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A Test of the Nonlinearity Hypothesis in Great-tailed Grackles (*Quiscalus mexicanus*)

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Abstract

Highly aroused or scared animals may produce a variety of sounds that sound harsh and are somewhat unpredictable. These sounds frequently contain nonlinear acoustic phenomena, and these nonlinearities may elicit arousal or alarm responses in humans and many animals. We designed a playback experiment to elucidate whether specific nonlinear phenomena can elicit increased responsiveness in great-tailed grackles (*Quiscalus mexicanus*). We broadcast two control sounds (a 0.5-s, 3-kHz pure tone and the song of tropical kingbirds (*Tyrannus melancholicus*) and three test sounds that all began with a 0.4-s, 3-kHz pure tone and ended with 0.1 s of either a 1- to 5-kHz band of white noise, an abrupt frequency jump to 1 kHz, or an abrupt frequency jump to 5 kHz. In response to these three nonlinear phenomena, grackles decreased their relaxed behavior (walking, foraging, and preening) and increased looking. A second experiment looked at the rapidity of the time course of frequency change and found that the abrupt frequency jump from 3 to 1 kHz, as opposed to a gradual downward frequency modulation over the same bandwidth, was uniquely arousing. These results suggest that while nonlinear phenomena may be generally evocative, frequency jumps may be the most evocative in great-tailed grackles. Future studies in other systems can evaluate this general hypothesis.

Ever since Darwin's 'Principle of Antithesis' (Darwin 1872) and Morton's 'motivation-structural rules' (Morton 1977), researchers have focused on determining the relationship between acoustic structure and function (Rendall & Owren 2010). This link between structure and function couples sound production systems with the resulting sounds that are produced by signalers in certain situations, and also to the responses to those sounds elicited in receivers. Sound production systems may, routinely or in specific situations, produce a set acoustic features that are referred to as nonlinear acoustic phenomena. These nonlinear acoustic phenomena may include rapid frequency jumps, subharmonics, biphonation, and deterministic chaos (which looks like noise on a spectrogram) (Wilden et al. 1998; Fitch et al. 2002). Sounds with rapid frequency jumps can function to capture attention (McConnell 1991) and may elicit aggressive responses (Hope 1980; Slocombe & Zuberbüler 2005). For instance, fear screams are 'noisy' and have a nonlinear structure that includes deterministic chaos and what appears to be noise (Gouzoules et al. 1984; Tokuda et al. 2002). Calls that function as mobbing calls are characterized by upward frequency shifts and noise, while alarm calls are characterized by chevron-shaped frequency modulations (Hope 1980). Importantly, animals hearing these sounds may have specific responses to them. For instance, tonal-harmonic signals may induce calm behavior, while abrupt signal onsets may increase arousal in mammals and birds (Morton 1977 & Götz & Janik 2011). Rapid up-sweeps that characterize whistles can capture attention and increase locomotion (McConnell 1991). The link between structure and function suggests that nonlinear acoustic phenomena should act generally to elicit arousal and antipredator responses in multiple species, although their potential utility is not restricted to antipredator behavior (Rendall & Owren 2010).

Nonlinear acoustic phenomena have the potential to be especially evocative to receivers because, in some cases, they result from over-blowing a producer's vocal system (Fitch et al. 2002), a phenomenon that may be associated with fearful events. Strictly, it is the vocal production system that is nonlinear, not the sound, but nonetheless, nonlinear acoustic phenomena have recognizable structures and share a defining characteristic of some degree of unpredictability. Receivers may pay attention to nonlinear sounds because their unpredictability makes them difficult to habituate to (Owren & Rendall 1997; Fitch et al. 2002; Blumstein & Récapet 2009). In marmots (*Marmota flaviventris*) and meerkats (*Suricata suricatta)*, alarm calls that contained nonlinear attributes were more evocative than alarm calls without nonlinear phenomena (Blumstein & Récapet 2009; Townsend & Manser 2011). Studies in humans show that the reactions of both parents and non-parents to infant cries were strongest in response to sounds with rapid frequency shifts (Green et al. 1987). Film sound tracks with simulated nonlinear acoustic phenomena may elicit fearful responses in humans (Blumstein et al. 2010).

Nonlinear acoustic phenomena have been shown to be generally evocative to receivers (Blumstein & Récapet 2009). If such sounds, specifically rapid frequency jumps and deterministic chaos, are generally evocative, we expect that receivers should be more aroused and increase antipredator behavior in response to sounds characterized by, or containing, nonlinear acoustic phenomena than in response to sounds without these features. Furthermore, we expect that more rapid frequency shifts will cause stronger responses. We tested these hypotheses by presenting several simulated nonlinear acoustic phenomena (white noise to simulate deterministic chaos, abrupt frequency jumps, and frequency modulations) to an island population of great-tailed grackles (*Quiscalus mexicanus*). Great-tailed grackles were used as a focal study species due to their abundance at our study site. Grackles were also easily approachable, ensuring that playbacks could be carried out consistently. By using novel synthetic sounds we were able to isolate the specific acoustic structure of the nonlinear acoustic phenomena. Because these sounds had no connection to individual species, they could be implemented to test our general hypothesis on any species.

Methods

All experiments were carried out at Calabash Caye Field Station in Calabash Caye, Belize (17.266667°N, 87.816667°W). Playback experiments were conducted from Oct. 8 to 24, 2011, between 05:45 and 10:00 h and 16:00 and 18:00 h. Calabash Caye is a 1.90 × 1.00 km island with no permanent residents, although it does have four private properties and a Belize Coast Guard forward operating base.

The initial experiment was designed to determine whether three simulated nonlinear acoustic phenomena caused a behavioral response and, if so, which were most evocative. The level of response was measured by an increased time spent 'looking' (more attentive), increased time spent in 'locomotion', or a decreased time in relaxed behaviors such as 'preening' or 'foraging'. The experiment included two control sounds: a 0.5-s, 3-kHz pure tone and the ~1.0-s vocalization of tropical kingbirds (*Tyrannus melancholicus*). The three simulated nonlinear acoustic phenomena all began with a 0.4-s, 3-kHz pure tone and ended in 0.1 s of either a 1- to 5-kHz, a band of white noise, a frequency jump to a 1-kHz pure tone (FJ Down), or a frequency jump to a 5-kHz pure tone (FJ Up) (Fig. 1). Tropical kingbird vocalizations served as an appropriate procedural control because tropical kingbirds were common on the island and often were heard vocalizing.

We synthesized sounds (16 bit, 44 kHz) using AVID Pro Tools HD, version 9.0.5 (Avid Technology, Inc., Burlington, MA, USA) with the DIGIRACK Signal Generator plug-in's sine and white noise functions. Our synthesized calls ranged between 1 and 5 kHz because this frequency range falls well within many birds' hearing range (Dooling et al. 1978). Because rapid onset of sounds may trigger a startle response, we ramped up the amplitude linearly to peak amplitude over 100 ms to avoid startling our subjects (Götz & Janik 2011). Sounds were stored in AIF format on Apple iPods (Apple Inc., Cupertino, CA, USA) and played back to subjects using a PAL Speaker (Tivoli Audio, Boston, MA, USA). Stimuli were broadcast at an amplitude of 84–86 dB SPL (measured at 1 m using a RadioShack digital sound level meter, weighting A, peak amplitude). For the control sounds, we obtained six tropical kingbird songs from a commercially produced CD (Oberle 2008).

Movement from site to site on the island throughout the day helped us avoid resampling individuals. When a suitable subject was located (stationary or slowly moving, not visibly interacting with conspecifics or heterospecifics), the experimenter came to approx. 10 m (mean = 8.99 m ± 2.03 SD) from the subject (experimenters were trained to estimate the distance to within approx. 1 m accuracy before data collection) to begin the focal observation. Each

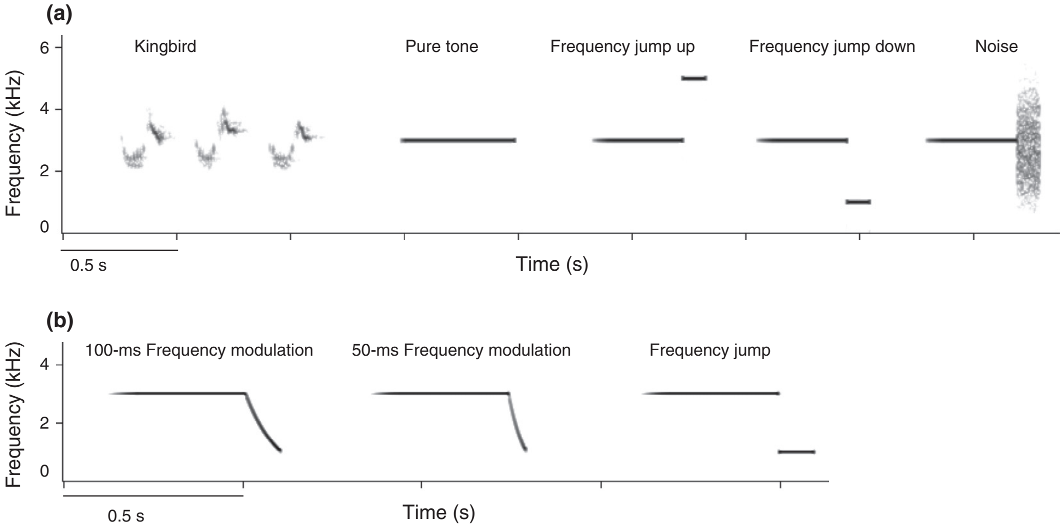

Fig. 1: Spectrograms (1024 point, 93.75% overlap, Hamming window) for playback experiments: (a) experiment 1: control (tropical kingbird call/song), pure tone, frequency jump up, frequency jump down, and noise; and (b) experiment 2: 100-ms frequency modulation, 50-ms frequency modulation, and frequency jump down.

treatment began with 30 s of silence, during which time the subject's behavior was observed and behavioral transitions were dictated quietly into a tape recorder (see Table 1 for ethogram used). During this 30-s period, we observed and recorded the individual's baseline behavior. After 30 s of silence, the acoustic stimulus was broadcast, and we continued our focal observation for another 60 s of silence, during which time we observed and dictated the subject's behavior. For this experiment, a total of 156 playback experiments were performed (35 'kingbird control', 32 'pure tone', 27 'frequency jump from 3 to 5 kHz', 29 'frequency jump from 3 to 1 kHz', and 33 'pure tone followed by white noise').

The second experiment aimed to determine whether the rate of frequency change influences response, which compared responses of grackle to frequency jumps (abrupt shifts in frequency) to the responses to frequency modulations (gradual down-sweeps and up-sweeps of frequency change). Three treatments were used: a 100-ms frequency modulation (0.4 s of 3-kHz, pure tone followed by a 100-ms sweep to 1-kHz pure tone), a 50-ms frequency modulation (0.4 s of 3-kHz, pure tone followed by a 50-ms down-sweep to 1-kHz pure tone), and a frequency jump (0.4 s of 3-kHz pure tone followed by 0.1 s of 1-kHz pure tone). For this experiment, we performed a total of 80 playback experiments (22 'frequency jump', 27 '50-ms frequency modulation', 31 '100-ms frequency modulation').

All focal observations were scored using JWatcher (v1.0 Blumstein & Daniel 2007), which was also used to calculate the proportion of time that grackles spent engaged in each behavior. A behavior's duration was

Table 1: Grackle ethogram used to quantify response to playback

Behavior	Description
Stand and Look	Immobile individual standing with head in a fixed position; scored each time head moved then fixed in a new position
Out of sight	Focal out of sight
Vocalization	Any type of call or song; new vocalization counted each time there was a pause
Locomotion	
Flight	Flying through the air (but not out of sight)
Hopping	Jumping from place to place, not flying; scored for each individual hop
Relaxed behavior	
Walk	Moving legs, taking steps
Preen	Bird standing, beak moving through feathers; scored each time the head was removed from the feathers for a break in preening
Forage	Bird standing, beak toward ground looking for food or food in beak; forage scored each time the bird put its beak down to the ground

calculated from the point when individuals started a behavior until the point when they switched to a new behavior. The two exceptions were looking [which was scored every time the head moved and then fixated (i.e., was immobile for >1 s)] and hopping (which was scored for each individual hop). In our analyses, however, only the proportion of time spent looking and the proportion of time spent hopping were used. We grouped behaviors for analysis into 'relaxed behaviors' and 'locomotion'. Walking, foraging, and preening were grouped and considered 'relaxed behaviors' because they are not antipredatory or defensive behaviors. Walking was included because grackles foraged on the ground and they were never seen fleeing by walking away from the site of playback. 'Locomotion' included flight and hop, and these behaviors were always directed away from the source of the playback sound.

By observing the behavior of the grackles in other situations, we noted that when faced with other potentially alarming sounds, such as the sound of a generator starting, grackles immediately left the area by flying or hopping. The proportion of time in sight engaged in locomotion and vigilance (looking, flying, and hopping) has been used by others to reflect fearful responses (see Boissy 1995; Searcy & Caine 2003; Ito & Mori 2010).

To quantify the response to playback, we used the 30 s before the playback as a baseline and compared those results to the first 15 s after the playback because examination of graphical depictions of the results showed that the most substantial changes from baseline occurred within 15 s after playback. We calculated 95% confidence intervals of the difference from baseline to post-playback proportions of time of each behavior to see whether the time allocated to each behavior changed significantly based on stimulus presentation. Using StatView (v 5.0.1 SAS Inc., Chicago, IL, USA), we fit ANOVA models and calculated Fisher's PLSD to determine how stimulus type explained variance in time allocation.

To ensure that our results were not confounded by other variables, we recorded a number of other factors during each trial. We fit one-way ANOVA models for each factor and determined that there were no significant differences between treatments for these variables. For the first experiment, we tested distance from speaker ($p = 0.916$), whether the individual was on the ground or in a tree ($p = 0.405$), the height of the individual in the tree ($p = 0.903$), percentage cloud cover at time of the playback ($p = 0.991$), the wind speed according to the Beaufort scale ($p = 0.573$), the number of conspecifics within 10 m of the individual ($p = 0.395$), the number of heterospecifics within 10 m of the individual ($p = 0.769$), and the distance from the individual to some type of cover ($p = 0.886$). For the second experiment, we tested the same variables and again found no significant differences by treatment: distance from speaker ($p = 0.765$), whether the individual was on the ground or in a tree ($p = 0.839$), the height of the individual in the tree ($p = 0.540$), percentage cloud cover at time of the playback ($p = 0.847$), the wind speed according to the Beaufort scale ($p = 0.421$), the number of conspecifics within 10 m of the individual ($p = 0.884$), the number of heterospecifics within 10 m of the individual ($p = 0.098$) and the distance from the individual to some type of cover ($p = 0.855$).

Grackles were not individually marked; it is likely that some individuals received more than one playback. To estimate the magnitude of this inadvertent pseudoreplication, we censused the grackles on the island using a modified point-count method. We were unable to randomly access much of the island because of dense mangrove vegetation, but we watched grackles move in and out of this habitat. On two different mornings, three observers simultaneously censused three separate areas of the island. Every 15 min from 06:15 to 09:00 h, observers counted and recorded the number of individual grackles seen or heard within 20 m. The maximum number of grackles counted across all three sites at any single point in time was 44. From this number we know that there were at least 44 grackles on the island. However, 80% of the island was not censused and grackles were observed moving at least 200 m at a time, including into and out of areas we could not easily access. Thus, we assume that there are substantially more individuals than we counted. Nevertheless, we recognize the possibility of some degree of pseudoreplication and suggest that, because animals were not marked, these results be treated with some caution.

Our playback protocol (systematically varying playback order and maintaining a minimum duration of 5 min between playbacks) helped prevent this from confounding interpretation. To reduce carryover effects, we used a Latin Square design to determine playback order while walking along trails. If anything, conducting repeated playbacks to an individual would cause that individual to selectively habituate. Such selective habituation would presumably be randomly distributed across treatments and would make it more difficult to detect significant differences between treatments. Given that we were often able to see grackles move around in the vicinity of where we worked, and we were able to successfully avoid conducting successive playbacks to the same individual, we find it very unlikely that any pseudoreplication biased our results. Again, however, animals were not marked and we should view the generality of these results with some caution.

Results

Grackles seem to trade off locomotion with vigilance; thus, it is the pattern of results that must be considered when interpreting the first experiment. This experiment showed that grackles hearing any of the three simulated nonlinear acoustic phenomena significantly decreased the proportion of time allocated to relaxed behavior (Fig. 2a). The frequency jump down caused a nearly significant increase in proportion of time allocated to locomotion (Fig. 2b) and was significantly different from both the control (Fisher's PLSD p = 0.021) and the pure tone (p = 0.017). Both the frequency jump up and the noise evoked significantly more time allocated to looking; the frequency jump down caused a nearly significant increase in proportion of time allocated to looking (Fig. 2c). Importantly, the control and pure tone playback experiments elicited no significant change from baseline time allocation in any of the dependent variables, indicating that all responses were due to the simulated nonlinear acoustic phenomena and not to playback novelty.

Our second experiment showed that birds hearing any of the three simulated nonlinear acoustic phenomena engaged in significantly less relaxed behavior (Fig. 2d), and significantly more looking (Fig. 2f). Grackles spent significantly less time engaged in relaxed behavior in response to the frequency jump down than either to the 100-ms frequency modulation (p = 0.003) or to the 50-ms frequency modulation (p = 0.008). Grackles spent significantly more time looking in response to the frequency jump as opposed to either the 100-ms frequency modulation (p = 0.019) or the 50-ms modulation (p = 0.037). There was, however, no effect on time allocated to locomotion (Fig. 2e).

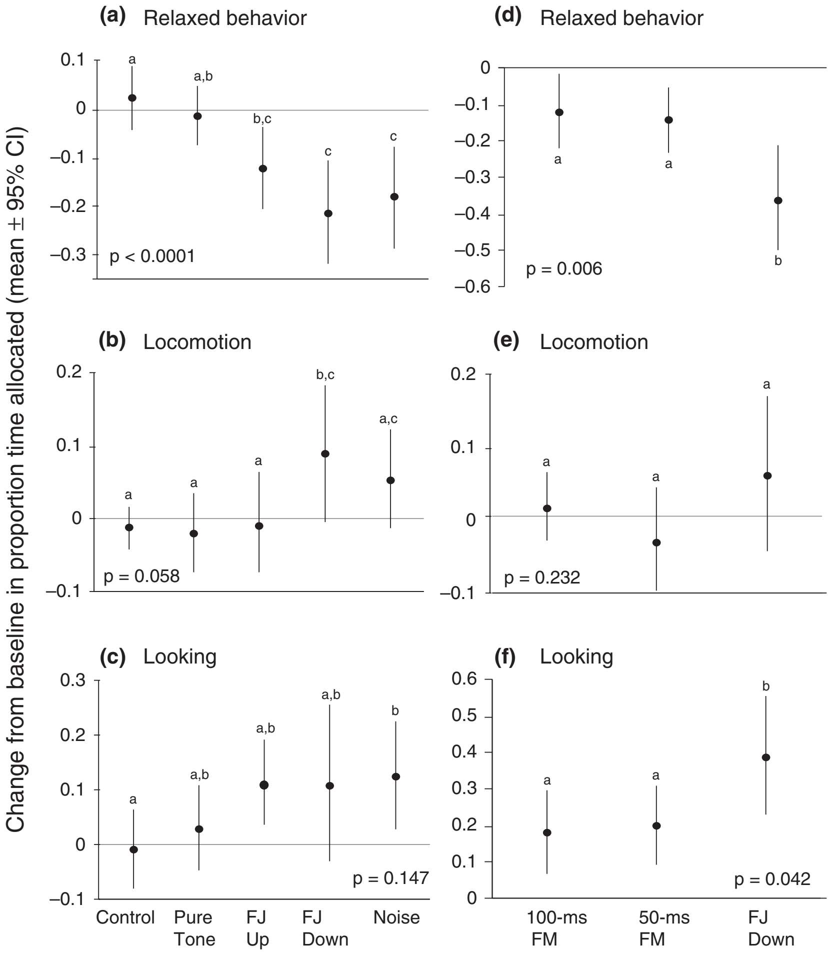

Fig. 2: Response of grackles to different playbacks. Pairs with the same letters represent non-significant (Fisher's PLSD p > 0.05) pairwise comparisons, while stimulus pairs with different letters are significantly different. (a–c) The grackles' responses to experiment 1 and illustrate the change (average ±95% CI) from baseline time allocation to (a) relaxed behavior, (b) locomotion, and (c) looking. (d–f) The grackles' responses to experiment 2 and illustrate the change (average ±95% CI) from baseline time allocation to (d) relaxed behavior, (e) locomotion, and (f) looking.

Discussion

Our results demonstrate that after the three types of simulated nonlinear acoustic phenomena were broadcast, grackles increased looking and reduced relaxed behavior. These results demonstrate that these sounds captured the listener's attention. We also infer that, given their nature (reduced relaxed behavior, heightened vigilance, increased locomotion compared with pre-playback baseline periods), these responses can be interpreted as an antipredatory response. Abrupt frequency jumps down and noise were more evocative than frequency jumps up. The grackles' response to the frequency jump up was never significantly different from their response to that elicited by a pure tone. The frequency jump down evoked significantly different responses than the pure tone in both relaxed behavior and looking, while noise evoked significantly different responses in relaxed behavior and locomotion.

More abrupt frequency changes were more evocative to grackles, suggesting that the time course of frequency change is salient. Frequency jumps, which are examples of nonlinear acoustic phenomena, are common in alarming vocalizations (Blumstein & Récapet 2009), and the simulated frequency jumps were more evocative to grackles than either the 50-ms or 100-ms frequency modulations. This may be because many species, including grackles, have naturally occurring frequency modulations that occur over 40–500 ms (Fig. 3). Thus, grackles may commonly hear such sounds and, as a result, may be relatively habituated such modulations. Abrupt frequency jumps may be less common and generally elicit antipredator responses, which would explain why they are present in screams, mobbing calls, and some alarm calls (Fitch et al. 2002; Blumstein & Récapet 2009). Because such frequency jumps are not present in most common grackle calls, they may not be habituated to this type of sound.

While our study focused on one species, nonlinear acoustic phenomena are present in many species' alarm calls and fear screams and thus are likely to act more generally to evoke antipredatory responses in animals hearing them (Gouzoules et al. 1984; Blumstein & Récapet 2009; Townsend & Manser 2011). We also acknowledge that such sounds can be used in a variety of non-predatory situations and can function as general attention-getting signals. Additional studies could combine our results with the knowledge that startle or fear reflexes occur in response to a specific type of rise time (i.e., those that are fast–Götz & Janik 2011; Owren & Rendall 2001) and by doing so identify the precise time course that elicits arousal.

Our results could also have implications for human and wildlife interactions specifically with respect to conservation and management. Previous studies have shown that startle-eliciting noises have long-term effects on the behavior of some animal populations, and increasing the stimulus rise time could decrease the amount of disturbance caused by anthropogenic sounds (Götz & Janik 2011). Many anthropogenic sounds contain sounds that resemble nonlinear acoustic phenomena, and these almost always include abrupt frequency jumps or noise, which our results show to be arousing and therefore possibly disturbing to animals. Such disturbance may include distraction from important activities (Chan & Blumstein 2011), reproduction (Peris & Pescador 2004), and other activities (Warren et al. 2005). One thing that may reduce the deleterious impact of anthropogenic sounds would be to reduce or eliminate nonlinear acoustic phenomena and noise. Of course, the reverse is also true: Nonlinear acoustic phenomena may be particularly good repellents that could be used to deter animals from certain areas (Götz & Janik 2011).

Our results for this species of bird show that simulated nonlinear acoustic phenomena are arousing to

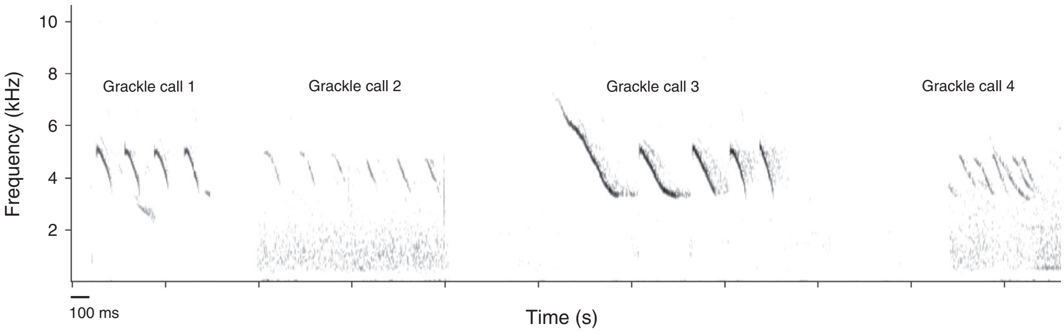

Fig. 3: Spectrograms (1024 point, 93.75% overlap, Hamming window) of four natural grackle vocalizations from a commercial CD (Oberle 2008). As can be seen in the spectrograms, natural grackle vocalizations contain rapid frequency modulations from a higher to lower frequency ranging in length from 50 to 300 ms.

receivers. Further experiments could reveal other functions of these sounds and demonstrate that naturally produced nonlinear acoustic phenomena are more than simply a by-product of vocal production mechanisms (Fitch et al. 2002), but rather may have been selected to influence or otherwise manipulate receiver behavior (Rendall & Owren 2010).

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