



# Sound repetition rate controls the duration of tonic immobility in chicks (*Gallus gallus*)



Sharon T. Pochron\*, Roger K.R. Thompson

Department of Psychology, Franklin and Marshall College, Lancaster, PA, 11760, USA

## ARTICLE INFO

### Keywords:

Alarm call  
Attraction call  
Death feigning  
Internote interval  
Note duration  
Thanatosis

## ABSTRACT

Tonic Immobility (TI) functions as anti-predator defense. Its duration depends on cues signaling predator proximity. One such cue includes alarm calls from conspecifics and non-conspecifics. This study aimed to determine the cue within alarm calls that controls TI duration. We induced TI in chicks (*Gallus gallus*) and found that their TI durations increased in the presence of adult conspecific alarm calls, non-conspecific alarm calls, and synthetic sounds made of white noise set to the repetition rate found in natural alarm calls. Moreover, chicks did not increase their TI durations when exposed to conspecific attraction calls, synthetic sounds made of white noise set to the repetition rate found in natural attraction calls, and derived sounds made of a natural alarm call lacking an internote interval. We then created: 1) sounds with white noise set to the internote interval found in natural alarm calls and the note duration found in natural attraction calls, and 2) sounds with white noise set to the internote interval found in natural attraction calls and the note duration found in natural alarm calls. Neither affected TI duration. We conclude that repetition rate acts as a salient cue that lengthens TI duration.

## 1. Introduction

To avoid death by predation, invertebrate and vertebrate prey species have evolved a diversity of anti-predator mechanisms, some of which require deployment late in the sequence of a predation event (Humphreys and Ruxton, 2018). Tonic Immobility (TI; sometimes called death feigning) is one such mechanism, used as a last resort, and generally occurring after the predator has physically restrained the prey. During TI, the prey adopts a relatively immobile state that can last from seconds to hours after the physical restraint has ceased (Gallup, 1974; Rogers and Simpson, 2014; Humphreys and Ruxton, 2018). TI can function to reduce the perceived need of the predator to further subdue the prey, thereby increasing opportunities for the prey to escape and survive (Sargeant and Eberhardt, 1975; Thompson et al., 1981; Miyatake et al., 2004; Cassill et al., 2008; Humphreys and Ruxton, 2018).

TI duration is sensitive to auditory and visual cues that signal the proximity of danger (Humphreys and Ruxton, 2018). For example, Gallup (1977) found that young chickens remained in TI longer when exposed to predators, artificial eyes, and a visual cliff, all cues that potentially signal imminent danger. Arduino and Gould (1984) found that young chickens demonstrated longer TI durations in situations where the bird might perceive the chance of escape to be lower (e.g.

when a hawk model faced the chick) compared to cases when this chance might be considered higher (e.g. when the hawk model faced away from the chick).

Thompson and Liebreich (1987) described a fear-caught alarm call and a follow-me attraction call; while researchers have not yet assessed what these sounds subjectively mean to the hens themselves, a link between behaviour and the call exists. Specifically, adult chickens emit the fear-caught call when captured, and when hens emit the follow-me call, their chicks follow them. Thompson and Liebreich (1987) reported that chicks remained in TI longer when exposed to the fear-caught call relative to the follow-me call. They also found that both aerial-predator and ground-predator alarm calls lengthened TI duration. Jones (1986) reported similar results to those of Thompson and Liebreich (1987) in adult chickens.

Consistent with Thompson and Liebreich's (1987) demonstration of functional differences between the fear-caught call and the follow-me call, Collias and Joos (1953) reported that these two calls differ acoustically. The fear-caught call has a relatively long sustained note duration of  $0.54 \pm 0.06$  s whereas the follow-me attraction call has a relatively short note duration of  $0.12 \pm 0.03$  s. Both studies used the same recordings, described in detail below, linking the acoustic structure of particular sounds to specific behaviours.

The fact that fear-caught and follow-me calls differ in both function

\* Corresponding author. Present address: Sustainability Studies Program, School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY, 11794, USA

E-mail address: [Sharon.pochron@stonybrook.edu](mailto:Sharon.pochron@stonybrook.edu) (S.T. Pochron).

<https://doi.org/10.1016/j.beproc.2019.103901>

Received 14 March 2019; Received in revised form 6 June 2019; Accepted 2 July 2019

Available online 02 July 2019

0376-6357/ © 2019 Published by Elsevier B.V.

(Thompson and Liebreich, 1987) and acoustic structure (Collias and Joos, 1953) suggests that a predictable acoustical feature may well influence TI duration. Specifically, chicks that hear noises consistent with danger (e.g. alarm calls) and remain in TI may evolutionarily outcompete chicks that ignore such information. Determining the acoustic feature of alarm calls that increases the duration of TI can elucidate the auditory cue to which young chickens attend.

When pilot studies in our laboratory suggested that the dominant frequency and rise/decay times of the fear-caught call did not significantly control TI duration (Kanik, 1984; Sanders, 1985), we turned our focus to repetition rate, which had been implicated in both the excitation and inhibition of locomotion in mallard ducklings (*Anas platyrhynchos*). Specifically, field observations of six mallard hens with their broods revealed that the vocal behaviour of ducklings was excited by a call that mothers use to attract their young, and the vocal behaviour of the young was inhibited by a different call that mothers use to elicit silence and locomotory freezing in their young; acoustically, the two types of calls were most clearly separable from one another on the basis of repetition rate (Miller, 1980; Miller and Blaich, 1986).

Repetition rate consists of two components: note duration and internote interval. Here, we tested the hypothesis that the repetition rate of the fear-caught call is the primary salient cue in controlling TI duration. To test our hypothesis, we played natural, transformed, and synthetic calls to chicks over five experiments and measured the duration of experimenter-induced TI. We predicted that if lab-made sounds mimicked the repetition rate of natural fear-caught calls, then chicks would increase TI duration to resemble that exhibited by chicks listening to the natural fear-caught calls. Conversely, we predicted that TI duration would not be enhanced if a sound's repetition rate differed from that of the natural fear-caught call. We then asked if note duration and/or internote interval *per se* more strongly predicted TI duration relative to repetition rate itself.

Domestic fowl (*Gallus gallus*) provide an excellent model to ask such questions, primarily because this species is particularly well studied. Their vocalization repertoire is well known and consists of a number of highly stereotyped vocalizations (Collias and Joos, 1953; Cowan, 1974; Kent, 1993; Marx et al., 2001; De Tommaso et al., 2019). Also, their habituation and locomotory freezing patterns are well understood (Chiandetti and Turatto, 2017; Chiandetti et al., 2018; Dissegna et al., 2018). Furthermore, their performance can be reliably compared with that of older animals and other species (Vallortigara and Chiandetti, 2017; Chiandetti, 2017; Vallortigara and Versace, 2017; Chiandetti et al., 2018), allowing for comparative perception studies and cognition research in several domains (Vallortigara, 2012; Chiandetti, 2018; Chiandetti et al., 2018).

## 2. Methods

### 2.1. Animals and ethical statement

All experiments used male Production Red X White Mountain (*Gallus gallus*) cockerels obtained from a local hatchery (Burlings, Oxford, PA) on day 1 post-hatch. The chicks were kept in a standard metal laboratory brooder placed in a  $1.8 \times 2.4 \times 2.7$  m. cinder block room maintained at about 37 °C. The brooder was bedded with pine shavings. The chicks were exposed to a 12/12 light/dark cycle (9.00–21.00), and they had constant access to water and Agway brand chick feed.

Franklin & Marshall's Animal Welfare Committee reviewed and approved the research, although the case number has been lost. We are confident that the case number once existed since the second author was an active member of that committee in 1988; his research involved a variety of primate species as well as chickens. Regarding animal welfare, the chicks had a dedicated lab technician to attend their needs, and none of them died during our project, despite the fact that they entered our facility as 1-day old chicks.

### 2.2. Apparatus

We used the same TI induction box described in Thompson & Liebreich (1987). The front of the induction box ( $48 \times 29 \times 31$  cm) consisted of a split black curtain; the remaining three wooden sides were painted matt black. The bottom was lined with paper towels, and the top of the box was plexiglass™, which permitted the investigator to observe the subject unobtrusively. The induction box was placed on a wooden desk ( $61 \times 91 \times 76$  cm), located in a sound-attenuation chamber (Controlled Acoustic Environment). TI duration was timed using a silent mercury clock (Standard Electric Time Corp). During the induction process, tapes of the sound were played on a Sony™ (TC-76) cassette-recorder. The speaker of the recorder was placed 16 cm from the induction box as in Thompson and Liebreich (1987).

### 2.3. Generation of test sounds

We used nine sounds over five experiments in this study. These sounds include: 1) a natural fear-caught call, 2) a natural follow-me call, 3) a natural death cry of a crow (*Corvus brachyrhynchos*), 4) a synthetic fear-caught sound, 5) a synthetic follow-me sound, 6) a continuous fear-caught sound, 7) the synthetic hybrid I sound, 8) the synthetic hybrid II sound, and 9) white noise. All durations are reported as means and standard deviations, unless otherwise noted.

We used the same fear-caught call and follow-me call as Thompson and Liebreich (1987). The crow death cry originated from a commercially available recording, "Johnny Stewart's Death Cry of a Crow" (Stewart, 1953). Stewart made a series of recordings still used by hunters to attract predators to particular sites, and he used live animals. Given the title of his recording, we presume that the crow used in this recording died. The attraction call used by Thompson and Liebreich (1987) was described by Collias and Joos (1953) and taped from a record disc, "The Sound of Animals" (Greenhall and Collias, 1954). This sound was originally collected by chicks living at Cornell Behavioral Farm.

We processed calls and created sounds with the aid of a receiver, cassette desk, and keyboard synthesizer interfaced by MacADIOS and MIDI to a Mac 512 computer using MacSpeech Lab, MacSound Lab, and Ensoniq Mirage Advanced Sampler's Operating System (MASOS) software.

We prepared natural calls by playing them on a JVC™ brand cassette deck; the sound was transferred, via the mixer, to the Ensoniq Mirage Digital Sampling Keyboard where it was stored. The digitized calls were then transferred to the computer via the MIDI interface, which produced serial sound waves from the digital information. On the computer, we used MacSound Lab software to visualize and edit the calls, enabling the creation of the non-natural sounds. MacSpeech software allowed us to generate sound spectrographs. The edited sound was returned to the Ensoniq keyboard and recorded on a TDK™ D60 brand cassette tape.

This study focused on the functionality of three acoustic features: note duration, internote interval, and repetition rate. We defined note duration as the time in seconds from the onset to the offset of each discrete sound pulse within the displayed signal (cf., Miller, 1980). We defined internote interval as the duration in seconds of the silent interval space between each note. We defined repetition rate as the interval in seconds between the onset of one note to the onset of the next note.

Experiments 1 and 2 used four discrete sounds: the fear-caught call, the crow death cry, the follow-me call, and white noise. The white noise recording was the same as that used by Thompson and Liebreich (1987). Fig. 1 provides spectrograms of the four sounds. Fig. 1a and 1b show that the temporal patterning of the fear-caught call resembles that of the crow death cry. Specifically, the fear-caught call had a repetition rate of 1.06 notes per second while the crow death cry had a repetition rate of 1.22 notes per second. The fear-caught call had a note duration

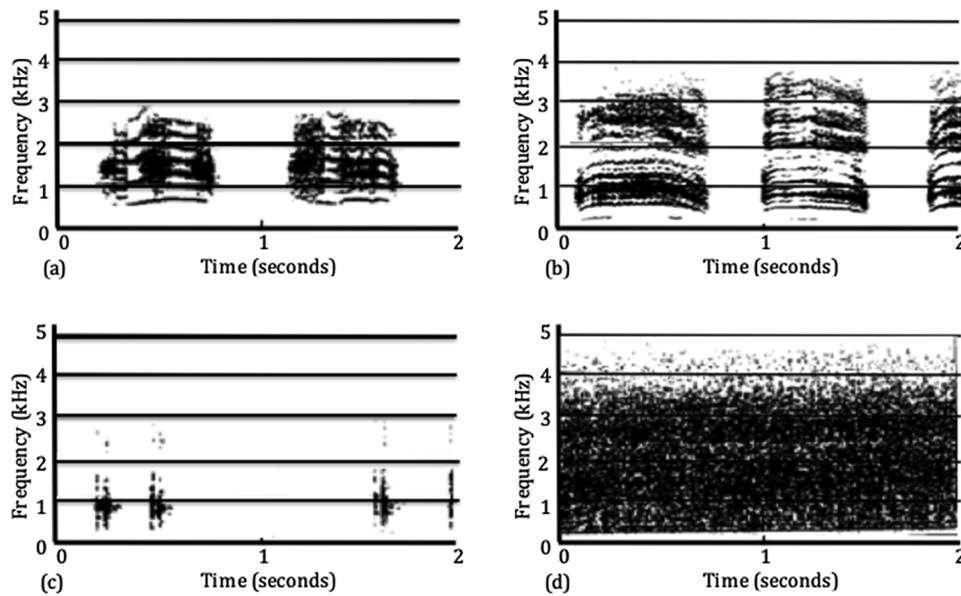


Fig. 1. Spectrographic illustrations of a) natural chicken fear-caught call, b) natural crow death cry, c) a natural chicken follow-me call, and d) white noise.

of  $0.54 \pm 0.60$  s and an internote interval of  $0.39 \pm 0.20$  s whereas the crow death cry had a note duration of  $0.55 \pm 0.11$  s and the internote interval of  $0.25 \pm 0.70$  s. Conversely, the follow-me call had a note duration of  $0.12 \pm 0.03$  s and an internote interval of  $0.18 \pm 0.11$  s. The follow-me call had a repetition rate of 3.27 notes per second. In Experiments 1 and 2, we also played continuous white noise; which by definition had no note duration, internote interval or repetition rate.

In Experiment 3 we used four sounds: two synthetic sounds (the synthetic fear-caught sounds and the synthetic, continuous fear-caught sound), white noise, and the natural fear-caught call. We generated the synthetic fear-caught sound, by setting white noise to the repetition rate found in the natural fear-caught call. Specifically, the synthetic fear caught alarm call had a note duration of  $0.54 \pm 0.01$  s and an internote interval of  $0.38 \pm 0.01$  s. These values produced a repetition rate of 1.09 notes per second which corresponded to the repetition rate of 1.08 notes per second found in the natural fear-caught call.

We generated the synthetic, continuous fear-caught call, by removing the  $0.39 \pm 0.18$  s internote interval from the natural fear-

caught call. This removal produced a continuous sound that contained many of the same characteristics of the natural fear-caught call, but lacked the repetition rate. Fig. 2 shows spectrographs of the synthetic fear-caught sound and continuous fear-caught sound.

In Experiment 4 we used two synthetic sounds: the synthetic fear-caught sound, described above for Experiment 3, and a synthetic follow-me sound. The synthetic follow-me sound, comprised of white noise, had a note duration of  $0.12 \pm 0.01$  s and an internote interval of  $0.18 \pm 0.01$  s, which produced a repetition rate of 3.33 notes per second. The corresponding repetition rate of the follow-me call used in Experiment 2 and by Thompson and Liebreich (1987) was 3.27 notes per second. Fig. 2 provides a spectrograph of the synthetic follow-me sound.

In Experiment 5 we used three synthetic sounds: the synthetic fear-caught sound, synthetic hybrid I, and synthetic hybrid II. We created the synthetic hybrid I by setting white noise to the note duration found in the follow-me call ( $0.12 \pm 0.01$  s) and the internote interval found in the fear-caught call ( $0.38 \pm 0.01$  s). Hybrid I had a repetition rate of

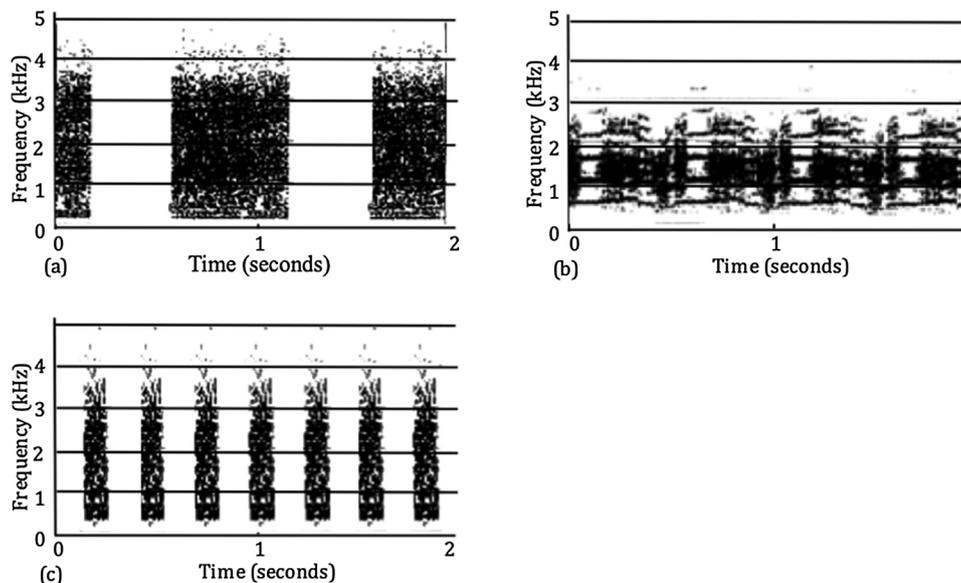


Fig. 2. Spectrographic illustrations of a) the synthetic fear-caught sound, b) the continuous fear-caught sound, and c) the synthetic follow-me call. We used these sounds in Experiments 3 and 4.

**Table 1**  
Acoustic features of the nine sounds used across the five experiments.

Sound Type	Note Duration		Internote Interval		Repetition Rate
	Mean (sec)	Standard Deviation	Mean (sec)	Standard Deviation	Mean (notes/sec)
Fear-caught call	0.54	0.06	0.39	0.18	1.06
Crow death cry	0.55	0.11	0.25	0.70	1.22
Follow-me call	0.12	0.03	0.18	0.11	3.27
White noise	na	na	na	na	na
Synthetic fear-caught sound	0.54	0.01	0.38	0.01	1.09
Continuous fear-caught sound	na	n	na	na	na
Synthetic follow-me sound	0.12	0.01	0.18	0.01	3.33
Synthetic hybrid I sound	0.12	0.01	0.38	0.01	2.00
Synthetic hybrid II sound	0.54	0.01	0.18	0.01	1.39

2.00 notes per second. We created the synthetic hybrid II sound by setting white noise to the note duration found in the fear-caught call ( $0.54 \pm 0.01$  s) and the internote interval found in the follow-me call ( $0.18 \pm 0.01$  s). Hybrid II had a repetition rate of 1.39 notes per second. Table 1 provides the note durations, internote intervals and repetition rates of all nine sounds.

Following Thompson and Liebreich (1987), once we created the experimental sounds and were prepared to play them to the chicks, we used an Industrial Acoustics™ (SS-375) sound meter, set at the C weighting scale, to measure sound intensities at 20 cm from the speaker used in experimental sessions. During testing, sounds were presented at a mean sound intensity level of 70 dB, which is perceptible but does not elicit startle responses (Fischer and Gilman, 1969; Hatton and Thompson, 1975).

#### 2.4. TI duration measurements

We used 24 chicks in each experiment for a total of 120 chicks. To statistically accommodate individual differences in chicks, we measured baseline TI duration and assigned chicks to treatment groups in a manner such that each treatment group had the same mean baseline TI duration as per Thompson and Liebreich (1987). To establish the baseline, on day 9 post-hatch, the chicks were induced into TI while the experimenter played a blank Maxell™ XLII cassette tape. Based on TI duration, chicks were then separated into groups with comparable means. Once testing began, each group was exposed to one sound condition on each subsequent daily trial as determined by a Latin Square, randomizing the order in which the birds heard the sounds. In each of the five experiments, all birds heard all sounds. No bird used in one experiment was used in another.

The chicks were tested individually; a chick was removed from the brooder, carried by hand to the sound attenuation chamber (a distance of about 9 m), and placed in the TI induction box. The chick was not

handled for one minute. After the initial 30 s of this period, the cassette recorder was started and played continuously throughout the remainder of the trial, up to a maximum of 12 min (720 s). The experimenter remained immobile throughout the trial.

All chicks were tested between 11.00 and 18.00 h. After the second 30 s of the initial 1 min interval elapsed, each subject was induced into TI by placing the chick on its left side, restraining it, and exerting pressure on its head and neck region for 15 s. TI measurement began as soon as the experimenter's hand was removed from the subject, and measurement ceased when the subject righted itself or at the 720-second (12-min) mark, whichever came first. If the chick did not enter TI, or if it remained in TI for less than 2 s, the experimenter waited 5 s and repeated the induction process. If after five attempts, the chick did not enter TI, it received a score of 0 s for TI duration. The cassette recorder was shut off as soon as TI ended and the tape was rewound while the experimenter returned the bird to the brooder and fetched the next subject.

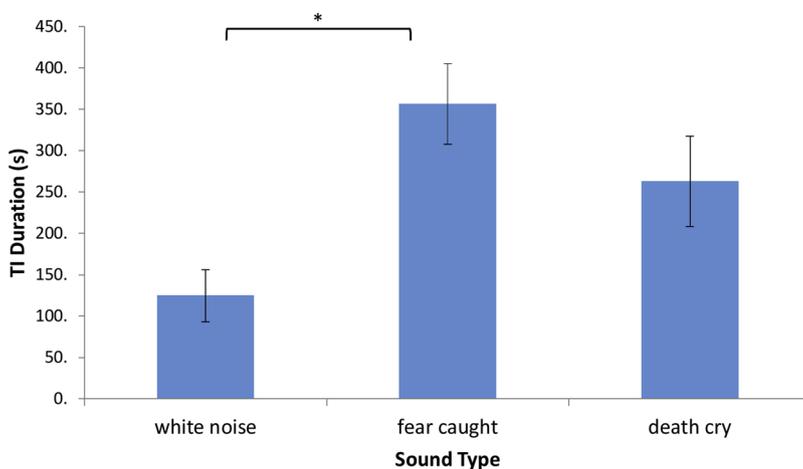
We used Excel Version 16.15 and StatPlus on a Macbook Air to conduct most of the statistics, specifically Friedman's ANOVAs, a non-parametric ANOVA that compares multiple related samples. To calculate effect size, we calculated the Cohen's *d* statistic, which assumes that the standard deviations are roughly equal (Cohen, 1988). We used an effect size calculator to find the Cohen's *d* (Ellis, 2009a).

### 3. Results

#### 3.1. Experiment 1: a fear-caught call versus crow death cry

As shown in Fig. 3, the mean and standard deviation of TI duration produced by chicks listening to the fear-caught call ( $356.5 \pm 266.5$  s) and the crow death cry ( $262.8 \pm 213.1$  s) exceeded that produced by chicks listening to white noise ( $124.8 \pm 154.3$  s).

With a Cohen's *d* of 1.064, the mean TI duration produced by chicks



**Fig. 3.** Mean TI duration in seconds of chicks listening to different sounds during Experiment 1. Error bars show standard error of the mean. The TI duration of chicks listening to the fear-caught call and the death cry of the crow exceeded that of chicks listening to white noise, and the difference was significant when comparing fear-caught to white noise.

listening to the fear-caught call differed from that of chicks listening to white noise by just over one standard deviation; this difference, according to Ellis (2009b), qualifies as *large*. Conversely, we calculated a Cohen's *d* of 0.39 when comparing the mean TI duration produced by chicks listening to the fear-caught call and the crow death cry. This can be categorized as *small* (Ellis, 2009b) since these groups differed by about 40% of a standard deviation. Lastly, we calculated a Cohen's *d* of 0.74 when comparing the mean TI duration of chicks listening to white noise to those listening to the crow death cry; this difference qualifies as *medium/large* according to Ellis (2009b).

A Friedman's ANOVA detected significant differences ( $X^2 = 8.56$ ,  $DF = 2$ ,  $P = 0.01$ ), and the post-hoc pairwise comparison reported that the TI duration associated with the fear-caught call significantly exceeded that associated with white noise ( $X^2 = 5.26$ ,  $DF = 1$ ,  $P = 0.02$ ). While the TI duration associated with the crow death cry did not significantly exceed that associated with white noise ( $X^2 = 3.52$ ,  $DF = 1$ ,  $P = 0.06$ ), the p-value was low, which is consistent with a Cohen's *d* score of *medium/large* (Ellis, 2009b).

Qualitatively, only one of 24 birds (4.2%) remained in TI for the maximum duration of 720 s while exposed to white noise, while four birds (16.7%) listening to the fear-caught call and four birds (16.7%) listening to the crow death cry remained in TI for the maximum duration.

### 3.2. Experiment 2: crow death cry versus the follow-me call

The mean and standard deviation of TI duration produced by chicks listening to the crow death cry ( $463.75 \pm 201.48$  s) exceeded that produced by chicks listening to the follow-me call ( $232.79 \pm 255.46$  s) and by chicks listening to white noise ( $182.8 \pm 263.39$  s). See Fig. 4.

With a Cohen's *d* of 1.00, the mean TI duration produced by chicks listening to the crow death cry differed from that of chicks listening to the follow-me call by just over one standard deviation; this difference, according to Ellis (2009b), qualifies as a *large*. When comparing the mean TI duration of chicks listening to the crow death cry to those listening white noise, we calculated a similar Cohen's *d* of 1.20, which also falls into the *large* category. Conversely, we calculated a Cohen's *d* of 0.19, a difference categorized as *trivial/small* (Ellis, 2009b) when comparing the mean TI duration produced by chicks listening to the follow-me call and white noise. Lastly, we calculated a Cohen's *d* of 0.74 when comparing the mean TI duration of chicks listening to white noise to those listening to the crow death cry; this difference qualifies as *medium/large* according to Ellis (2009b).

A Friedman's ANOVA detected significant differences ( $X^2 = 16.49$ ,  $DF = 2$ ,  $P = 0.0003$ ). The post-hoc pairwise comparison reported that the TI duration associated with the crow death cry significantly exceeded that associated with follow-me call ( $X^2 = 10.71$ ,  $DF = 1$ ,

$P = 0.001$ ) and that the TI duration associated with the crow death cry significantly exceeded that associated with white noise ( $X^2 = 10.71$ ,  $DF = 1$ ,  $P = 0.001$ ).

Qualitatively, exposure to the crow death cry caused 11 of the 24 birds (45.8%) to remain in TI for the maximum duration of 720 s, while exposure to white noise and the follow-me call caused only three birds (12.5%) to remain in TI for the maximum duration.

### 3.3. Experiment 3: natural fear-caught call versus two modified versions

The mean and standard deviation of TI duration produced by chicks listening to the synthetic fear-caught sound ( $395.01 \pm 264.17$  s) and to the natural fear-caught call ( $356.50 \pm 279.45$  s) exceeded that produced by chicks listening to white noise ( $207.90 \pm 244.52$  s) and by chicks listening to the continuous fear-caught sound ( $121.25 \pm 149.27$  s). See Fig. 5.

With a Cohen's *d* of 0.14, the mean TI duration produced by chicks listening to the natural fear caught call differed from that of chicks listening to the synthetic fear caught call by about 15% of one standard deviation; this difference, according to Ellis (2009b), qualifies as a *trivial*. Similarly, when comparing the mean TI duration of chicks listening to white noise to those listening the continuous fear-caught call, we calculated a Cohen's *d* of 0.43, which falls into the *small* category. Conversely, we calculated a Cohen's *d* of 0.74, a difference categorized as *medium/large* (Ellis, 2009b) when comparing the mean TI duration produced by chicks listening to the synthetic fear-caught call and white noise. We also calculated a Cohen's *d* of 0.57 when comparing the mean TI duration of chicks listening to white noise to those listening to the natural fear-caught call; this difference qualifies as *medium* according to Ellis (2009b).

Lastly, we found the biggest effect differences when comparing the fear-caught calls containing repetition rates to the fear-caught call lacking a repetition rate. Specifically, when comparing the mean TI duration of chicks listening to a synthetic fear-caught call to those listening to the continuous fear-caught call, we calculated a Cohen's *d* of 1.28, which qualifies as *large/really large* according to Ellis (2009b). Similarly, we calculated a Cohen's *d* of 1.05 when we compared the mean TI duration of chicks listening to a natural fear-caught call to those listening to the continuous fear-caught call. Differing by more than one standard deviation, this *d* value qualifies as *large*, according to Ellis (2009b).

A Friedman's ANOVA detected significant differences ( $X^2 = 14.36$ ,  $DF = 3$ ,  $P = 0.002$ ). The post-hoc pairwise comparison reported that the TI duration associated with the natural fear-caught call significantly exceeded that associated with continuous fear-caught sound ( $X^2 = 4.17$ ,  $DF = 1$ ,  $P = 0.04$ ); the TI duration associated with the synthetic fear-caught sound significantly exceeded that associated with

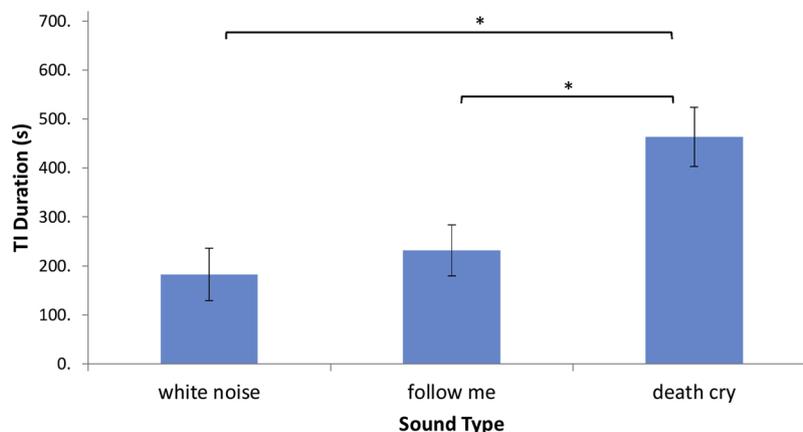


Fig. 4. Mean TI duration in seconds of chicks listening to different sounds during Experiment 2. Error bars show standard error of the mean. TI duration of chicks listening to the death cry of the crow significantly exceeded that of chicks listening to a chicken follow-me call and white noise.

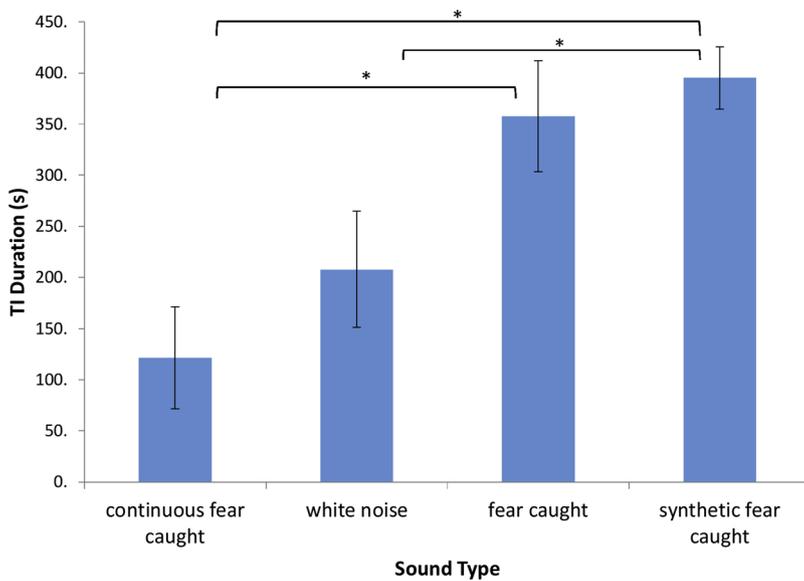


Fig. 5. Mean TI duration in seconds of chicks listening to different sounds during Experiment 3. Error bars show standard error of the mean. Chicks listening to the natural fear-caught call and chicks listening to white noise set to the repetition rate of the natural fear-caught call remain in TI longer than chicks listening to a natural fear-caught call that had had its internote interval removed.

the continuous fear-caught sound ( $X^2 = 10.67$ ,  $DF = 1$ ,  $P = 0.001$ ); and, consistent with a Cohen's  $d$  of 0.735, the TI duration associated with the synthetic fear-caught sound approached a significant difference when compared to the TI duration associated with the white noise ( $X^2 = 3.52$ ,  $DF = 1$ ,  $P = 0.006$ ).

Qualitatively, exposure to the natural fear-caught call caused five of 24 birds (20.1%) to remain in TI for the maximum duration, and exposure to the synthetic fear-caught call caused two birds (8.3%) to remain in TI for the maximum duration. Exposure to white noise caused one bird (4.2%) to remain in TI for the maximum duration while no bird (0%) exposed to the continuous fear-caught call remained in TI for the full length of 720 s.

### 3.4. Experiment 4: synthetic fear-caught sound versus +/- Synthetic follow-me sound

The mean and standard deviation of TI duration ( $433.13 \pm 232.18$  s) produced by chicks listening to the synthetic fear-caught sound (white noise set to the repetition rate of the natural fear-caught call) exceeded the mean TI duration ( $249.17 \pm 245.16$  s) produced by chicks listening to the synthetic follow-me sound (white noise set to the repetition rate of the natural follow-me call) and by chicks listening to white noise ( $204.96 \pm 155.20$  s). See Fig. 6.

With a Cohen's  $d$  of 0.22, the mean TI duration produced by chicks listening to the synthetic follow-me call differed from that of chicks listening to the white noise by less than 25% of one standard deviation;

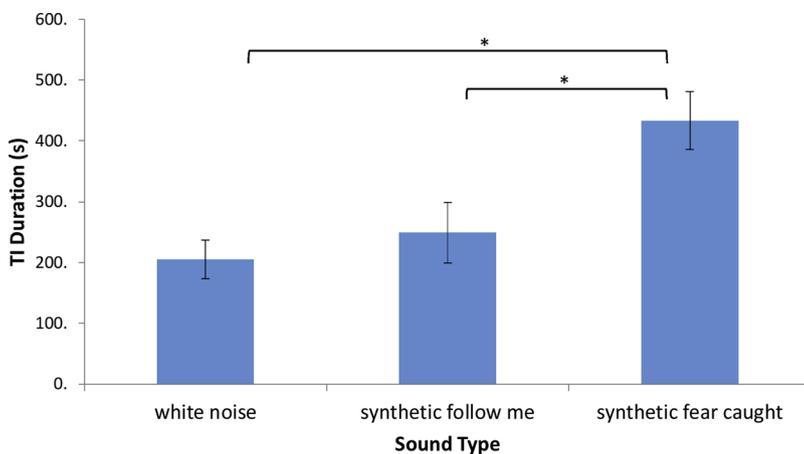


Fig. 6. Mean TI duration in seconds of chicks listening to different sounds during Experiment 4. Error bars show standard error of the mean. Results from this experiment show that setting white noise to the repetition rate of a natural follow-me call and a natural fear-caught call causes chicks to behave as if they were listening to the natural sounds.

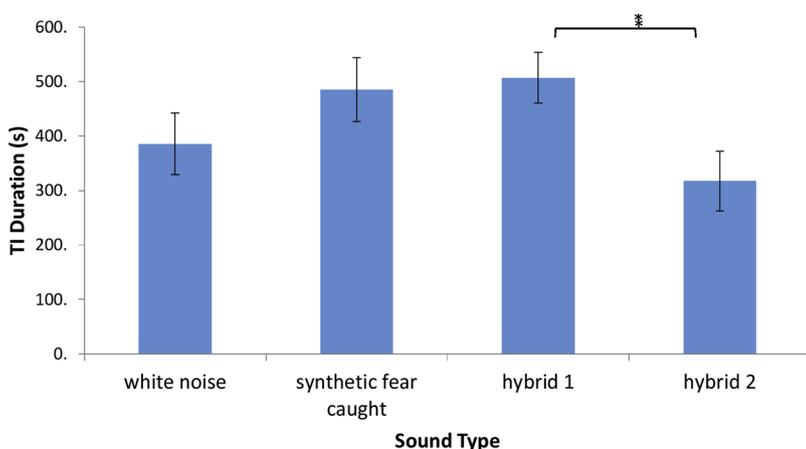
this difference, according to Ellis (2009b), qualifies as a *trivial/small*. When comparing the mean TI duration of chicks listening to the synthetic fear-caught sound to those listening white noise, we calculated a Cohen's  $d$  of 1.16, which also falls into the *large* category. We calculated a Cohen's  $d$  of 0.77, a difference categorized as *medium/large* (Ellis, 2009b) when comparing the mean TI duration produced by chicks listening to the synthetic fear-caught sound and the synthetic follow-me sound.

A Friedman's ANOVA detected significant differences ( $X^2 = 6.47$ ,  $DF = 2$ ,  $P = 0.04$ ). The post-hoc pairwise comparison reported that the TI duration associated with the synthetic fear-caught sound significantly exceeded that associated with synthetic follow-me sound ( $X^2 = 3.85$ ,  $DF = 1$ ,  $P = 0.047$ ), and that the TI duration associated with the synthetic fear-caught sound significantly exceeded that associated with white noise ( $X^2 = 4.17$ ,  $DF = 1$ ,  $P = 0.04$ ).

Qualitatively, exposure to the synthetic fear-caught call caused eight of the 24 birds (33.3%) to remain in TI for the maximum duration while only three birds (12.5%) exposed to the synthetic follow-me call remained in TI for 720 s and no bird (0%) exposed to white noise remained in TI for the maximum duration.

### 3.5. Experiment 5: internote interval versus the repetition rate

Regarding means and standard deviations of TI durations, chicks listening to the synthetic fear-caught sound remained in TI for  $485.5 \pm 287.97$  s; chicks listening to the synthetic hybrid I sound, which had the



**Fig. 7.** Mean TI duration in seconds of chicks listening to different sounds during Experiment 5. Error bars show standard error of the mean. The mean TI duration generated by listening to *hybrid 1*, which had the note duration of the follow-me call and the internote interval of the fear-caught call, significantly exceeded that generated by listening to *hybrid 2*, which had the note duration of the fear-caught call and the internote interval of the follow-me call. Because chicks have a tendency to react more similarly to the *hybrid 1* sound and the synthetic fear-caught sound than to the *hybrid 2* sound and the synthetic fear-caught sound, this experiment suggests that internote interval may have a stronger impact on TI duration than does note duration.

note duration of the follow-me call and the internote interval of the fear-caught call, remained in TI for  $507.17 \pm 227.83$  s; chicks listening to the synthetic hybrid II sound, which had the note duration of the fear-caught call and the internote interval of the follow-me call, remained in TI for  $317.08 \pm 267.66$  s; and chicks listening to white noise remained in TI for  $385.93 \pm 278.12$  s. See Fig. 7.

A Friedman's ANOVA did not detect significant differences ( $X^2 = 5.80$ ,  $DF = 3$ ,  $P = 0.120$ ). The post-hoc pairwise comparison reported only one specific significant difference; the length of TI inspired by the synthetic hybrid I sound significantly exceeded that inspired by listening to the synthetic hybrid II sound ( $X^2 = 5.00$ ,  $DF = 1$ ,  $P = 0.025$ ).

The ANOVA results are consistent with the effect size calculations. When comparing the mean TI duration exhibited by chicks listening to the synthetic hybrid I call to that produced by chicks listening to the synthetic hybrid II call, we calculated a Cohen's  $d$  of 0.77, which qualifies as *medium/large*, according to Ellis (2009b). We calculated a Cohen's  $d$  of 0.61, which is *medium* according to Ellis (2009b), when we compared the mean TI duration of chicks listening to the synthetic fear-caught sound to those of the synthetic hybrid II call. All other effect-size calculations for these treatments qualified as *trivial* or *small*, according to Ellis (2009b).

Exposure to the synthetic fear-caught call caused 12 of 24 birds (50%) to remain in TI for the maximum duration, and exposure to the synthetic hybrid I sound caused 11 birds (45.8%) to remain in TI for the maximum duration. Exposure to white noise and to the synthetic hybrid II sound both caused four birds (16.7%) to remain in TI for the maximum duration.

#### 4. Discussion

We designed this set of experiments to identify the cue within alarm calls that controls TI duration in naïve chicks (*Gallus gallus*). Informed by prior findings (Jones, 1986; Thompson and Liebreich, 1987) we specifically tested the hypothesis that the repetition rate of the fear-caught call is the primary salient cue controlling TI duration. Results from Experiment 1 suggest that young chicks perceive both the chicken fear-caught call and the crow death cry similarly frightening in that exposure to both novel sounds caused them to remain in TI longer than listening to white noise. Results from Experiment 2 revealed the non-specific crow death cry elicited significantly longer TI durations than did a hen's follow-me call, despite the novelty of both calls. Taken together, results from both experiments suggest that some component—found in both the crow death cry and the chicken fear-caught call, but not in the follow-me call—compels chicks to lengthen the amount of time they remain in TI.

Because the chicken fear-caught call and the crow death cry have similar repetition rates, we designed Experiment 3 to address the

question of whether or not repetition rate alone was sufficient to lengthen TI duration. Toward that end, we exposed the chicks to white noise set to a repetition rate consistent with the fear-caught call and the crow death cry. TI durations in response to exposure to the white-noise based fear-caught sound did not differ significantly from that generated by exposure to the natural fear-caught call. Furthermore, both sounds were associated with significantly longer TI durations relative to the durations associated with the fear-caught call that had its repetition rate removed. (The natural fear-caught call elicited longer TI durations than did white noise, but the difference was not significant.) Overall, these results suggest that young chicks selectively attend to the repetition rate of calls while in TI, and if the repetition rate mirrors that found in conspecific alarm calls, the chicks increase their TI duration.

To assure ourselves that the repetition rate of the synthetic fear-caught call and not some unmeasured component of the white noise drove the lengthened TI duration, we designed Experiment 4. Here we found that TI duration in the presence of the synthetic fear-caught sound (white noise set to the repetition rate of a fear-caught call) significantly exceeded TI durations associated with the synthetic follow-me call or white noise.

Because repetition rate is derived from both note duration and internote interval, we designed Experiment 5 to determine if either of those components was perceptually more salient in lengthening TI duration than repetition rate *per se*. The synthetic hybrid I sound had the internote interval of the fear-caught call and the note duration of the attraction call, whereas the synthetic hybrid II sound had the internote interval of the follow-me call and the note duration found in the fear-caught call.

Chicks did not clearly vary their TI duration in response to any of these above sounds; however, the synthetic hybrid II sound, with its internote interval based on the follow-me call, appears to have been less frightening than the synthetic hybrid I sound, with its internote interval corresponding to that of the fear-caught call. Collectively, the results from the five experiments suggest that repetition rate *per se* drives TI duration, but internote interval may merit additional exploration.

Because the crow death cry and the fear-caught death call share a repetition rate that lengthens TI duration, it might be tempting to conclude that young birds hearing calls emitted at a rate of about 1 per second, will react defensively regardless of the species eliciting or even emitting the call. Support exists for such a view. For instance, when Japanese great tit parents (*Parus minor*) give a "chicka" alarm call in response to sighting a crow, chicks hide in the bottom of their nest. When those same parents give a "jar" alarm call in response to sighting a snake, those same chicks jump from their nest. The "chicka" call and the "jar" call have repetition rates of 1.7 and 1.5 calls per second, respectively (Suzuki, 2016). Our fear-caught call and the crow death cry had repetition rates of 1.08 and 1.25 calls per second respectively. (See

Table 1.) Similarly, Arabian babblers (*Turdoides squamiceps*) use a call with a repetition rate of 1 call per second when mobbing cats (Naguib et al., 1999), Australian magpies (*Gymnorhina tibicen*) have a generic alarm call with a repetition rate of 1 call per second that causes adults to scan the sky (Kaplan and Rogers, 2013), Siberian jays (*Perisoreus infaustus*) have an alarm call with a repetition rate of 1.1 calls per second that they use when they spot a perched hawk and another alarm call with a repetition rate of 1 call per second that elicits freezing (Griesser, 2009), and the Southern house wren (*Troglodytes musculus*) uses Type 1 alarm calls with a repetition rate of 1 to 1.4 calls per second when humans or predators approach (Fasanella and Fernandez, 2009).

Interestingly, however, other bird species have repetition rates in their alarm calls that resemble our chicken follow-me attraction call of 3.27 calls per second but they elicit a very different response. (See Table 1.) For example, the same Siberian jays mentioned above have an attack call that prompts conspecifics to hide or mob with a repetition rate of 3 calls per second (Griesser, 2009), and adult white-browed scrubwrens (*Sericornis frontalis*) use a "trill" alarm call with a repetition rate of 4 calls per second to quiet their young, but not their youngest, chicks (Platzen and Magrath, 2005). Domestic chicks (*Gallus gallus*) seem to prefer hen's clucks that have a repetition rate of 2 calls per second, among other features (Kent, 1993; De Tommaso et al., 2019); this repetition rate is shorter than our attraction call, but longer than our alarm call.

Still other bird species emit alarm calls with repetition rates that fall far outside our measurements. For example, the white-browed scrubwrens mentioned above have a "buzz" ground alarm call with a repetition rate of 6.5 calls per second (Platzen and Magrath, 2005). Tufted titmouse (*Baeolophus bicolor*) adults use a "seet" alarm call with a repetition rate of 0.2 calls per second, which cause birds to freeze. The same Arabian babblers mentioned above that had a alarm call with a repetition rate of 1 call per second when mobbing cats use a call with a repetition rate of 0.5 calls per second when mobbing owls (Naguib, et al. 1999). The Australian magpies mentioned above have an alarm call that works for both urban and rural populations called an "eagle" alarm call. It has no repetition rate because it is constant (Kaplan and Rogers 2013). De Tommaso et al. (2019) demonstrate that domestic chicks, similarly to those used in our experiments, did not respond to continuous sound.

While the repetition rates of alarm calls vary across species, information contained in alarm calls allows receivers to act adaptively in the face of danger (Ellis, 2008). The information also varies within species where birds use distinct calls for distinct predator types (e.g. Suzuki, 2016), across the level of threat a particular predator presents (Naguib et al., 1999; Baker and Becker, 2002; Ellis, 2008), and across populations (Kaplan and Rogers, 2013).

Presumably, if such variation in alarm-call structure is functional, particular call variants should elicit responses appropriate to the context in which those variants are produced (Ellis, 2008). While a particular repetition rate might not be constantly important in alarm calls for birds, repetition rate itself commonly serves as the variant (or sometimes one of several variants) that elicits the appropriate response.

For example, American robins (*Turdus migratorius*) communicate predator type and intensity of need for nest defense by varying repetition rate (Gottfried et al., 1985). Arabian babblers vary their call repetition rate to differentiate between calling to mob a cat versus calling to mob an owl (Naguib et al., 1999). Reed warblers (*Acrocephalus scirpaceus*) increase the repetition rate of their mobbing calls to attract more individuals (Welbergen and Davies, 2008). Japanese great tits encode information about predator type by using repetition rate, production specificity, and note combinations of discrete alarm calls (Suzuki, 2016), and white-throated magpie jays varied several acoustic parameters across threats, but repetition rate remained constant across all threats (Ellis, 2008).

While the repetition rates of avian alarm calls vary markedly across the globe, the literature provides abundant evidence that within

species, call repetition rate commonly tells conspecific listeners (or birds of other species sharing the same ecology *sensu* Fallow and Magrath, 2010 and Magrath and Bennet, 2011) what kind of predator is approaching and/or how much danger the approaching predator presents. Despite the fact that our subjects were not only amongst the youngest birds compared to those reviewed in the literature but also the only domesticated studied, the behaviour of our chicks fits logically within the behaviour of the reviewed avian species.

## Acknowledgements

First we thank all of the computer technicians who helped us back up data files between 1988 and 2018. We thank Jeff Coleman who helped set up the recording equipment and taught the authors how to use it. We thank Rocky Abessinio for caring for the chicks. More recently, we thank Dr. Kathy Twiss for her critique of an early draft of the manuscript., and two anonymous reviewers who helped improve the final versions. We also thank Dr. Katherine Aubrecht, the Chair of the Sustainability Studies Program, and Dr. Paul Shepson, Dean of the School of Marine and Atmospheric Science. Support for this research was provided in part by a grant from Franklin & Marshall College's Hackman Scholars Program to support undergraduate participation in research.

## References

- Arduino, P.J., Gould, J.L., 1984. Is tonic immobility adaptive? *Anim. Behav.* 32 (3), 921–923. [https://doi.org/10.1016/S0003-3472\(84\)80173-6](https://doi.org/10.1016/S0003-3472(84)80173-6).
- Baker, M.C., Becker, A.M., 2002. Mobbing calls of black-capped chickadees: effects of urgency on call production. *Wilson Bull.* 114 (4), 510–516. [https://doi.org/10.1676/0043-5643\(2002\)114\[0510:MCOBCC\]2.0.CO;2](https://doi.org/10.1676/0043-5643(2002)114[0510:MCOBCC]2.0.CO;2).
- Cassill, D.L., Vo, K., Becker, B., 2008. Young fire ant workers feign death and survive aggressive neighbors. *Naturwissenschaften* 95 (7), 617–624. <https://doi.org/10.1007/s00114-008-0362-3>.
- Chiandetti, C., 2018. Hier bin ich: wo bist du? The affiliative imprinting phenomenon in the modern study of animal cognition. *Gestalt Theory* 40 (2), 189–205. <https://doi.org/10.2478/gth-2018-0016>.
- Chiandetti, C., Turatto, M., 2017. Context-specific habituation of the freezing response in newborn chicks. *Behav. Neurosci.* 131 (5), 437 <https://doi-org.proxy.library.stony-brook.edu/10.1037/bne0000212>.
- Chiandetti, C., Dissegna, A., Turatto, M., 2018. Rapid plasticity attenuation soon after birth revealed by habituation in newborn chicks. *Dev. Psychobiol.* 60 (4), 440–448. <https://doi.org/10.1002/dev.21628>.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*. (2nd). New Jersey: Laurence Erlbaum Associates, Publishers, Hillsdale.
- Collias, N.E., Joos, M., 1953. The spectrographic analysis of sounds signals of the domestic fowl. *Behavior* 76, 25–61.
- Cowan, P.J., 1974. Selective responses to the parental calls of different individual hens by young *Gallus gallus*: auditory discrimination learning versus auditory imprinting. *Behav. Biol.* 10, 541–545. [https://doi.org/10.1016/S0091-6773\(74\)92196-8](https://doi.org/10.1016/S0091-6773(74)92196-8).
- Dissegna, A., Turatto, M., Chiandetti, C., 2018. Short-term memory in habituation and dishabituation of newborn chicks' freezing response. *J. Exp. Psychol. Anim. Learn. Cogn.* 44 (4), 441. <https://doi.org/10.1037/xan0000182>.
- Ellis, J.M., 2008. Which call parameters signal threat to conspecifics in white-throated magpie-jay mobbing calls? *Ethology* 114 (2), 154–163. <https://doi.org/10.1111/j.1439-0310.2007.01439.x>.
- Ellis, P.D., 2009a. Effect Size Calculators. " website: <http://www.polyu.edu.hk/mm/sizefaq/calculator/calculator.html> accessed on May 23, 2019. .
- Ellis, P.D., 2009b. Result Whacker. website: <http://www.polyu.edu.hk/mm/sizefaq/calculator/result.html> accessed on May 23, 2019. .
- Fallow, P.M., Magrath, R.D., 2010. Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Anim. Behav.* 79 (2), 411–417. <https://doi.org/10.1016/j.anbehav.2009.11.018>.
- Fasanella, M., Fernández, G.J., 2009. Alarm calls of the Southern house wren *Troglodytes musculus*: variation with nesting stage and predator model. *J. Ornithol.* 150 (4), 853–863. <https://doi.org/10.1007/s10336-009-0406-2>.
- Fischer, G.J., Gilman, S.C., 1969. Following during imprinting as a function of auditory stimulus intensity. *Dev. Psychol.* 1, 216–218. <https://doi.org/10.1037/h0027303>.
- Gallup Jr, G.G., 1974. Animal hypnosis: factual status of a fictional concept. *Psychol. Bull.* 81, 836–853. <https://doi.org/10.1037/h0037227>.
- Gallup Jr, G.G., 1977. Tonic immobility: the role of fear and predation. *Psychol. Rec.* 27 (Suppl 1), 41–61. <https://doi.org/10.1007/BF03394432>.
- Gottfried, B.M., Andrews, K., Haug, M., 1985. Breeding robins and nest predators: effect of predator type and defense strategy on initial vocalization patterns. *Wilson Bull.* 97, 183–190. <http://www.jstor.org/stable/4162070>.
- Greenhall, A.M., Collias, N., 1954. *Sounds of Animals*. Folkway Records, Cornell, New York, NY, pp. 6124.
- Griesser, M., 2009. Mobbing calls signal predator category in a kin group-living bird

- species. Proc. R. Soc. Lond., B, Biol. Sci. 276 (1669), 2887–2892. <https://doi.org/10.1098/rspb.2009.0551>.
- Hatton, D.C., Thompson, R.W., 1975. Termination of tonic immobility in chickens by auditory stimuli. Bull. Psychon. Soc. 5, 61–62. <https://doi.org/10.3758/BF03336705>.
- Humphreys, R.K., Ruxton, G.D., 2018. A review of thanatosis (death feigning) as an anti-predator behaviour. Behav. Ecol. Sociobiol. (Print) 72 (2), 22. <https://doi.org/10.1007/s00265-017-2436-8>.
- Jones, R.B., 1986. Conspecific vocalizations, tonic immobility and fearfulness in the domestic fowl. Behav Process 13, 217–225. [https://doi.org/10.1016/0376-6357\(86\)90085-9](https://doi.org/10.1016/0376-6357(86)90085-9).
- Kanik, A.B., 1984. The Acoustic Components of Domestic Fowl Protection Calls Underlying the Enhancement of Tonic Immobility in Domestic Chicks (*Gallus Gallus*). Unpublished Senior Thesis. Franklin and Marshall College, Lancaster, PA.
- Kaplan, G., Rogers, L.J., 2013. Stability of referential signaling across time and locations: testing alarm calls of Australian magpies (*Gymnorhina tibicen*) in urban and rural Australia and in Fiji. PeerJ 1, e112. <https://doi.org/10.7717/peerj.112>.
- Kent, J.P., 1993. The chick's preference for certain features of the maternal cluck vocalization in the domestic fowl (*Gallus gallus*). Behaviour 125, 177–187. <https://doi.org/10.1163/156853993X00227>.
- Magrath, R.D., Bennett, T.H., 2011. A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proc. R. Soc. Lond., B, Biol. Sci. 279 (1730), 902–909. <https://doi.org/10.1098/rspb.2011.1362>.
- Marx, G., Leppelt, J., Ellendorff, F., 2001. Vocalisation in chicks (*Gallus gallus dom.*) during stepwise social isolation. Appl. Anim. Behav. Sci. 75, 61–74. [https://doi.org/10.1016/S0168-1591\(01\)00180-0](https://doi.org/10.1016/S0168-1591(01)00180-0).
- Miller, D.B., 1980. Maternal vocal control of behavioral inhibition in Mallard ducklings (*Anas platyrhynchos*). J. Comp. Physiol. Psychol. 94, 606–623. <https://doi.org/10.1037/h0077696>.
- Miller, D.B., Blaich, C.F., 1986. Alarm call responsivity of mallard ducklings: III. Acoustic features affecting behavioral inhibition. Dev. Psychobiol. 19, 291–301. <https://doi.org/10.1002/dev.420190402>.
- Miyatake, T., Katayama, K., Takeda, Y., Nakashima, A., Sugita, A., Mizumoto, M., 2004. Is death-feigning adaptive? Heritable variation in fitness difference of death-feigning behaviour. Proc. R. Soc. Lond., B, Biol. Sci. 271 (1554), 2293–2296. <https://doi.org/10.1098/rspb.2004.2858>.
- Naguib, M., Mundry, R., Ostreiher, R., Hultsch, H., Schrader, L., Todt, D., 1999. Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. Behav. Ecol. 10 (6), 636–640. <https://doi.org/10.1093/beheco/10.6.636>.
- Platzen, D., Magrath, R.D., 2005. Adaptive differences in response to two types of parental alarm call in altricial nestlings. Proc. R. Soc. Lond., B, Biol. Sci. 272 (1568), 1101–1106. <https://doi.org/10.1098/rspb.2005.3055>.
- Rogers, S.M., Simpson, S.J., 2014. Thanatosis. Curr Biol 24, R1031–R1033. <https://doi.org/10.1016/j.cub.2014.08.051>.
- Sanders, E.B., 1985. The Role of the Rise and Decay Times of the Fear-Caught Call in Enhancement of Tonic Immobility Duration in Naïve Domestic Chicks (*Gallus Gallus*). Unpublished Senior Thesis. Franklin and Marshall College, Lancaster, PA.
- Sargeant, A.B., Eberhardt, L.E., 1975. Death feigning by ducks in response to predation by red foxes (*Vulpes fulva*). Am. Midl. Nat. 94, 108–119. <https://doi.org/10.2307/2424542>.
- Stewart, J., 1953. Death Cry of a Crow." Game Call, Waco Texas, GC 201, 45 RPM, Copyright, Outdoor Products.
- Suzuki, T.N., 2016. Semantic communication in birds: evidence from field research over the past two decades. Ecol. Res. 31 (3), 307–319. <https://doi.org/10.1007/s11284-016-1339-x>.
- Thompson, R.K.R., Foltin, R.W., Boylan, R.J., Sweet, A., Graves, C.A., Lowitz, C.E., 1981. Tonic immobility on Japanese quail can reduce the probability of sustained attack by cats. Anim. Learn. Behav. 9, 145–149. <https://doi.org/10.3758/BF03212037>.
- Thompson, R.K.R., Liebreich, M., 1987. Adult chicken alarm calls enhance tonic immobility in chicks. Behav Process 14, 49–61. [https://doi.org/10.1016/0376-6357\(87\)90066-0](https://doi.org/10.1016/0376-6357(87)90066-0).
- De Tommaso, M., Kaplan, G., Chiandetti, C., Vallortigara, G., 2019. Naïve 3-day-old domestic chicks (*Gallus gallus*) are attracted to discrete acoustic patterns characterizing natural vocalizations. J. Comp. Psychol. 133 (1), 118–131. <https://doi.org/10.1037/com0000132>.
- Vallortigara, G., 2012. Core knowledge of object, number, and geometry: a comparative and neural approach. Cogn. Neuropsychol. 29 (1–2), 37–41. <https://doi.org/10.1080/02643294.2012.654772>.
- Vallortigara, G., Chiandetti, C., 2017. Objects and space in an avian brain. In: Carel ten Cate, C., Healy, S.D. (Eds.), Avian Cognition. Cambridge University Press, Cambridge, pp. 141–162.
- Vallortigara, G., Versace, E., 2017. Laterality at the neural, cognitive, and behavioral levels. In: Call, J., Burghardt, G.M., Pepperberg, I.M., Snowdon, C.T., Zentall, T. (Eds.), APA Handbooks in Psychology. APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior. American Psychological Association, Washington, DC, US, pp. 557–577. <https://doi.org/10.1037/0000011-027>.
- Welbergen, J.A., Davies, N.B., 2008. Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. Anim. Behav. 76 (3), 811–822. <https://doi.org/10.1016/j.anbehav.2008.03.020>.