

Fowl communicate the size, speed and proximity of avian stimuli through graded structure in referential alarm calls

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Many animals produce alarm calls that warn conspecifics about predators. In some species, alarm calls communicate continuous traits associated with a predator encounter, such as its level of threat. In other species, alarm calls communicate categorical traits, such as predator class (e.g. avian versus terrestrial), and are consequently considered functionally referential. In theory, functionally referential alarm calls can simultaneously communicate continuously distributed traits, though examples of such calls are rare. Such dual-function calls could be adaptive because they would enable receivers to tailor their responses to a specific predator class, as well as to more subtle characteristics of individual attacks. Here, we tested whether male fowl (*Gallus gallus*) communicate continuous variation in avian stimuli through graded structure in their functionally referential aerial alarm calls. In the first experiment, we held male fowl in an indoor test cage and allowed them to view wild birds flying past a window. We recorded their alarm calls and compared the structure to the size, speed, and proximity of the eliciting stimuli. Stimuli that appeared closer, larger, and faster elicited alarm calls that were shorter, louder, clearer, and lower in frequency. In the second experiment, we broadcast alarm calls to foraging females and compared their responses to the graded structural changes documented earlier. Females exhibited greater initial responses and finished feeding later in response to louder alarm calls. Together, these results show that fowl communicate the size, speed and proximity of avian stimuli through graded variation in their functionally referential aerial alarm calls.

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Many animals produce alarm calls that alert conspecifics to the presence of predators (reviewed in Zuberbühler 2009). In some species, alarm calls also communicate continuous variation in some aspect of the predator encounter, such as the caller's motivational state or the predator's proximity, size or speed of attack (Darwin 1872; Morton 1977; Blumstein & Armitage 1997; Templeton et al. 2005). These traits can be important correlates of a predator's hunting success, so they may be especially important for determining a receiver's antipredator response (Howland 1974; FitzGibbon 1989). These traits can also be measured for all types of predators and thus may be important to receivers in a wide variety of predator contexts.

In some communication systems, callers produce acoustically distinct alarm calls that correspond to specific external referents (production specificity), such as different types of predators (e.g. Seyfarth et al. 1980) or different types of predator behaviours (e.g.

Griesser 2008). Receivers, upon hearing such calls, show antipredator behaviours that are appropriate for the specific external referent that evoked the alarm (perception specificity). Alarm calls that show both production and perception specificity are termed 'functionally referential' (Macedonia & Evans 1993; Evans 1997), and they have been documented in primates, suricates (*Suricata suricatta*), Gunnison's prairie dogs, *Cynomys gunnisoni*, and birds (Seyfarth et al. 1980; Evans et al. 1993a; Zuberbühler et al. 1999; Manser 2001; Manser et al. 2001; Fichtel & Kappeler 2002; Kiriazis & Slobodchikoff 2006). In general, functionally referential alarm calls are associated with species that use different escape strategies for different types of predators (Macedonia & Evans 1993). In some species, social factors, such as the need to coordinate group movements during foraging, can also contribute to the evolution of functionally referential alarm calls (Furrer & Manser 2009).

Theory predicts that functionally referential alarm calls can simultaneously communicate continuous variation in some aspect of a predator encounter (Marler et al. 1992; Macedonia & Evans 1993). Furthermore, there are no obvious mechanistic constraints. Predator class can be communicated by producing structurally discrete types of alarm calls, whereas continuous traits associated with a predator

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attack can be communicated through graded features of a particular call type (Evans 1997). In principle, there are several ways in which a signal could be designed to simultaneously encode predator class and other information. For example, an animal could produce a functionally referential alarm call repeatedly and encode a continuous trait, such as predator distance, through a sequence-level parameter, such as calling rate. Alternatively, callers could encode a continuous trait in the graded structure of a functionally referential call. For example, highly aroused individuals generally produce harsh, low-frequency calls, whereas less aroused individuals generally produce calls that are clearer and higher in frequency (Morton 1977). Regardless of the specific encoding mechanism, functionally referential alarm calls that simultaneously communicate continuous traits could be highly adaptive because they would allow receivers to tailor their antipredator responses to a specific predator class, as well as to more subtle characteristics of individual predator attacks.

Functionally referential alarm calls that simultaneously communicate continuous traits have only been documented definitively in suricates (Manser 2001; Manser et al. 2001). Callers in this species produce acoustically distinct alarm calls in response to avian and terrestrial predators, and they simultaneously encode the predator's distance into the graded structure of calls. When alarm calls are broadcast in the absence of predators, receivers show antipredator behaviours that are appropriate for both the class and distance of predator that evoked the call (Manser 2001; Manser et al. 2001). Other species, such as tufted capuchin monkeys, *Cebus apella nigrinus*, produce functionally referential alarm calls in some contexts and separate alarm calls that communicate continuous traits in others (Wheeler 2010). However, capuchins are not known to produce functionally referential alarm calls that simultaneously communicate continuous traits (Wheeler 2010). Such dual-function calls probably exist in other species, but the necessary experiments have yet to be conducted. For example, white-browed scrubwrens, *Sericornis frontalis*, communicate the distance to aerial predators by grading the number of elements in their trilled aerial alarm calls (Leavesley & Magrath 2005). Whether trilled aerial alarm calls are functionally referential, however, remains unclear because formal tests of their production specificity have yet to be conducted; calls may be elicited specifically by avian predators, or by all predators more generally (Leavesley & Magrath 2005). Similarly, the mobbing calls of Siberian jays, *Perisoreus infaustus*, encode the type of threat (hawk, owl) and the level of threat (low to high) that is associated with perched raptors (Griesser 2009). Playback experiments necessary for assessing call perception have yet to be conducted, however, so it remains unclear whether mobbing calls communicate predator type and predator threat to receivers in jays (Griesser 2009).

Fowl (*Gallus gallus*) are ideal for studying alarm calling behaviour because they produce two functionally referential alarm calls (Evans

et al. 1993a). The 'terrestrial alarm call' is a loud series of broadband pulses that is produced by both sexes specifically in response to predators approaching on the ground, such as foxes (*Vulpes vulpes*) or racoons (*Procyon lotor*). In response to terrestrial alarm calls, fowl assume an erect posture and scan the horizontal plane (Evans et al. 1993a). The 'aerial alarm call' is acoustically distinct from the terrestrial alarm call and has a highly variable structure (Table 1, Fig. 1, Supplementary Material; see also Figure 4 in Evans et al. 1993a). It is produced only by males in response to a broad class of objects moving overhead, including insects, airplanes and predatory and nonpredatory birds (Gyger et al. 1987; Evans & Marler 1995). Larger and faster aerial stimuli that are shaped like raptors have the greatest probability of evoking these calls (Evans et al. 1993b; Evans & Marler 1995). In response to aerial alarm calls, fowl crouch, scan the sky and seek shelter (Evans et al. 1993a).

The objective of the current study was to determine whether the functionally referential aerial alarm calls of male fowl also communicate continuous traits associated with avian stimuli. In the first experiment (i.e. call production), we held males in an indoor test cage and allowed them to view wild birds flying past a window. In the past, we have noticed males housed indoors producing aerial alarm calls in response to wild birds flying past outside. We therefore took advantage of this opportunity and compared the structure of males' alarm calls to the size, speed and proximity of the eliciting avian stimuli. In the second experiment (i.e. call perception), we played back aerial alarm calls to females and compared variation in their antipredator responses to gradation in the structure of the eliciting calls. We predicted that female responses would be explained best by the acoustic parameters that were correlated with avian stimulus attributes in the call production experiment. By assessing both call production and call perception, we were able to test whether fowl communicate continuous variation in avian stimuli through gradation in their referential aerial alarm calls.

METHODS

Experiment 1: Call Production

In the first experiment, we placed male fowl into an indoor test cage and permitted them to view wild birds and other objects flying past a window outside. To monitor and quantify the naturally occurring stimuli observed by the subjects, we videorecorded the window from the male's perspective and quantified the apparent size, speed and proximity of the stimuli. We also audiorecorded the subject's vocal response, so that we could test for relationships between variation in avian stimulus attributes and gradation in alarm call structure.

Table 1

Description of 334 aerial alarm calls produced by male fowl and the avian stimuli that evoked them in the call production experiment

| Variable | Minimum | Maximum | Average | Coefficient of variation (%) |
|-----------------------------|------------|-------------|-------------|------------------------------|
| Alarm call structure | | | | |
| Length (ms) | 403 (349) | 2154 (882) | 1048 (308) | 53 (19) |
| Amplitude (dB(C)) | 60 (5) | 78 (7) | 69 (5) | 9 (3) |
| Dominant frequency (Hz) | 673 (196) | 1473 (370) | 992 (218) | 26 (10) |
| Entropy (%) | 21 (3) | 33 (4) | 27 (3) | 15 (3) |
| Avian stimuli | | | | |
| Diameter (mm) | 1.5 (1.3) | 35.2 (15.2) | 14.2 (5.8) | 81 (14) |
| Speed (cm/s) | 4.3 (1.8) | 68.1 (34.6) | 23.1 (10.2) | 88 (21) |
| Proximity (index) | 1.1 (0.4) | 2.9 (0.3) | 1.9 (0.4) | 41 (11) |
| PC1 | -1.1 (0.2) | 1.6 (1.1) | 0.0 (0.5) | — |

For each variable, we calculated four parameters for each male (minimum, maximum, average, coefficient of variation). Shown is the average (standard deviation) of each parameter from among the 24 males. 'PC1' is a principal component that incorporates the maximum size, average speed and proximity to subject. Coefficient of variation could not be calculated for PC1 because it involved division by zero. All values are shown prior to transformation.

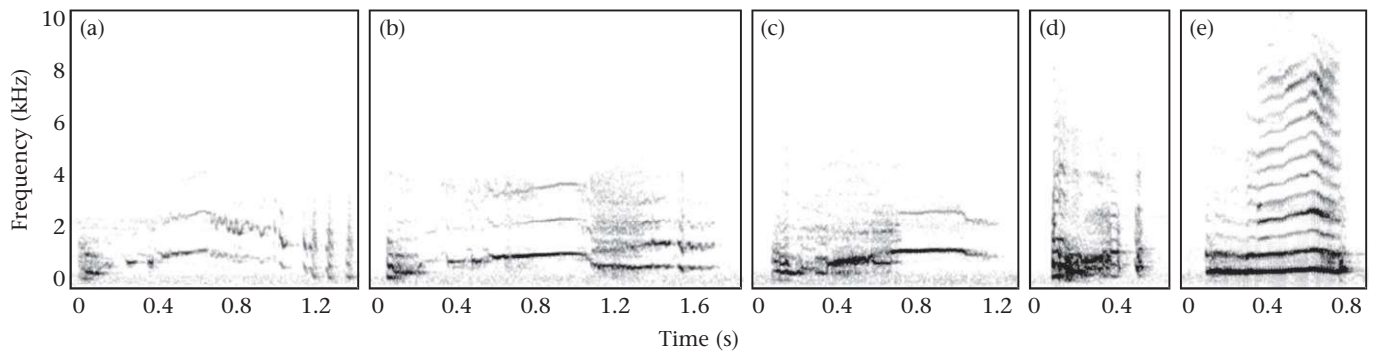


Figure 1. Graded structure of aerial alarm calls. The five calls shown here (a–e) were produced by a single male in the call production experiment, and were used as one of the four sets of playback stimuli in the call perception experiment. Calls are arranged in order of ascending amplitude because amplitude was the only acoustic feature that correlated with both avian stimulus attributes and receiver responses. Spectrograms were generated using a 1024-point FFT, 87.5% overlap, and a Hamming window, which resulted in a frequency resolution of 43 Hz and a temporal resolution of 2.9 ms. Calls were filtered with a band-pass filter (200–12 000 Hz) and are shown at original amplitude. Greyscale represents an amplitude range of 50 dB.

Subjects

Subjects were 24 sexually mature male golden Sebright fowl that were between 1 and 3 years of age. When not being tested, they were kept in a climate-controlled holding facility (temperature: 21 °C; light: overhead incandescent lighting for 12 h, beginning at 0600 hours, as well as natural light from surrounding windows). Each male was paired with one female in a separate wire cage (1 m long, 1 m wide, 0.8 m high) that contained food, water, wooden perches and straw bedding.

Apparatus

During recording sessions, we held subjects in a wire test cage (1.12 m long, 0.45 m wide, 0.73 m high) that had an artificial grass mat, wooden perches and a continuous supply of food and water. The test cage was housed inside a climate-controlled test room (temperature: 21 °C; lighting: incandescent lights for 12 h, beginning at 0600 hours each day) that had a single window to the outside (1.11 m wide, 0.82 m high). The test cage was positioned on a small table, such that its floor was level with the bottom of the window. The longitudinal axis of the test cage was aligned with the centre of the window, and the narrow end of the cage was placed facing the window at a distance of 1.7 m. To reduce acoustic interference from outside the test room, as well as reverberation from within the test cage, we attached 10 cm thick ‘Sonex’ sound-attenuating foam baffles (Illbruck Acoustic, Inc., Minneapolis, MN, U.S.A.) to the back and both sides of the cage, as well as to the wire overhead.

The view from the test cage through the test room window was dominated by several large trees (*Eucalyptus*) in the foreground (0–15 m from window), three small buildings in the mid-ground (15–30 m from window) and several large trees in the background. Sky was visible between tree branches in the upper half of the field of view, and green grass was visible between trees and buildings in the lower half of the field of view. When a subject was in the end of the cage nearest the window (i.e. 1.7 m from window), its horizontal and vertical fields of view through the window were approximately 36° and 27°, respectively. When a subject was in the opposite end of the cage (i.e. 2.8 m from window), its horizontal and vertical fields of view through the window were approximately 22° and 17°, respectively.

We videorecorded aerial stimuli from the subject’s perspective using a Sony Handicam (model: HDR-HC7; format: HDV 1080i50; shutter speed: 1/100 s). The camera was mounted on a tripod at approximately the subject’s eye-height (27 cm above the floor of the test cage) and was placed outside the subject’s cage midway along the side of the cage that faced the test room window. We adjusted the focal length so that the camera’s field of view included the entire window for the remainder of the experiment, so that the

apparent size, speed and proximity of stimuli could be compared across recording sessions. Because the camera was slightly closer to the window, it captured the subject’s complete field of view through the window, regardless of his position within the cage. Video was recorded digitally (format: HDV 1080i50) to the hard drive of a Macintosh computer using QuickTime Pro software (version 7; Apple, Inc., Cupertino, CA, U.S.A.).

We recorded the subject’s vocalizations with a Sennheiser MKH 40-P48 microphone (cardioid pickup pattern; 40–20 000 Hz frequency response, ±1 dB deviation) that was suspended from the centre of the subject’s cage. Calls were digitized using a MOTU UltraLite-mk3 digital interface (48 kHz sampling rate; 24-bit amplitude encoding) and were recorded to the digital sound track (WAVE format, 48 kHz sampling rate, 16-bit amplitude encoding) of the video file that was recording the aerial stimuli. By recording to the same digital file, we ensured precise temporal synchronization of the audio and video tracks. We calibrated our system by recording 30 s of continuous white noise, which we broadcast at 76 dB(C) SPL (measured at a distance of 1 m with a RadioShack sound level meter, model 33-4050, slow response) through a Nagra Kudelski DSM monitor, which was placed on the centre of the test cage floor. After this initial calibration procedure, we did not adjust the gain on the audio-recording system for the remainder of the experiment, which ensured that all vocalizations were recorded at the same level.

Procedure

We recorded subjects between 13 February and 7 May 2008. We began a recording session at 1200 hours by transferring a subject and his female cagemate from the holding facility to the test cage inside the test room. The female was included because males only produce alarm calls in the presence of a conspecific audience (Karakashian et al. 1988; Evans & Marler 1992). The pair was given until 3 h before sunset to acclimate to the test cage (time of sunset determined at –33°50′00″ latitude, 151°15′00″ longitude). Audio and video recording began at that time and continued until sunset, at which time the birds went up to roost and became silent. We resumed recording the next morning at sunrise and continued for an additional 4 h, resulting in a total of 7 h of audio and video recording per subject. We programmed all recordings to begin and end automatically, thus eliminating the need for a human observer to enter the test room during a recording session. Following a recording session, we returned the subject and his mate to the holding facility, replaced the food, water and artificial grass mat in the test cage, and cleaned the test room window.

Our goal was to record at least 10 alarm calls per subject. To achieve this, we reviewed the audio recordings following the first

round of 24 recording sessions (see Sound Analysis details below). Males that had not produced 10 alarm calls in the first round were recorded again in a second round. The recording procedure for the second round was identical to that of the first, and subjects were recorded in the same order. Of the 24 subjects recorded in the first round, 16 were recorded in the second round, resulting in a total of 280 h of audio and video recording.

Quantifying stimulus attributes and alarm call structure

We identified alarm calls on the original recordings using Soundtrack Pro software (version 2.0.2; Apple, Inc., Cupertino, CA, U.S.A.). For each recording, we listened to the audio track at approximately natural amplitude while simultaneously viewing the video track and a scrolling real-time spectrogram of the audio track (512-point fast Fourier transform (FFT), 87.5% overlap, Hamming window). When we detected an alarm call (see example spectrograms in Fig. 1; example audio files are provided in the [Supplementary Material](#)), we noted the exact time (40 ms resolution) on a permanent time code that we had superimposed on the video track, and then saved the alarm call into two separate digital files. The first file contained the video track only (format: HDV 1080i50) and was used to characterize the aerial stimuli that evoked the alarm calls. The second file contained the audio track only (WAVE format, 44.1 kHz sampling rate, 16-bit amplitude encoding) and was used to quantify alarm call structure. Both files included 30 s of the original recording before and after the alarm call. Females do not produce aerial alarm calls, so we were confident that the male subject produced all recorded calls.

Extracted video clips were displayed on a high-resolution external video monitor (1920 × 1080 pixels resolution) that we controlled with Final Cut Pro software (version 6.0.6; Apple, Inc.). For each of the 695 video clips, we searched frame by frame for aerial stimuli during a 5 s measurement window that immediately preceded the alarm call. The beginning and end of the measurement window were selected relative to the video's permanent time code, thus keeping the observer blind to the structure and sound of the corresponding alarm call. After detecting a stimulus, we categorized it as avian or nonavian and excluded all nonavian stimuli (e.g. flying invertebrates, falling leaves) from subsequent analysis ($N = 217$ clips). We also excluded clips in which an avian stimulus was airborne for less than two video frames (i.e. <80 ms) during the measurement window ($N = 39$ clips) because it was not possible to measure the speed of such stimuli. If more than one avian stimulus was present during the measurement window ($N = 52$ clips), we measured only the one closest in time to the alarm call.

We measured the following three variables for every avian stimulus: (1) maximum diameter (a measure of the size of the avian stimulus from the subject's perspective), (2) average speed and (3) proximity to subject. To determine maximum diameter, we measured the largest diameter of the stimulus in every video frame in which it was visible during the 5 s measurement window, and then noted the maximum value of these measures. Measurements were made by placing a transparent ruler directly onto the video monitor. To determine average speed, we divided the linear distance travelled by the stimulus during the 5 s measurement window by the period of time for which it was visible. Linear distance was measured by placing a transparent ruler directly onto the monitor and stepping frame by frame through the video; the measure did not incorporate deviations from a linear flight path. To determine the proximity to the subject, we compared the position of the stimulus to landmarks in the video (e.g. trees, buildings). Based on known distances between the landmarks and the video camera, we could approximate the minimum distance between the stimulus and the camera. The resolution of this method was limited by the spacing of landmarks and the difficulty of estimating depth from a two-dimensional video; consequently, we

quantified proximity using an ordinal scale that was based on landmark positions (1 = 0–15 m; 2 = 15–30 m; 3 = 30+ m).

For each avian stimulus that we measured, we also measured the fine structure of the corresponding alarm call using SASLab Pro software (version 4.40; Avisoft Bioacoustics, Berlin, Germany). We filtered each extracted audio file with a band-pass filter (200–12 000 Hz), which removed background noise without affecting the structure of the alarm call (Wilson & Evans 2010). We then generated a spectrogram (1024-point FFT, 87.5% overlap, Hamming window, 2.9 ms temporal resolution, 43 Hz frequency resolution; Fig. 1) and used the 'automatic parameter measurements' feature (settings: holdtime, 100 ms; threshold, -30 dB relative to maximum amplitude) to select the alarm call and measure its structure. If the subject produced more than one alarm call in response to a particular avian stimulus, then we selected and measured only the first. We measured four structural features, including (1) call length, (2) amplitude, (3) dominant frequency and (4) entropy. Amplitude is the root-mean-square amplitude of the entire call, and dominant frequency is the frequency with the highest amplitude. Entropy is a measure of sound purity that approaches 0 for pure tones and 100 for white noise; it is the ratio of the geometric mean to the arithmetic mean of the spectrum, multiplied by 100. Dominant frequency and entropy were measured from every FFT within the alarm call and were then averaged (separately for each variable) for statistical analysis.

Statistical analysis

Preliminary analyses revealed that the three independent variables (i.e. maximum diameter, average speed, proximity to subject) were highly intercorrelated. To avoid potential problems associated with multicollinearity, we conducted a principal components analysis on the three independent variables (see Table 2) and used only the derived factor scores in subsequent statistical analyses.

We used linear mixed model analysis to test for relationships between avian stimulus attributes and alarm call structure. A single principal component derived from the three original avian stimulus variables was entered as a covariate with fixed effects, and male identity was entered as a subject variable with random effects to account for repeated measures of the same individuals. A separate model was constructed for each of the four measures of alarm call structure. For each model, we estimated fixed effects using the restricted maximum likelihood method and modelled the subject effect by assuming a variance components covariance structure. Residuals were not normally distributed for three of the four models, but were corrected by applying a square-root transformation to call length and a log transformation to dominant frequency and entropy. All other model assumptions were satisfied. Tests were two tailed, and we considered results to be statistically

Table 2
Details of the principal components analysis used to describe 334 avian stimuli recorded in the call production experiment

| Variable | PC1 |
|------------------------|-------|
| Diameter (mm) | 0.94 |
| Speed (cm/s) | 0.88 |
| Proximity (index) | -0.89 |
| Eigenvalue | 2.45 |
| Variance explained (%) | 81.7 |

Component loadings are provided for the single extracted principal component (PC1). Analysis was based on the correlation matrix and unrotated components were extracted when eigenvalues exceeded 1. Sampling adequacy was assessed using Bartlett's test, and the hypothesis that the correlation matrix contained only zero correlations was rejected ($\chi^2_3 = 595.8$, $P < 0.001$). Component scores were generated using the regression method.

significant when $P \leq 0.05$. All analyses were conducted in PASW (version 18.0 for Macintosh; Chicago, IL, U.S.A.).

Experiment 2: Call Perception

In the second experiment, we tested whether female fowl respond appropriately to gradation in the structure of aerial alarm calls. We played back alarm calls, and then compared female responses to variation in call structure, which we quantified according to the structural measures described in experiment 1.

Subjects

Subjects were 32 sexually mature female golden Sebright fowl that were between 2 and 7 years of age. Of the 32 females tested, 24 had served as a conspecific audience in the first experiment. When not being tested, subjects were paired with males and kept in the same conditions and climate-controlled holding facility as in the call production study.

Apparatus

During playback trials, we held subjects in a wire test cage (1.12 m long, 0.45 m wide, 0.73 m high) that was placed on the floor in the centre of a sound-attenuating chamber (Ampliscience, model 10070; Robassomero, Italy). The chamber measured 2.38 m wide \times 2.38 m long \times 2.15 m high and was lined with 10 cm thick 'Sonex' foam baffles on the walls and 15 cm thick baffles on the ceiling to prevent reverberation. The cage had an artificial grass mat, a continuous supply of water, and light provided by two incandescent lamps (60 W). A remotely operated food dispenser was placed above the cage and was used to deliver fresh corn to the centre of the cage floor during trials. To broadcast alarm call stimuli, we placed a Nagra Kudelski DSM monitor midway along the length of the test cage, abutting the side. The monitor was connected through a conduit panel in the chamber wall to a Behringer digital-to-analogue converter (model FCA202, 24 bits/96 kHz) and a Macintosh computer that played stimuli using QuickTime Pro software (version 7; Apple, Inc.). Subjects were monitored with a Panasonic video camera (model WV-CL320) and a Sennheiser microphone (model MHK 40-P48) connected to a Canopus analogue-to-digital converter (model ADV110) through the conduit panel. This was connected to a second Macintosh computer, which recorded trials using QuickTime Pro software.

Prior to commencing playbacks, we calibrated the playback system by broadcasting the white noise that we had recorded during the call production study. We adjusted the playback level so that the white noise measured precisely 76 dB(C) SPL at a distance of 1 m (i.e. the same level used during recording). The playback level was not adjusted for the remainder of the playback experiment, which ensured that each alarm call was broadcast at the same amplitude at which it had been produced (mean \pm SD = 70 \pm 8 dB(C) SPL at a distance of 1 m).

Stimuli

Playback stimuli were 20 high-quality aerial alarm calls recorded during the call production study (Table 3, Fig. 1, Supplementary

Material). For each of four males, we selected five calls that were, as far as possible, evenly distributed across the range of variation observed in the call production study (Table 1, 3, Fig. 1, Supplementary Material). Using Raven Interactive Sound Analysis software (version 1.3 Pro, Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, NY, U.S.A.), we extracted the calls from the original recordings, plus 100 ms of silence before and after each call. We removed background noise with a band-pass filter (200–12 000 Hz; Wilson & Evans 2010), and then saved the calls as separate digital files (WAVE format, 48 kHz sample rate, 16-bit amplitude encoding). We did not normalize the sound files because we wanted to preserve natural amplitude gradation among calls.

Procedure

We tested subjects between 2 August and 9 September 2008 using a randomized complete block design. We assigned the 32 hens at random to four equal-sized groups (i.e. eight per group), and then tested each group daily during a different 5-day period. Each group was tested with alarm calls derived from different stimulus males (i.e. four stimulus males corresponding to four groups of subjects, with the constraint that subjects were not tested with alarm call stimuli recorded from their cagemates), and each subject within the group was tested with the same set of five alarm calls (i.e. one alarm call per day in a random order). Subjects were tested individually each day in either the morning (0800–1100 hours) or the afternoon (1500–1800 hours) to correspond to peak foraging periods. A given hen was always tested at the same time each day.

Prior to testing a group, we habituated each subject in the group to the test apparatus. We placed one of the eight subjects into the test cage and allowed her to move freely around the cage for approximately 15 min. During that time, we delivered five kernels of fresh corn to the centre of the test cage floor using the remotely operated food dispenser. We repeated this habituation procedure each day until every subject in the group walked readily around the cage, did not become startled by the food dispenser, and consumed all of the corn that was delivered (range 3–11 habituation cycles per subject).

We began testing a group on the day after all birds had habituated to the test apparatus. A trial began by placing one of the eight subjects into the test cage, closing the chamber door and initiating the recording procedure. The observer controlled the experiment from outside the chamber, viewing the subject remotely on the computer monitor. When the subject began moving around the cage, we delivered five kernels of fresh corn to the centre of the test cage floor. As soon as the subject pecked at the corn, we broadcast an alarm call stimulus and continued recording the subject until she consumed all of the remaining corn (4–59 s), or for 10 min if she did not resume feeding. We then returned the subject to the holding facility, replaced the mat in the test cage and reloaded the food dispenser with fresh corn.

Quantifying female responses

Prior to scoring female responses, we viewed the trial recordings using QuickTime Pro software. When the corn was delivered, we stepped frame by frame through the video and noted the exact time

Table 3
Description of the 20 aerial alarm calls that were used as stimuli in the call perception experiment

| Variable | Minimum | | Maximum | | Average | | Coefficient of variation (%) | |
|-------------------------|---------|------|---------|-------|---------|------|------------------------------|-----|
| Length (ms) | 473 | (48) | 1361 | (180) | 958 | (75) | 38 | (7) |
| Amplitude (dB(C)) | 61 | (4) | 81 | (4) | 70 | (1) | 11 | (2) |
| Dominant frequency (Hz) | 655 | (99) | 1165 | (214) | 926 | (30) | 22 | (1) |
| Entropy (%) | 24 | (3) | 33 | (3) | 28 | (1) | 13 | (4) |

For each variable, we calculated four parameters for each male (minimum, maximum, average, coefficient of variation). Shown is the average (standard deviation) of each parameter from among the four stimulus males.

at which the alarm call stimulus was played, relative to the video's time code (40 ms resolution). We then scored female responses to alarm call stimuli by viewing the recordings again with the audio track muted. This method allowed us to score female responses relative to when the alarm call was played, but ensured that the observer was not influenced by listening to the eliciting call.

We measured two dependent variables from every trial: (1) initial response and (2) time to finish feeding. Initial response was scored as the immediate reaction to the onset of the alarm call and was quantified according to the six-level ordinal scale defined by Evans et al. (1993b) as follows.

- (1) No visible response.
- (2) Looking upwards (typically by rolling the head to fixate with one eye).
- (3) Looking upwards and flexing the neck, so as to draw the head towards the body.
- (4) Responses 2 and 3, together with perceptible crouching.
- (5) Responses 2 and 3, together with pronounced crouching, so that the body makes contact with the floor.
- (6) Responses 2, 3 and 5, together with running in a crouched posture.

Time to finish feeding was designed to reflect the trade-off between foraging and vigilance. It was defined as the time from the onset of the alarm call stimulus to when the subject consumed the last kernel of corn. If a subject did not consume all of the corn after the alarm call was played, we set time to the maximum value observed among the 32 subjects on that particular test day (i.e. test days 1–5). Subjects did not consume all of the corn in 7 of the 160 playback trials.

Statistical analysis

We used linear mixed model analysis to test for relationships between alarm call structure (independent variables) and female response (dependent variables). Our measures of alarm call structure were derived directly from the call production study (see above), and included call length, amplitude, dominant frequency and entropy. These four measures, as well as test day (i.e. 1–5), were entered into the model as covariates with fixed effects. Female identity was entered as a subject variable with random effects to account for repeated measures of the same individuals. We constructed a separate model for each measure of female response. For each model, we estimated fixed effects using the restricted maximum likelihood method and modelled the subject effect by assuming a variance components covariance structure. Preliminary analyses revealed a two-way interaction between test day and amplitude in the model explaining initial response. Therefore, in the final model explaining initial response, we included as covariates with fixed effects all two-way interactions between test day and the four measures of alarm call structure. No interaction effects were detected in the model explaining time to finish feeding, so interactions were not included in this model. Residuals were not normally distributed in the model describing time to finish feeding, but were corrected by applying a log transformation to the dependent variable. All other model assumptions were satisfied. Tests were two tailed, and we considered results to be statistically significant when $P \leq 0.05$.

RESULTS

Experiment 1: Call Production

Of 695 aerial alarm calls produced by 24 subjects during 280 h of recording, 373 (54%) were associated with a clear avian stimulus, 217 (31%) with a nonavian stimulus (e.g. invertebrates, falling leaves) and 105 (15%) with no discernable aerial stimulus. Of the 373 calls

that were associated with an avian stimulus, we excluded 39 because the stimulus was not present on two or more video frames. Analyses were therefore based on 334 aerial alarm calls that were associated with a clear avian stimulus during the 5 s immediately preceding the call (mean \pm SD = 1.3 ± 0.9 calls/subject/h; range 0.1–4.0 calls per subject per h). In general, we could not ascertain the species of avian stimuli because the lighting conditions (i.e. dim light inside the test room, bright light outside the test room) caused the avian stimuli to appear very dark on the video recordings. The few stimuli that we could identify included predatory birds, such as Australian magpies, *Cracticus tibicen*, kookaburras, *Dacelo novaeguinae*, and unidentified raptors, as well as nonpredatory birds, such as parrots (Cacatuidae, Psittacidae) and honey-eaters (Meliphagidae). The brown goshawk, *Accipiter fasciatus*, was the only raptor that was observed regularly at our study site.

Avian stimuli were highly variable in terms of maximum diameter, average speed and proximity to subject, as measured from the video on an external monitor (Table 1). In addition, the three variables were highly intercorrelated and thus loaded heavily onto a single principal component that explained 82% of the variance in the original three variables (Table 2). Maximum diameter and average speed loaded positively onto the principal component, whereas proximity to subject loaded negatively onto the principal component. Consequently, a high principal component score reflects a close, large and fast-moving avian stimulus.

The principal component describing the avian stimuli accounted for a significant amount of the gradation in alarm call structure (Fig. 2). In response to stimuli that appeared larger, closer and faster moving, subjects produced shorter alarm calls (linear mixed model analysis: $F_{1,327} = 40.8$, $P < 0.001$) with higher amplitude ($F_{1,323} = 38.5$, $P < 0.001$), lower dominant frequency ($F_{1,322} = 39.4$, $P < 0.001$) and less random energy distribution ($F_{1,325} = 8.7$, $P = 0.003$). In contrast, stimuli that appeared smaller, more distant and slower moving elicited longer alarm calls that had lower amplitude, higher dominant frequency and more randomly distributed energy (Fig. 2).

Experiment 2: Call Perception

Females usually responded to the playback of male alarm calls by crouching, rolling their head to the side and looking upwards with one eye. They also stopped consuming corn and remained still for up to 1 min. Alarm call structure and test day both had a significant effect on female response (Fig. 3). The initial response was stronger in response to louder alarm call stimuli, but declined significantly over the 5-day test period (Fig. 3a). Furthermore, the effect of amplitude on initial response diminished over time, as reflected by a significant interaction between test day and amplitude (linear mixed model analysis: test day: $F_{1,138} = 8.1$, $P = 0.005$; amplitude: $F_{1,142} = 16.3$, $P < 0.001$; test day \times amplitude interaction: $F_{1,139} = 14.5$, $P < 0.001$; Fig. 3a). Initial response was not affected by the other measures of alarm call structure, or by their interactions with test day (linear mixed model analysis: call length: $F_{1,145} = 0.0$, $P = 0.903$; dominant frequency: $F_{1,139} = 0.5$, $P = 0.494$; entropy: $F_{1,140} = 0.4$, $P = 0.510$; test day \times call length interaction: $F_{1,147} = 0.3$, $P = 0.571$; test day \times dominant frequency interaction: $F_{1,139} = 0.6$, $P = 0.439$; test day \times entropy interaction: $F_{1,136} = 0.0$, $P = 0.900$). As with initial response, the time to finish feeding was longer in response to louder alarm call stimuli, but declined significantly over the 5-day test period (linear mixed model analysis: test day: $F_{1,124} = 33.8$, $P < 0.001$; amplitude: $F_{1,150} = 8.0$, $P = 0.005$; Fig. 3b). Time to finish feeding was not affected by the other measures of alarm call structure (linear mixed model analysis: call length: $F_{1,140} = 1.9$, $P = 0.166$; dominant frequency: $F_{1,154} = 2.5$, $P = 0.114$; entropy: $F_{1,153} = 2.3$, $P = 0.128$).

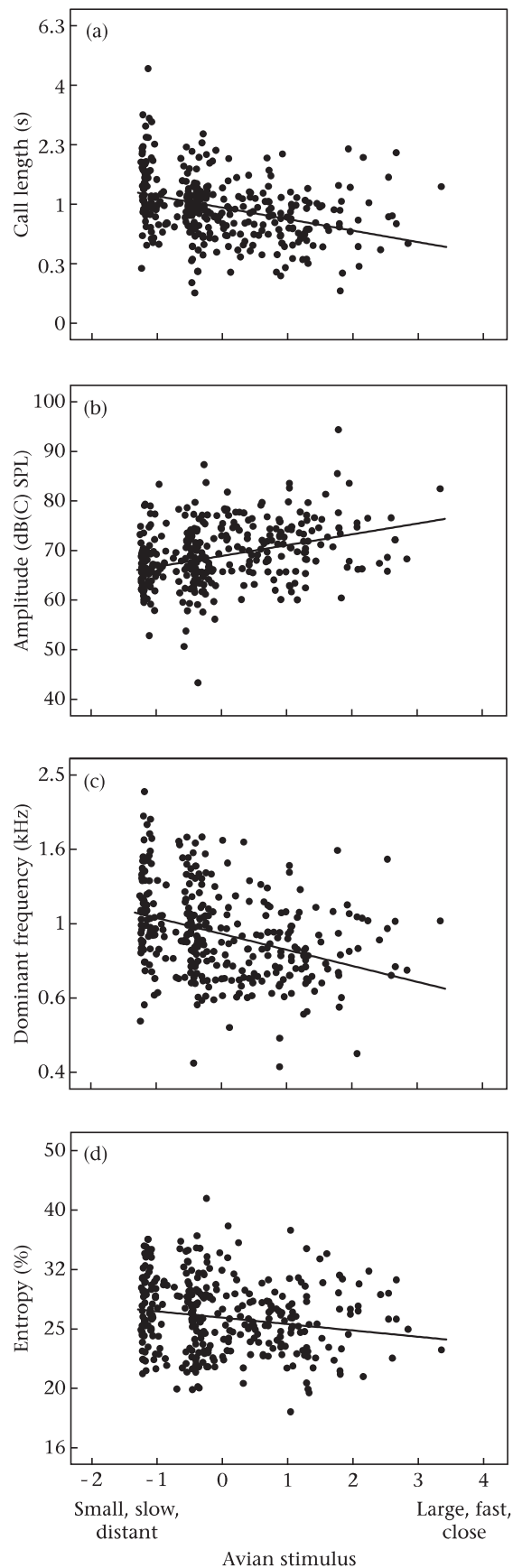


Figure 2. Relationship between avian stimulus attributes and alarm call structure. Shown on the abscissa is a principal component that incorporates the size, speed and

DISCUSSION

Male fowl encoded continuous traits associated with avian stimuli into several graded parameters of their functionally referential aerial alarm calls. Stimuli that appeared closer, larger and faster elicited alarm calls that were shorter, louder, clearer and lower in frequency. Female receivers ignored gradation in the duration, frequency and entropy of alarm calls, but responded appropriately to gradation in alarm call amplitude. In response to louder alarm calls, females showed stronger initial responses and took longer to finish feeding. Together, these results show that fowl communicate continuous variation in avian stimuli through graded structure in their functionally referential aerial alarm calls.

Gradation in the structure of alarm calls correlated with continuous variation in both stimulus attributes and receiver responses. This pattern is consistent with urgency-based calling, which has been described in ground squirrels, birds, suricates and primates (Owings & Hennessy 1984; Blumstein & Armitage 1997; Manser 2001; Manser et al. 2001; Warkentin et al. 2001; Fichtel & Hammerschmidt 2002; Leavesley & Magrath 2005; Templeton et al. 2005; Fallow & Magrath 2010). As in these other systems, however, the precise cause of gradation in alarm call structure is unclear (Evans 1997). It could reflect the size, speed or proximity of avian stimuli, or the risk of predation associated with these physical properties. Another possibility is that gradation in call structure instructs receivers about how to respond (i.e. imperative), rather than denoting stimulus characteristics per se (i.e. denotative; Cheney & Seyfarth 1990; Marler et al. 1992). Finally, gradation could reflect the caller's affective state, which logically correlates with those stimulus characteristics that predict attack (Morton 1977; Evans 1997). Future studies could address this latter possibility by testing whether predator attributes affect physiological measures that are associated with the caller's affective state (Cabanac & Aizawa 2000; Walker et al. 2006).

Gradation in the amplitude of alarm calls affected female responses and thus had communicative value. In addition, receivers appeared to respond adaptively to this gradation, since they resumed feeding sooner in response to quieter calls that were putatively associated with less dangerous predators (FitzGibbon 1989). Female responses also diminished over time, which could reflect habituation to a novel environment. We have observed similar effects in male fowl, whose alarm calling rates declined steadily for several weeks following their introduction to a novel outdoor environment (Wilson & Evans 2008; Wilson et al. 2010). Alternatively, reduced female responsiveness could reflect caller reliability. In our experimental design, we repeatedly broadcast alarm calls from the same male in the absence of predators, which made him progressively less reliable. Since the alarm calls of fowl are individually distinctive (Bayly & Evans 2003), it is possible that females became less responsive as the alarm calls of an individual male consistently failed to predict aerial predators. Richardson's ground squirrels, *Spermophilus richardsonii*, yellow-bellied marmots, *Marmota flaviventris*, and vervet monkeys, *Chlorocebus aethiops*, all discriminate between the alarm calls of reliable and unreliable individuals (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004).

proximity of 334 avian stimuli. Shown on the ordinates are the (a) call length, (b) amplitude, (c) dominant frequency and (d) entropy of the 334 corresponding alarm calls ($N = 24$ males). Note the nonlinear ordinate scales for call length, dominant frequency and entropy (see text for details of associated transformations). To elucidate the relationship between avian stimulus attributes and within-male gradation in alarm call structure, we removed between-male differences in alarm call structure by centering each male's measurements for a given variable on that variable's overall sample mean. Regression lines were calculated from the slope and intercept coefficients generated by the linear mixed model analyses.

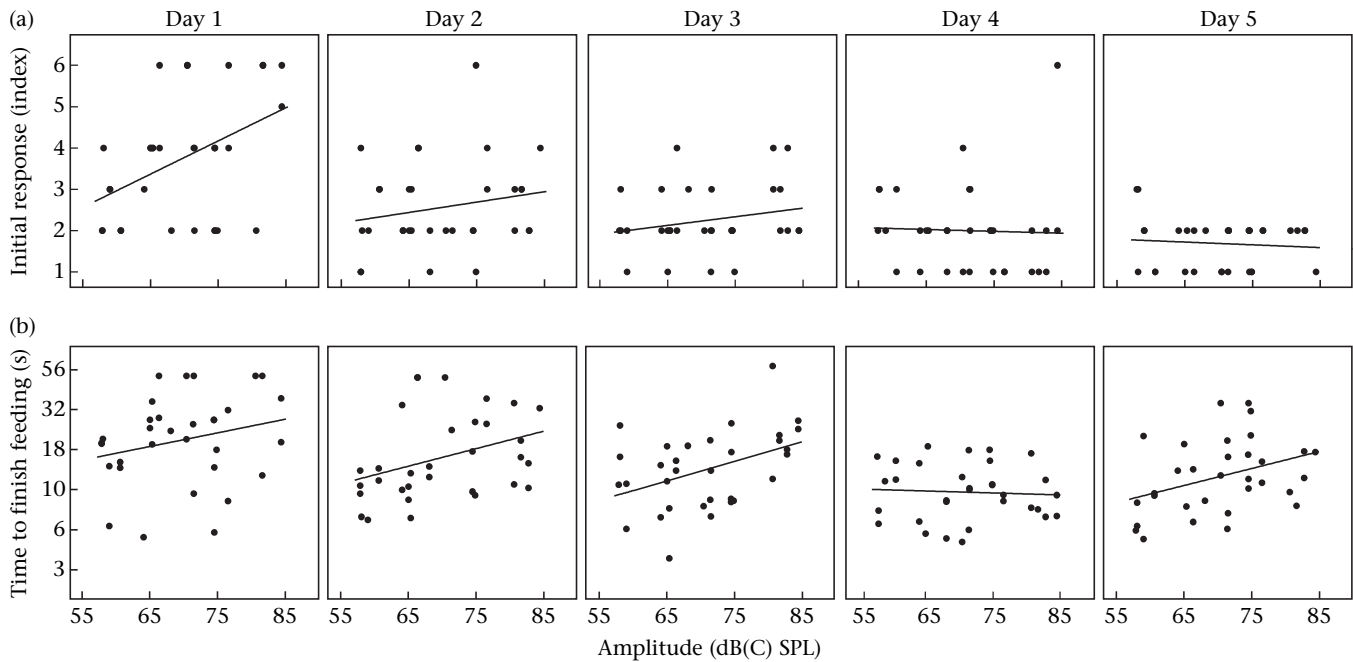


Figure 3. Relationship between alarm call structure and female response over a 5-day test period ($N = 32$). Shown on the abscissa is the amplitude of the eliciting alarm call stimulus. Shown on the ordinates are (a) initial response and (b) time to finish feeding. Note the nonlinear ordinate scale for time to finish feeding.

Amplitude was the only acoustic feature we measured that correlated with both stimulus attributes and receiver responses. In general, animals produce louder calls when they are highly aroused (Darwin 1872; Driver & Humphries 1969; Scherer 1985; Conover 1994; Jurisevic & Sanderson 1998; Rendall 2003; Soltis et al. 2009; but see Searcy & Nowicki 2006). Furthermore, louder calls are generally more evocative than quiet calls (Brenowitz 1989; Blumstein & Armitage 1997; Fichtel & Hammerschmidt 2002; Lampe et al. 2010; Brumm & Ritschard 2011). Gradation in call amplitude thus provides a simple, noncognitive mechanism for adapting receiver responses to those predator attributes that directly influence a caller's affective state. A potential disadvantage of using amplitude gradation for communication is that amplitude can vary as a function of wind gusts, topography, vegetation, movement of the caller's head, and other, presumably irrelevant, factors. Furthermore, calls necessarily attenuate as they travel from caller to receiver (Bradbury & Vehrencamp 1998). In fowl, however, the effects of attenuation and these other miscellaneous factors are probably minimal because males only produce aerial alarm calls when accompanied closely by a conspecific audience (Karakashian et al. 1988; Evans & Marler 1992). In social groups, most aerial alarm calls are given by alpha males, which associate closely with hens and keep other males at a distance (Wilson et al. 2008, 2009; Kokolakis et al. 2010).

Avian stimuli affected several acoustic parameters of alarm calls that failed to predict receiver responses. These relationships potentially can be explained by mechanisms that also are unrelated to receiver responses. For example, the apparent effect of avian stimulus attributes on call length could be an artefact of varying call amplitude. In order to produce a loud, continuous call, the caller must expel the air in its air sacs at a high rate, which rapidly depletes its air supply and results in a short call (Plummer & Goller 2008). Similarly, the effect of stimulus attributes on dominant frequency can be explained by Morton's (1977) motivation-structural rules, which predict that animals will produce lower-frequency sounds in highly arousing situations. In contrast to dominant frequency, the observed effect of stimulus attributes on alarm call entropy contradicts Morton's (1977) motivation-

structural rules, which predict that animals will produce noisier calls (i.e. greater entropy) when they are highly aroused. Surprisingly, fowl produced alarm calls with lower entropy in response to stimuli that we assume were highly arousing. Similar results have also been found in other species, suggesting that highly aroused individuals may produce clearer vocalizations more generally. For example, yellow-bellied marmots (Blumstein & Chi 2011), piglets, *Sus scrofa* (Puppe et al. 2005) and goats, *Capra hircus* (Siebert et al. 2011) all produce clearer vocalizations when they are highly aroused.

By grading the structure of alarm calls in relation to predator distance, callers can potentially mitigate the predation costs associated with calling. For example, Richardson's ground squirrels remain cryptic by producing short-range ultrasonic alarm calls in lieu of long-range audible alarm calls when predators are distant and unlikely to have detected them (Wilson & Hare 2006). Our results suggest that fowl use a similar strategy for reducing predation risk. When predators were distant and unlikely to have noticed potential callers, males produced low-amplitude, high-frequency alarm calls that are known to be cryptic (Marler 1955; Klump & Shalter 1984; Wood et al. 2000). This finding is consistent with a recent study on risk management, which showed that male fowl have a greater probability of producing alarm calls when concealed under cover (Kokolakis et al. 2010). In contrast, when predators were close and likely to have already noticed the caller, males produced loud, low-frequency alarm calls. These characteristics typically indicate a caller's willingness to defend itself and may consequently function as threat signals (Morton 1977). Furthermore, these calls were similar to the 'distress calls' produced by many birds. Distress calls are thought to startle predators during the final stages of attack (Driver & Humphries 1969; Conover 1994), so this may be an additional function of the loud, low-frequency alarm calls observed in our study.

In conclusion, fowl have a remarkably complex alarm communication system in which they produce acoustically distinct alarm calls in response to aerial and terrestrial predators. Receivers, upon hearing alarm calls, respond with categorically distinct

antipredator behaviour that is specific to the type of predator that evoked the call. By recording males' alarm-calling responses to naturally occurring avian stimuli, and by comparing variation in females' responses to gradation in alarm call structure, the current study reveals additional complexity in this system. Specifically, we show that male fowl encode continuous variation in avian stimuli through gradation in the fine structure of their functionally referential aerial alarm calls. Stimuli that appear closer, larger and faster elicit alarm calls that are shorter, louder, clearer and lower in frequency. We also show that females ignore gradation in the duration, frequency and entropy of alarm calls, but respond appropriately to gradation in call amplitude. In response to louder alarm calls, females show stronger initial responses and take longer to finish feeding. Together, these results provide the first definitive evidence that a bird can communicate continuous variation in avian stimuli through gradation in the fine structure of their functionally referential alarm calls.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.11.033.

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