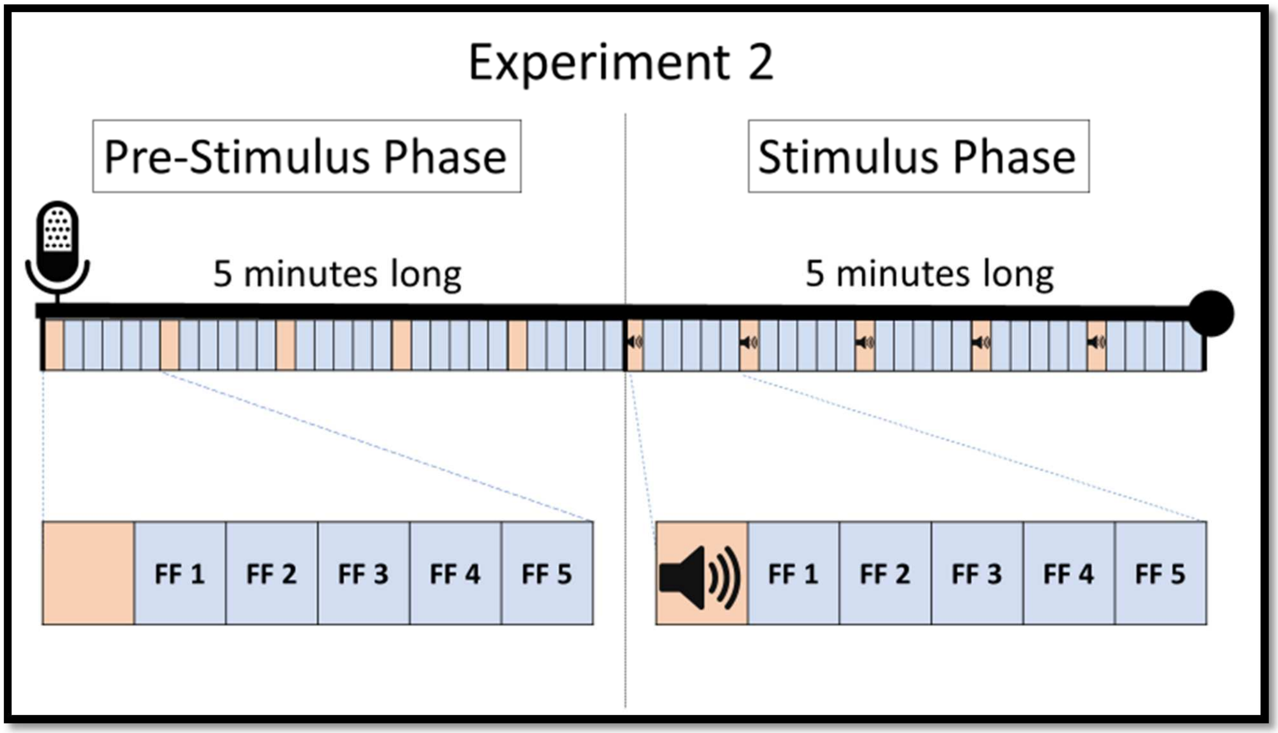


Figure 7. Illustration of the Experiment 2 phases. Each phase lasted for 5 minutes, and each minute was divided into 10-second intervals. The first interval of every minute was the stimulus interval (red), during which I either did nothing (pre-stimulus phase), or played the assigned stimulus call through the speaker (stimulus phase). The remaining 5 intervals of every minute were observation intervals (blue), during which I collected data by conducting a focal follow (FF) of whichever crow was closest to the speaker. There were 25 focal follow intervals for each phase.

Name of Measure	**Definition**	**Significance of Behavior**	**Prediction if stimulus call signifies:**		
			Ally Recruitment	**Territorial Advertisement**	**Danger Warning**
Avg. Adults Present	The total number of adult crows within 33 m of the speaker.	This measure can test whether a stimulus call attracts crows, repels crows, or neither over a wide area.	Increase	No change	Increase
Vocalization	The number of vocalizations given by the focal during the interval	The focal crow is sending a signal to other crows in a large area.	No change	Increase	Increase
Flight	The focal crow was in flight at some point during interval	The focal crow desires to move to a new location, either to escape from a threat or locate an object of interest.	Increase	Increase	Increase
Proximity to Speaker	The focal crow came within 7 m of the speaker during interval	The focal crow is attempting to locate the source of the stimulus calls.	No change	Increase	No change
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 wing-tips slightly upward 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

Table 2. The behaviors I recorded in Experiment 2. Apart from avg. adults present and vocalizations given, I only counted a behavior as present/absent for each 10-second focal follow interval, then summed all the intervals where the behavior was observed for that phase. For the avg. adults present, I averaged the number of adults present across all 25 intervals for that phase.

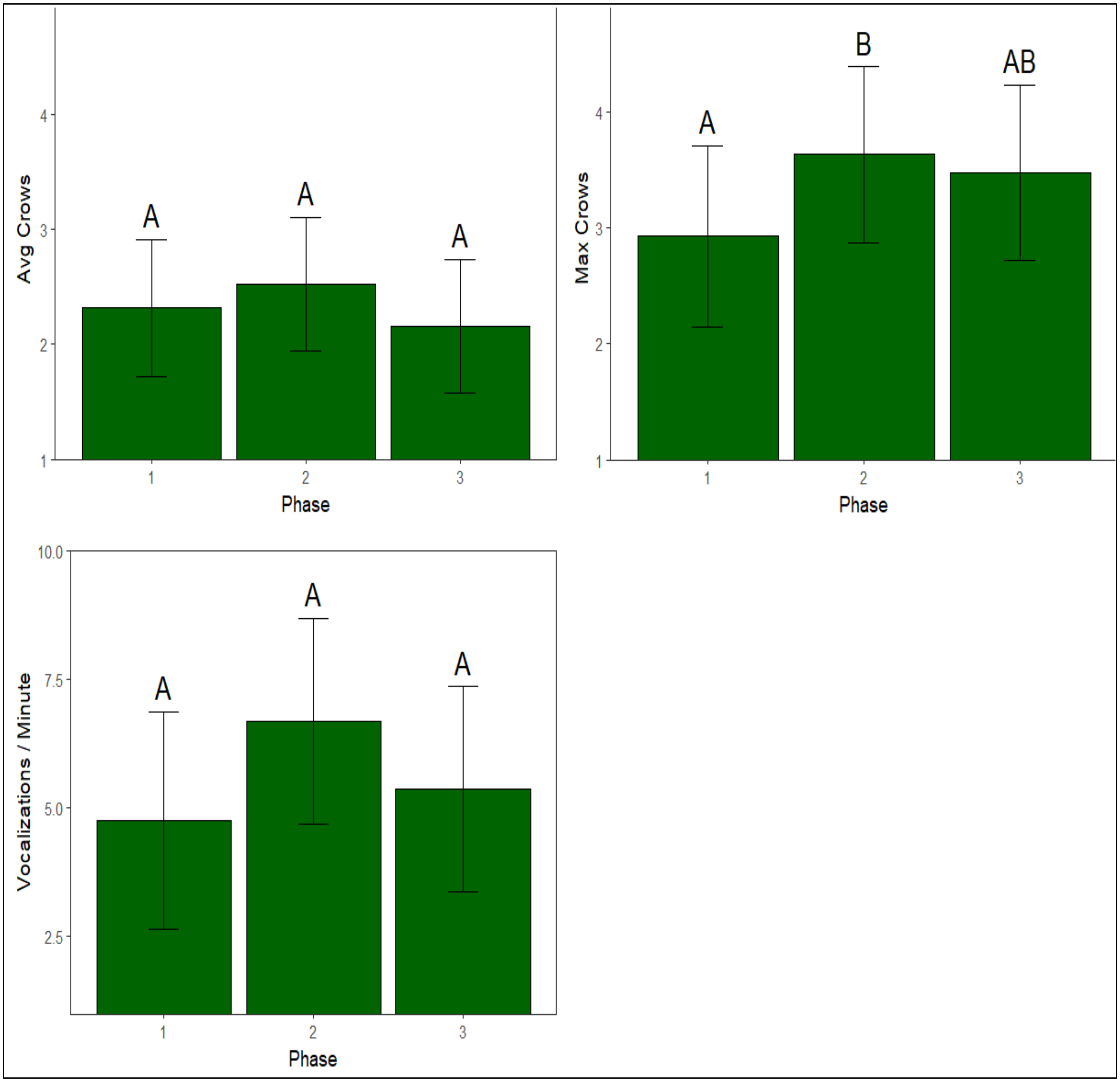


Figure 8. Comparison of the behaviors observed during the pre-stimulus (Phase 1), stimulus (Phase 2), and post-stimulus (Phase 3) phases of the Food Response experiment. Displays mean response ± 95% CI for average crows present (top left), maximum crows present (top right), and call rate (bottom left). These plots include data from all three peanut treatments and both feeder treatments, and ignores the distinction between them. The values used in this table can be found in **Appendix 3**.

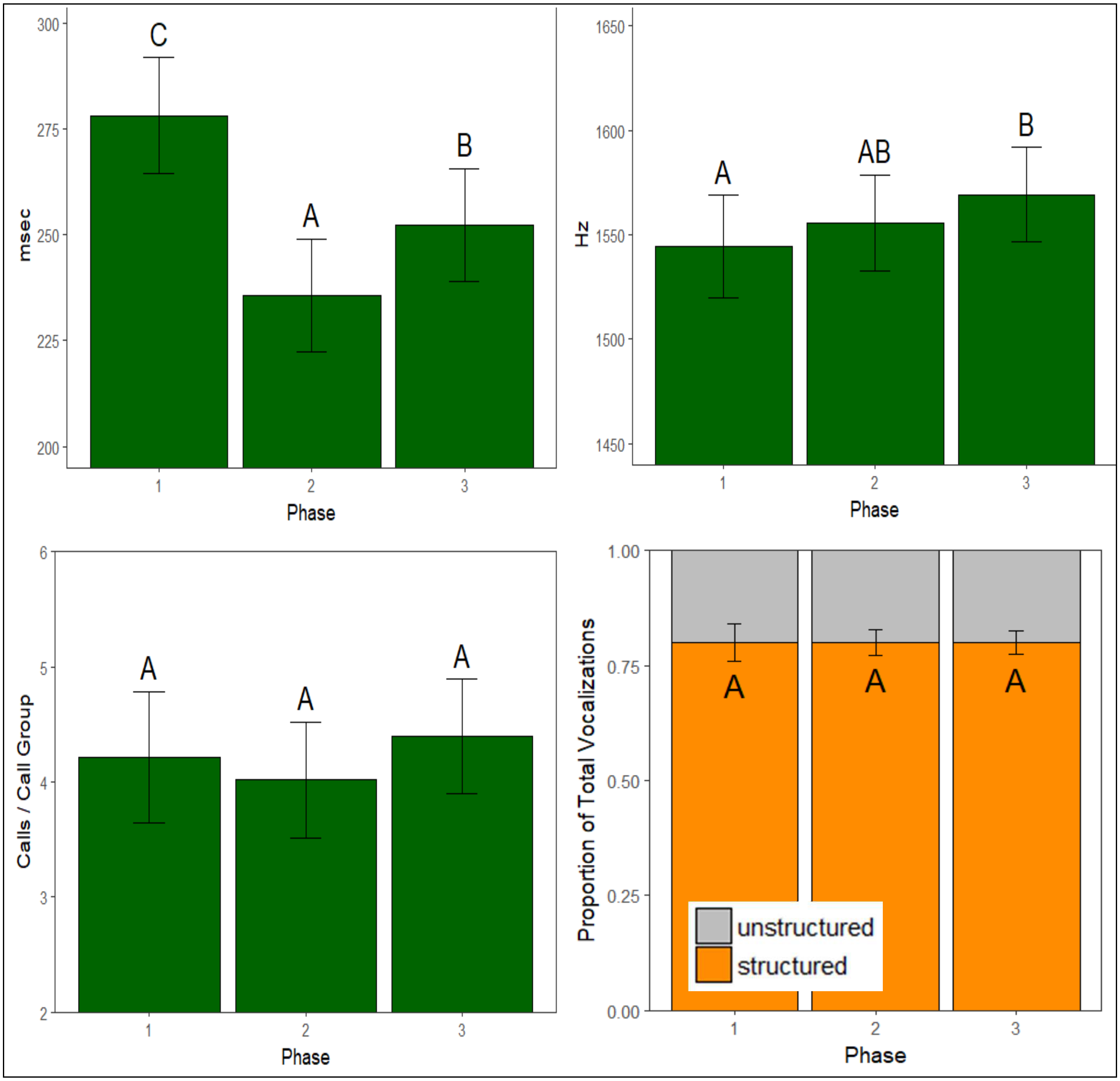


Figure 9. Comparison of the various micro-structural measures of the vocalizations uttered during the pre-stimulus (Phase 1), stimulus (Phase 2), and post-stimulus (Phase 3) phases of the Food Response experiment. Displays mean response for call duration (top left), peak frequency (top right), vocalizations per call group (bottom left), and proportion of structured vs unstructured call groups (bottom right). Call duration and peak frequency use all vocalizations uttered, while call group size and group structure use a single randomly chosen call per call group (to avoid oversampling).These plots include data from all three peanut treatments and both feeder treatments, and ignores the distinction between them. The values used in this table can be found in **Appendix 3**.

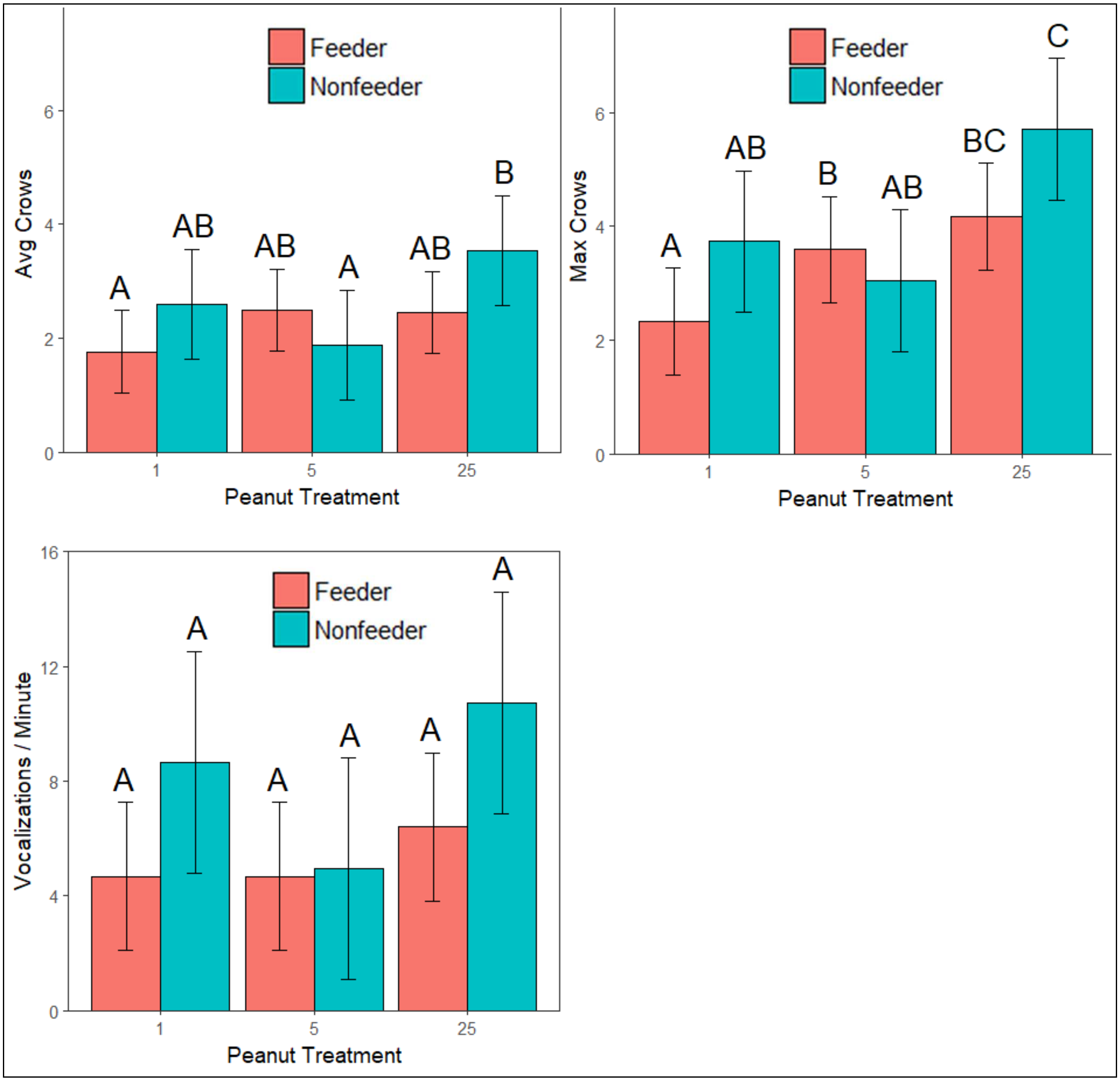


Figure 10. Comparison of the effect peanut treatment and feeder treatment had on the behaviors observed during the Food Response experiment. Displays mean response ± 95% CI for average crows present (top left), maximum crows present (top right), and call rate (bottom left). Because pre-stimulus (Phase 1) data could not be collected for the nonfeeder treatments, this figure only uses data collected during the stimulus (Phase 2) and post-stimulus (Phase 3) phases, and ignores the distinction between them. The values used in this table can be found in **Appendix 4**.

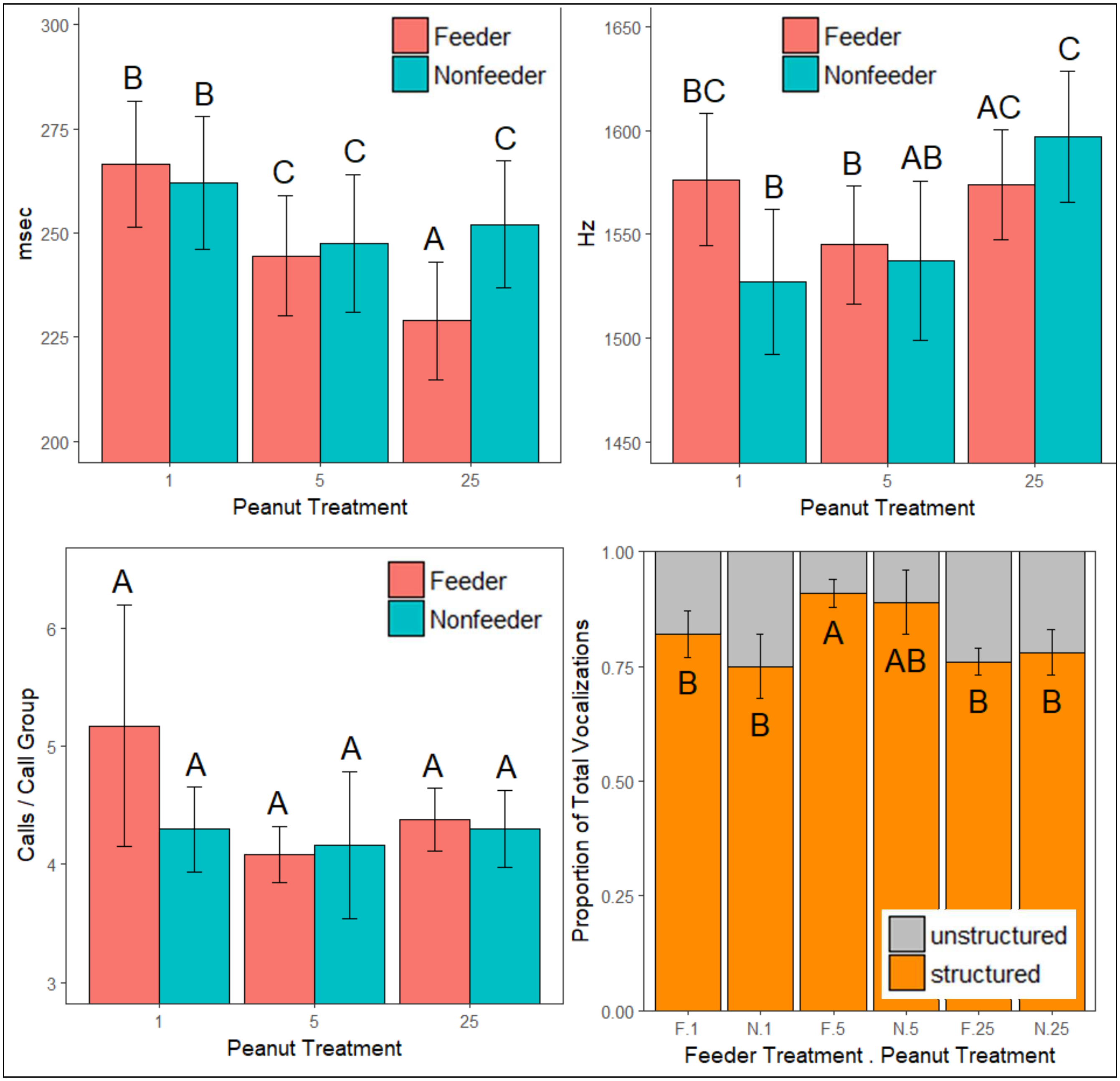


Figure 11. Comparison of the effect peanut treatment and feeder treatment had on the micro-structural qualities of the vocalizations uttered by the crows during the Food Response experiment. Displays mean response ± 95% CI for call duration (top left), peak frequency (top right), vocalizations per call group (bottom left), and proportion of structured vs unstructured call groups (bottom right). Call duration and peak frequency use all vocalizations uttered, while call group size and group structure use a single randomly chosen call per call group (to avoid oversampling). Because pre-stimulus (Phase 1) data could not be collected for the nonfeeder treatments, this figure only uses data collected during the stimulus (Phase 2) and post-stimulus (Phase 3) phases, and ignores the distinction between them. The values used in this table can be found in **Appendix 5**

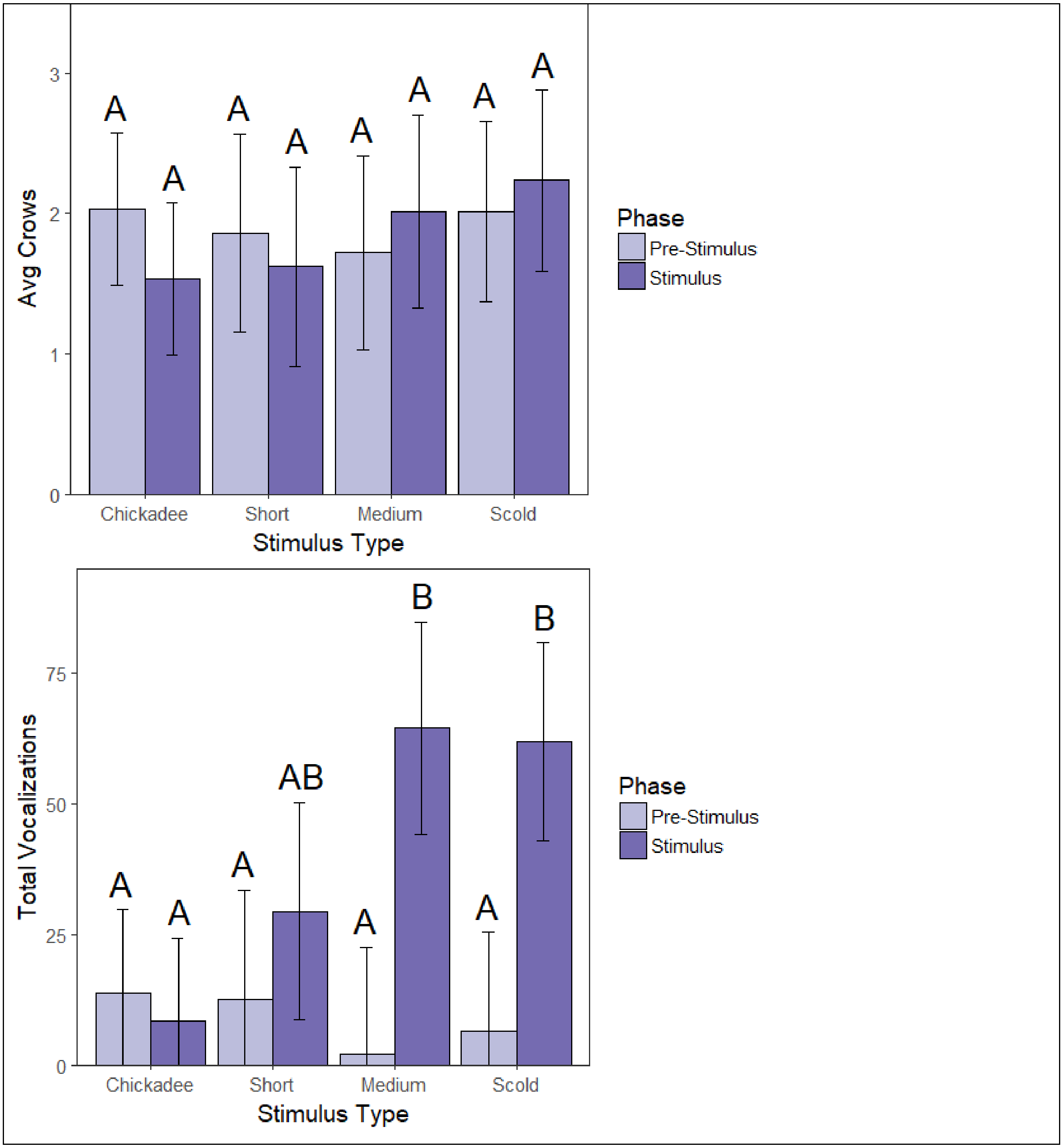


Figure 12. Comparison of the effect each stimulus had on the behaviors observed during the Call Playback experiment. Displays mean response for average crows present (top), and total vocalizations by the focal crow (bottom). The values used in this table can be found in **Appendix 8**.

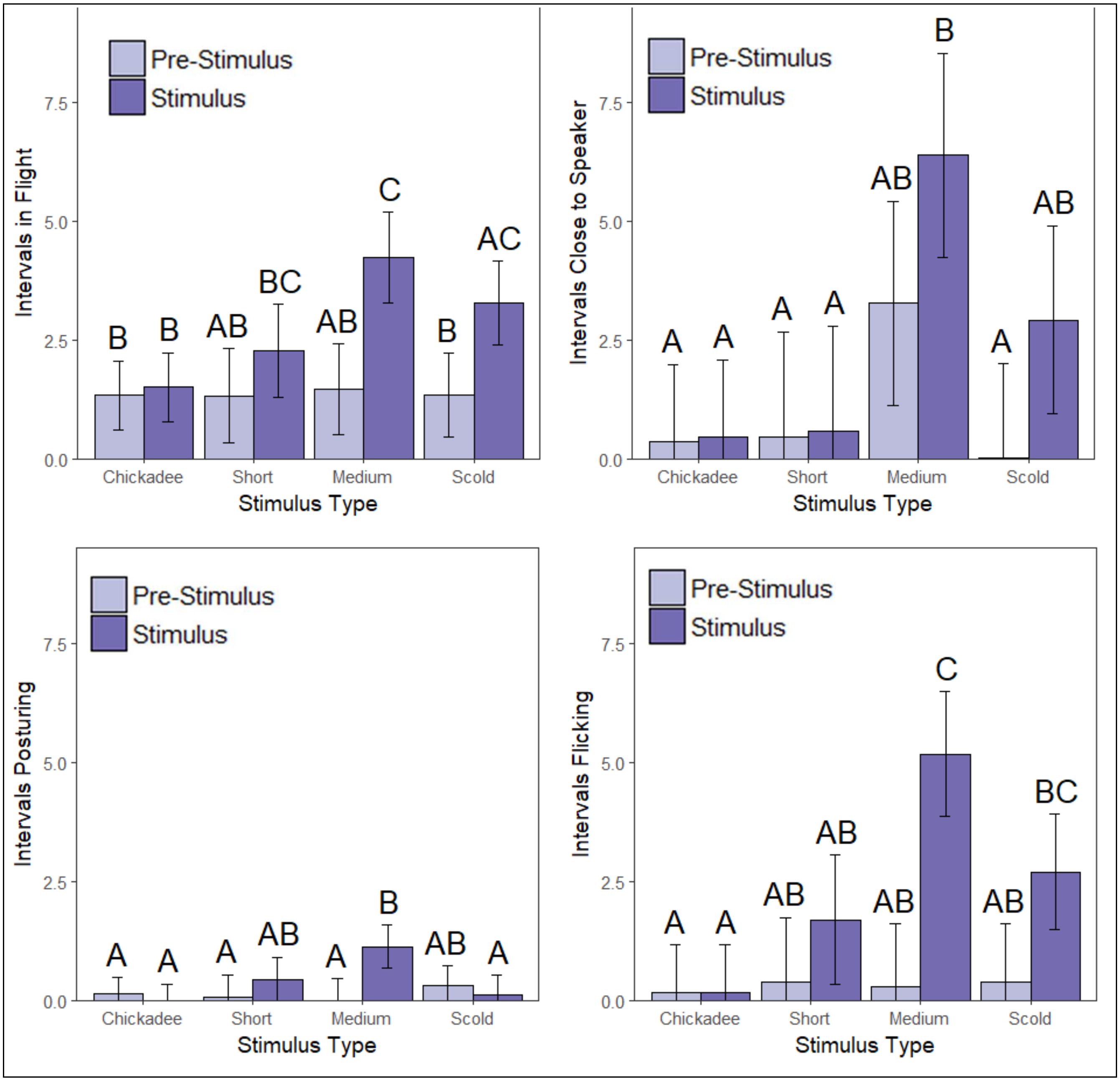


Figure 13. Comparison of the effect each stimulus had on the behaviors observed during the Call Playback experiment. Displays mean focal follow intervals during which the behavior was observed for flight (top left), <7m proximity to speaker (top right), dominance posturing (bottom left), and wing/tail flicking (bottom right) by the focal crows. The axes remain consistent to demonstrate relative magnitude. The values used in this table can be found in **Appendix 8**.

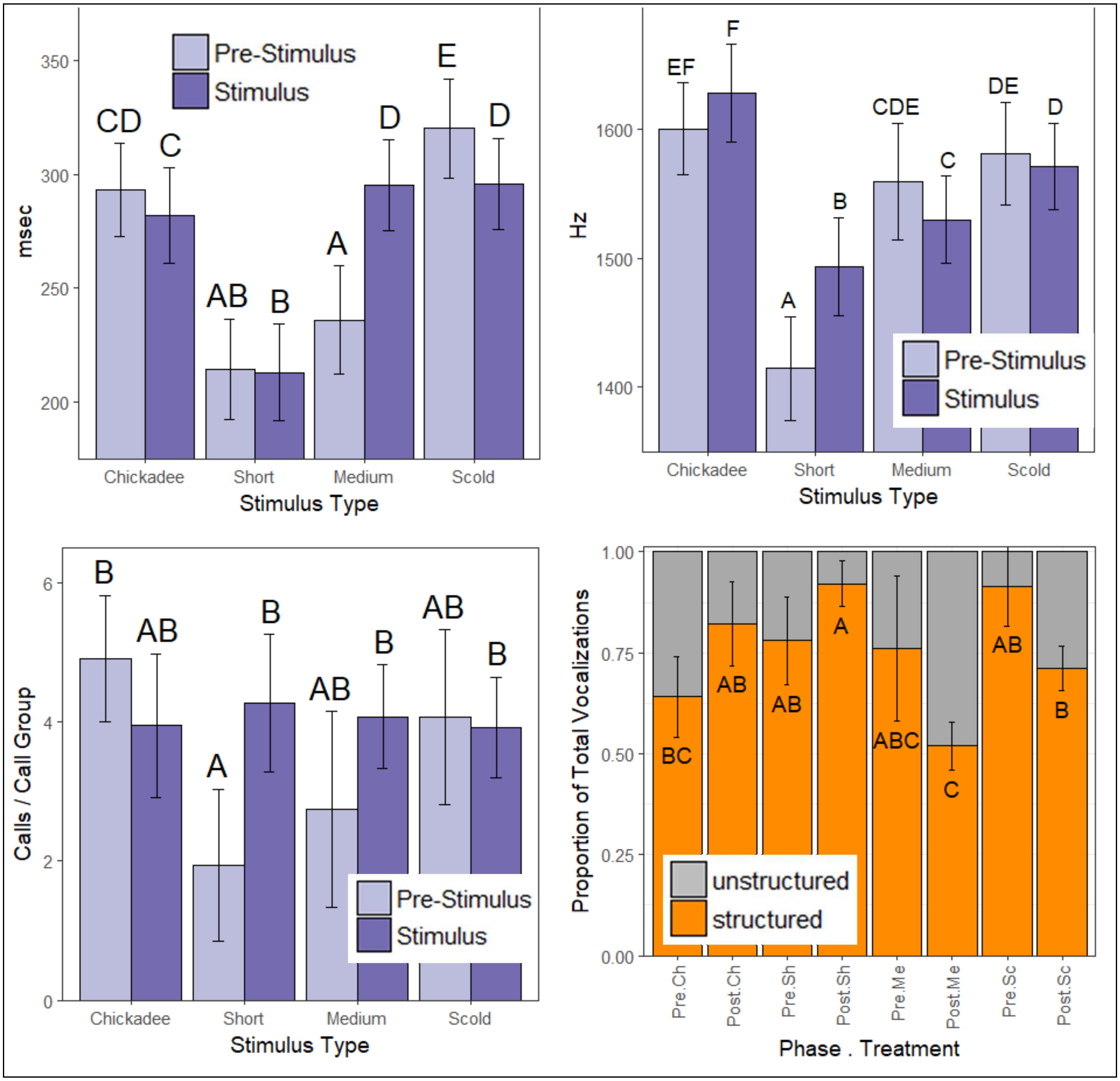


Figure 14. Comparison of the effect each stimulus had on the microstructure of the vocalizations uttered by the focal crow during the Call Playback experiment. Displays mean response for call duration (top left), peak frequency (top right), vocalizations per call group (bottom left), and proportion of structured vs unstructured call groups (bottom right). Call duration and peak frequency use all vocalizations uttered, while call group size and group structure use a single randomly chosen call per call group (to avoid oversampling). The values used in this table can be found in **Appendix 9**.

Behavior Measured	**Stimulus Type**	**Comparing change of conspecific treatment against heterospecific control (chickadee)**					
		N	**$\Delta \bar{X}$**	**Δ Std. Error**	**DF**	**t-value**	**P-value**
Avg. Adults Present	Chickadee	30	-0.50	0.27	67.9	-1.87	0.066
	Short	16	-0.12	0.39	56.9	0.96	0.34
	Medium	17	0.22	0.38	56.4	1.88	0.065
	Scold	20	0.19	0.36	54.8	1.91	0.061
Vocalizations	Chickadee	30	-5.47	9.786	79.0	-0.56	0.58
	Short	16	16.87	16.50	65.7	1.35	0.18
	Medium	17	62.27	16.18	64.8	4.19	$3.7e^{-05}$ **
	Scold	20	55.30	15.40	62.4	3.95	$2.0e^{-04}$ **
Flight	Chickadee	30	0.17	0.53	78.5	0.32	0.75
	Short	16	0.92	0.87	66.9	0.86	0.39
	Medium	17	2.76	0.85	66.3	3.04	$3.4e^{-03}$ **
	Scold	20	1.97	0.81	64.4	2.22	0.030 *
Speaker Proximity	Chickadee	30	0.10	1.14	77.7	0.09	0.93
	Short	16	-0.05	1.85	63.5	-0.08	0.94
	Medium	17	3.03	1.81	62.9	1.62	0.11
	Scold	20	2.80	1.71	60.8	1.57	0.12
Dominance Posture	Chickadee	30	-0.13	0.24	79.0	-0.55	0.59
	Short	16	0.38	0.41	68.7	1.25	0.22
	Medium	17	1.12	0.40	68.0	3.11	$2.7e^{-03}$ **
	Scold	20	-0.20	0.38	66.0	-0.17	0.86
Wing/Tail Flicking	Chickadee	30	0.00	0.70	78.3	0.00	1.0
	Short	16	1.39	1.16	62.4	1.20	0.24
	Medium	17	4.82	1.14	61.6	4.24	$7.6e^{-05}$ **
	Scold	20	2.35	1.08	59.2	2.18	0.033 *

Table 3. The statistical results found by comparing the difference in behavior from the pre-stimulus phase to the stimulus phase (delta) of each conspecific treatment against the heterospecific control for each behavior using a Welch two-sample t-test. The chickadee control is tested for significance against zero. The values were calculated using a linear mixed model with location as a random effect, and use Satterthwaite approximations to degrees of freedom.

* indicates significance at the α=0.05 level.

** indicates significance at the Bonferroni corrected α=0.0083 level

APPENDIX

Appendix 1. Photos of 6 disguises. The disguises are designed to obscure my identity and appear dissimilar to one another. They are also meant to appear non-threatening to human bystanders.

Microstructure Measure	**Stimulus Classification**	**Mean**	**Std. Deviation**	**Std. Error**	**95% CI**
Call Duration (msec)	Short	191	30	3.0	± 19.8
	Medium	359	77	9.2	± 20.4
	Scold	265	56	3.9	± 18.7
Peak Frequency (Hz)	Short	1536	287	28.8	± 51.4
	Medium	1528	85	10.2	± 54.9
	Scold	1628	120	8.5	± 45.0
Vocalizations per Call Group	Short	4.62	1.17	0.12	± 1.20
	Medium	2.57	0.63	0.08	± 1.22
	Scold	9.12	4.95	0.35	± 1.16
Call Group Structure (proportion total vocalizations)	**Stimulus Classification**	**Proportion Structured**	**Std. Deviation**	**Std. Error**	**95% CI**
	Short	1.00	0.00	0.00	± 0.00
	Medium	1.00	0.00	0.00	± 0.00
	Scold	0.00	0.00	0.00	± 0.00

Appendix 2. Table of the statistical values of the microstructure measures of the stimulus calls used during the Call Playback experiment. There were 99 individual short calls, 70 individual medium calls, and 201 individual scold calls.

Behavior Measure	**Phase**	**N**	**Mean**	**Std. Deviation**	**Std. Error**	**95% CI**
Average crows present	1	150	2.31	1.94	0.16	± 0.60
	2	186	2.52	2.73	0.20	± 0.58
	3	186	2.16	2.93	0.21	± 0.58
Maximum crows present	1	150	2.93	2.28	0.19	± 0.78
	2	186	3.64	3.54	0.26	± 0.76
	3	186	3.48	3.93	0.29	± 0.76
Call Rate (vocalizations per minute)	1	150	4.76	10.6	0.87	± 2.1
	2	186	6.69	11.3	0.83	± 2.0
	3	186	5.37	10.8	0.79	± 2.0
Microstructure Measure	**Phase**	**N**	**Mean**	**Std. Deviation**	**Std. Error**	**95% CI**
Call Duration (msec)	1	1766	278	87	2.1	± 14
	2	3557	236	79	1.3	± 13
	3	4185	252	85	1.3	± 13
Peak Frequency (Hz)	1	1766	1544	217	5.2	± 25
	2	3557	1556	260	4.4	± 23
	3	4185	1569	261	4.0	± 23
Vocalizations per Call Group	1	386	4.22	3.77	0.19	± 0.57
	2	800	4.02	2.82	0.10	± 0.50
	3	899	4.39	4.50	0.15	± 0.50
Call Group Structure (proportion total vocalizations)	**Phase**	**N**	**Proportion Structured**	**Std. Deviation**	**Std. Error**	**95% CI**
	1	386	0.80	0.40	0.020	± 0.040
	2	800	0.80	0.40	0.014	± 0.028
	3	899	0.80	0.40	0.013	± 0.026

Appendix 3. Table of the statistical values for the behaviors observed during the pre-stimulus (Phase 1), stimulus (Phase 2), and post-stimulus (Phase 3) phases of the Food Response experiment. This table uses data from all 3 peanut treatments and both feeder treatments.

Behavior Measure	Treatment	N	Mean	Std. Deviation	Std. Error	95% CI
Average crows present	Feeder + 1 Peanut	88	1.76	1.07	0.11	± 0.72
	Feeder + 5 peanuts	88	2.50	3.93	0.42	± 0.72
	Feeder + 25 Peanuts	88	2.45	3.08	0.33	± 0.72
	Nonfeeder + 1 Peanut	36	2.60	1.87	0.31	± 0.97
	Nonfeeder + 5 Peanuts	36	1.88	1.28	0.21	± 0.97
	Nonfeeder + 25 Peanuts	36	3.54	3.49	0.58	± 0.97
Maximum crows present	Feeder + 1 Peanut	88	2.33	1.29	0.14	± 0.94
	Feeder + 5 peanuts	88	3.59	4.90	0.52	± 0.94
	Feeder + 25 Peanuts	88	4.17	4.14	0.44	± 0.94
	Nonfeeder + 1 Peanut	36	3.74	3.21	0.54	± 1.24
	Nonfeeder + 5 Peanuts	36	3.05	1.88	0.31	± 1.24
	Nonfeeder + 25 Peanuts	36	5.71	4.27	0.71	± 1.24
Call Rate (vocalizations per minute)	Feeder + 1 Peanut	88	4.67	12.50	1.33	± 2.59
	Feeder + 5 peanuts	88	4.67	7.91	0.84	± 2.59
	Feeder + 25 Peanuts	88	6.40	10.88	1.16	± 2.59
	Nonfeeder + 1 Peanut	36	8.66	14.33	2.39	± 3.87
	Nonfeeder + 5 Peanuts	36	4.93	5.04	0.84	± 3.87
	Nonfeeder + 25 Peanuts	36	10.73	13.96	2.33	± 3.87

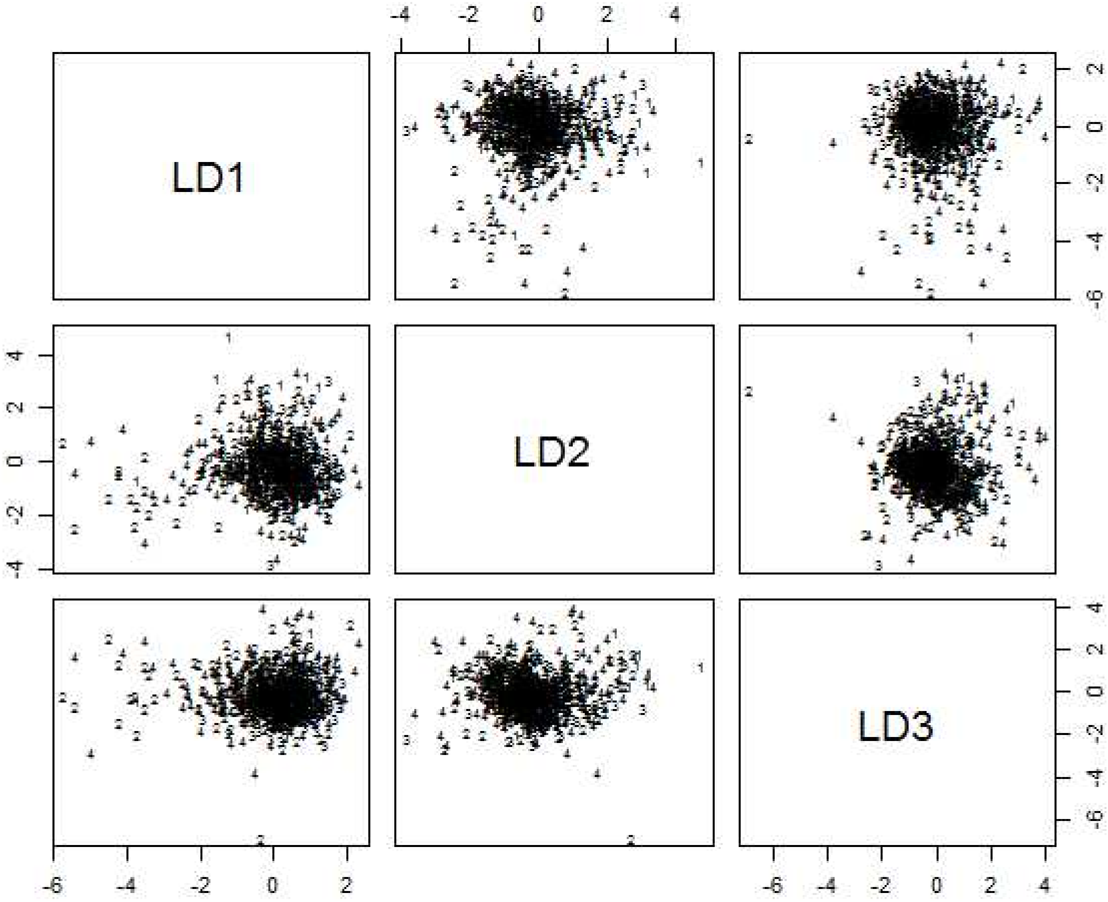
Appendix 4. Table of the statistical values for each combination of peanut treatment and feeder treatment for the behaviors observed during the Food Response experiment. Because pre-stimulus (Phase 1) data could not be collected for the nonfeeder treatments, this table only uses data collected during the stimulus (Phase 2) and post-stimulus (Phase 3) phases.

Microstructure Measure	**Treatment**	**N**	**Mean**	**Std. Deviation**	**Std. Error**	**95% CI**
Call Duration (msec)	Feeder + 1 Peanut	1112	267	76	2.28	± 15
	Feeder + 5 peanuts	1196	245	101	2.93	± 15
	Feeder + 25 Peanuts	2874	229	73	1.38	± 14
	Nonfeeder + 1 Peanut	742	262	74	2.70	± 16
	Nonfeeder + 5 Peanuts	395	248	102	5.14	± 16
	Nonfeeder + 25 Peanuts	1450	252	84	2.21	± 15
Peak Frequency (Hz)	Feeder + 1 Peanut	1112	1576	168	5.05	± 32
	Feeder + 5 peanuts	1196	1545	233	6.74	± 28
	Feeder + 25 Peanuts	2874	1574	237	4.44	± 26
	Nonfeeder + 1 Peanut	742	1527	139	5.10	± 35
	Nonfeeder + 5 Peanuts	395	1537	211	10.60	± 38
	Nonfeeder + 25 Peanuts	1450	1597	399	10.48	± 32
Vocalizations per Call Group	Feeder + 1 Peanut	208	5.17	7.49	0.52	± 1.02
	Feeder + 5 peanuts	287	4.08	2.07	0.12	± 0.24
	Feeder + 25 Peanuts	618	4.38	3.36	0.14	± 0.27
	Nonfeeder + 1 Peanut	169	4.30	2.34	0.18	± 0.36
	Nonfeeder + 5 Peanuts	91	4.16	2.97	0.31	± 0.62
	Nonfeeder + 25 Peanuts	326	4.30	2.99	0.17	± 0.33
Call Group Structure (Proportion)	**Treatment**	**N**	**Proportion Structured**	**Std. Deviation**	**Std. Error**	**95% CI**
	Feeder + 1 Peanut	208	0.82	0.39	0.03	± 0.05
	Feeder + 5 peanuts	287	0.91	0.28	0.02	± 0.03
	Feeder + 25 Peanuts	618	0.76	0.43	0.02	± 0.03
	Nonfeeder + 1 Peanut	169	0.75	0.44	0.03	± 0.07
	Nonfeeder + 5 Peanuts	91	0.89	0.31	0.03	± 0.07
	Nonfeeder + 25 Peanuts	326	0.78	0.42	0.02	± 0.05

Appendix 5. Table of the statistical values for each combination of peanut treatment and feeder treatment for the micro-structural measures of vocalizations recorded during the Food Response experiment. Because pre-stimulus (Phase 1) data could not be collected for the nonfeeder treatments, this table only uses data collected during the stimulus (Phase 2) and post-stimulus (Phase 3) phases.

	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
Center 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

Appendix 6. List of linear discriminants for comparing the microstructure of the calls recorded in the Food Response experiment. 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 7. Plot of the clusters formed using linear discriminant analysis on the 11 micro-structure measures from each vocalization recorded in the Food Response experiment. 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.

Behavior Measured	Stimulus Type	N	Pre-stimulus Phase				Stimulus Phase			
			Mean	Std. Deviation	Std. Error	95% CI	Mean	Std. Deviation	Std. Error	95% CI
Avg. Adults Present	Chickadee	30	2.03	2.16	0.39	± 0.54	1.53	1.34	0.25	± 0.54
	Short	16	1.86	1.31	0.33	± 0.71	1.62	1.43	0.36	± 0.71
	Medium	17	1.72	1.41	0.34	± 0.69	2.01	1.01	0.24	± 0.69
	Scold	20	2.01	1.39	0.31	± 0.64	2.23	1.01	0.23	± 0.64
Vocalizations	Chickadee	30	13.87	39.08	7.14	± 15.87	8.40	27.14	4.95	± 15.87
	Short	16	12.65	23.63	5.91	± 20.92	29.46	37.52	9.38	± 20.92
	Medium	17	2.17	12.72	3.08	± 20.37	64.53	81.67	19.81	± 20.37
	Scold	20	6.52	24.57	5.49	± 18.93	61.97	67.47	15.09	± 18.93
Flight	Chickadee	30	1.33	1.24	0.23	± 0.72	1.50	1.22	0.22	± 0.72
	Short	16	1.32	1.82	0.45	± 0.99	2.26	2.67	0.67	± 0.99
	Medium	17	1.46	1.23	0.30	± 0.96	4.22	3.70	0.90	± 0.96
	Scold	20	1.33	1.18	0.26	± 0.88	3.28	2.39	0.53	± 0.88
Speaker Proximity	Chickadee	30	0.37	1.83	0.33	± 1.62	0.47	2.56	0.47	± 1.62
	Short	16	0.45	1.75	0.44	± 2.21	0.58	2.00	0.50	± 2.21
	Medium	17	3.27	6.65	1.61	± 2.15	6.38	8.74	2.12	± 2.15
	Scold	20	0.02	0.00	0.00	± 1.98	2.92	6.40	1.43	± 1.98
Dominance Posture	Chickadee	30	0.13	0.73	0.13	± 0.34	0.00	0.00	0.00	± 0.34
	Short	16	0.06	0.25	0.06	± 0.47	0.44	0.81	0.20	± 0.47
	Medium	17	0.00	0.00	0.00	± 0.45	1.12	2.39	0.58	± 0.45
	Scold	20	0.30	0.98	0.22	± 0.42	0.1	0.31	0.07	± 0.42
Wing/Tail Flicking	Chickadee	30	0.17	0.46	0.08	± 0.99	0.17	0.46	0.08	± 0.99
	Short	16	0.38	0.87	0.22	± 1.36	1.69	2.99	0.75	± 1.36
	Medium	17	0.29	0.61	0.15	± 1.32	5.17	6.48	1.57	± 1.32
	Scold	20	0.39	0.67	0.15	± 1.21	2.69	4.15	0.93	± 1.21

Appendix 8. Table of the statistical values for the behaviors observed during the pre-stimulus and stimulus phases of the Call Playback experiment. These values were calculated using a linear mixed model with location as a random effect.

Microstructure Measure	Stimulus Type	Pre-stimulus Phase					Stimulus Phase				
		N	Mean	Std. Deviation	Std. Error	95% CI	N	Mean	Std. Deviation	Std. Error	95% CI
Call Duration (msec)	Chickadee	442	293	44	2.10	± 21	242	282	57	3.65	± 21
	Short	164	214	62	4.85	± 22	340	213	65	3.55	± 21
	Medium	86	236	57	6.16	± 24	1144	295	76	2.26	± 20
	Scold	175	320	57	4.27	± 22	1185	296	71	2.06	± 20
Peak Frequency (Hz)	Chickadee	442	1600	149	7.06	± 36	242	1628	171	11.00	± 38
	Short	164	1414	251	19.63	± 41	340	1493	147	7.95	± 38
	Medium	86	1559	289	31.15	± 46	1144	1530	93	2.76	± 34
	Scold	175	1581	121	9.17	± 10	1185	1571	167	4.86	± 34
Vocalizations per Call Group	Chickadee	92	4.91	3.36	0.35	± 0.91	56	3.95	2.72	0.36	± 1.04
	Short	59	1.94	1.25	0.16	± 1.10	89	4.27	1.75	0.19	± 0.99
	Medium	25	2.74	2.47	0.49	± 1.41	264	4.08	3.54	0.22	± 0.74
	Scold	35	4.07	2.65	0.45	± 1.25	260	3.92	3.92	0.24	± 0.73
Call Group Structure (Proportion)	**Stimulus Type**	**N**	**Proportion Structured**	**Std. Deviation**	**Std. Error**	**95% CI**	**N**	**Proportion Structured**	**Std. Deviation**	**Std. Error**	**95% CI**
	Chickadee	92	0.64	0.48	0.05	± 0.10	56	0.82	0.37	0.05	± 0.10
	Short	59	0.78	0.42	0.05	± 0.11	89	0.92	0.27	0.03	± 0.06
	Medium	25	0.76	0.44	0.09	± 0.18	264	0.52	0.50	0.03	± 0.06
	Scold	35	0.91	0.28	0.05	± 0.10	260	0.71	0.45	0.03	± 0.06

Appendix 9. Table of the statistical values for the microstructural measures of the vocalizations uttered by the focal crow during the pre-stimulus and stimulus phases of the Call Playback experiment. These values were calculated using a linear mixed model with location as a random effect.