Received: 20 June 2017 | Revised: 15 August 2017 | Accepted: 4 September 2017

DOI: 10.1111/eth.12702

RESEARCH PAPER

WILEY ethology

Do birds differentiate between white noise and deterministic chaos?

Daniel T. Blumstein[1,2] | Jessica Whitaker[2] | Judith Kennen[2] | Gregory A. Bryant[3]

[1]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

[2]Rocky Mountain Biological Laboratory, Crested Butte, CO, USA

[3]Department of Communication, Center for Behavior, Evolution, and Culture, University of California, Los Angeles, CA, USA

Correspondence
Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA.
Email: marmots@ucla.edu

Funding information
Division of Biological Infrastructure, Grant/Award Number: 1226713; NSF, Grant/Award Number: DBI-1226713

Editor: W. Koenig

Abstract

Noisy, unpredictable sounds are often present in the vocalizations of fearful and stressed animals across many taxa. A variety of structural characteristics, called nonlinear acoustic phenomena, that include subharmonics, rapid frequency modulations, and deterministic chaos are responsible for the harsh sound quality of these vocalizations. Exposure to nonlinear sound can elicit increased arousal in birds and mammals. Past experiments have used white noise to test for effects of deterministic chaos on perceivers. However, deterministic chaos differs structurally from white noise (i.e., random signal with equal energy at all frequencies), and unlike white noise, may differ dramatically depending on how it is produced. In addition, the subtle structural variation of chaos may not be distinguishable in the environment due to the attenuation and degradation of sound over distance and different habitat types. We designed two experiments to clarify whether American robins (*Turdus migratorius*) and warbling vireos (*Vireo gilvus*) discriminate between white noise and deterministic chaos. We broadcast and re-recorded white noise and two exemplars of deterministic chaos—one generated with a Chua oscillator and the other generated using a logistic equation—at 1, 10, 20, 30, 40, and 80 m across open and forested habitat and used spectrogram correlations to compare stimuli along this degradational gradient. We found that sounds degraded similarly in both habitats when compared to a reference distance of 1 m. Comparing pairs of stimuli across distances suggested that Chua chaos was more easily distinguishable from noise and logistic chaos. In addition, all stimuli became more distinctive over increased distance. The second experiment tested behavioral responses of robins and warbling vireos to control sounds of tropical kingbird (*Quiscalus mexicanus*), white noise, and two exemplars of deterministic chaos (Chua and logistic). Neither American robins nor warbling vireos responded differently to at least two types of deterministic chaos and white noise, validating previous playback studies that used white noise as a surrogate for deterministic chaos. Uniform responses to a variety of nonlinear features in these birds possibly reflect error management in alarm signal detection.

KEYWORDS
acoustic discrimination, deterministic chaos, noise, nonlinear acoustics

1 | INTRODUCTION

Typically, unpredictable sounds elicit attentive responses better than melodic, pure tones. For example, the cries of human babies cause physiological responses in adult listeners associated with preparation for caregiving (Tkaczyszyn et al., 2013). Noisy screams, cries, and other sounds often contain specific structural characteristics that are particularly evocative to listeners. These nonlinear acoustic phenomena are found in vocalizations from a variety of taxa including terrestrial mammals (Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008; Charlton, 2015; Charlton, Watchorn, & Whisson, 2017; Rendall et al. 2009; Riede, Arcadi, & Owren, 2007; Stoeger, Baotic, Li, & Charlton, 2012; Stoeger, Charlton, Kratochvil, & Fitch, 2011; Tokuda, Riede, Neubauer, Owren, & Herzel, 2002; Wilden, Herzel, Peters, & Tembrock, 1998), marine mammals (Tyson, Nowacek, & Miller, 2007), frogs (Pettitt, Bourne, & Bee, 2012), toadfish (Rice, Land, & Bass, 2011), and birds (Fee, Shraiman, Pesaran, & Mitra, 1998).

Nonlinear acoustic phenomena, such as rapid frequency jumps, subharmonics, biphonation, and deterministic chaos, can affect the behavior of listeners and are emotionally evocative. These sounds, whether natural or artificially synthesized, appear to decrease time spent engaged in relaxed behaviors in marmots (Blumstein & Recapet, 2009), meerkats (Townsend & Manser, 2011), and birds (Blesdoe & Blumstein, 2014; Slaughter, Berlin, Bower, & Blumstein, 2013). Recently, Charlton et al. (2017) found that subharmonics in koala (*Phascolarctos cinereus*) female rejection calls increased their auditory impact in a playback experiment with male koalas. Further, nonlinear phenomena present in film soundtracks have been used to elicit fearful responses in humans (Blumstein, Davitian, & Kaye, 2010). Some singers intentionally incorporate biphonation, subharmonics, and abrupt frequency changes into their vocal performances to add musical effect (Neubauer, Edgerton, & Herzel, 2003), and studies have shown that nonlinearities added to music are emotionally evocative (Blumstein, Bryant, & Kaye, 2012).

Vocal production dynamics underlie nonlinear acoustic phenomena in the sound generating system of birds (Fee et al., 1998; Larsen & Goller, 1999; Zollinger, Riede, & Suthers, 2008) and mammals (Fitch, Neubauer, & Herzel, 2002; Wilden et al., 1998), often in relation to excessive sound pressure levels. Evidence indicates these phenomena might serve adaptive functions (Morton 1977; Fitch et al., 2002). For example, vocalizations with nonlinearities may allow listeners to better differentiate between individuals of the same species (Rendall, Notman, & Owren, 2009) and, in particular, subharmonics may alter the way listeners behave around the communicating individual by indicating size or dominance (Fitch et al., 2002; Morton, 1977), or caller arousal levels (Charlton et al., 2017). Also, calls containing noise or rapid jumps in frequency from tonal sound to noise may be more difficult to habituate to and function to get receivers' attention (Blumstein & Recapet, 2009; Townsend & Manser, 2011). Other functions are possible as well. For example, nonlinearities in vocalizations of giant panda (*Ailuropoda melanoleuca*) neonates communicate cub arousal and ensure attention from the mother (Stoeger et al., 2012).

Similar to the functioning of laryngeal tissue during phonation, syringeal labia oscillate during birdsong production as indicated by endoscopic imaging and in vivo analyses (Larsen & Goller, 1999). As opposed to human vocal production, birdsong variations seem to be more a product of syringeal vibratory regimes rather than varying vocal tract configurations (Laje, Gardner, & Mindlin, 2002). Models of songbird neuromuscular events have demonstrated that a low number of oscillating parameters underlying vocal production can explain a tremendous amount of variation in song form acoustics. This suggests that the number of parameters responsible for chaos might also be relatively low and specifically might involve oscillatory patterns of syringeal tissue similar to vocal folds oscillation in terrestrial mammals. But the ratio of vocal tract cross-sectional width to vocal tract length can be much greater in some bird species than humans, and thus, feedback processes between source and filter are also likely responsible for nonlinear phenomena in many bird species' repertoire (Laje et al., 2002).

Most researchers examining nonlinear sound function have used mammals as model systems, while only two experimental studies have investigated the effects of nonlinear sound on birds (Blesdoe & Blumstein, 2014; Slaughter et al., 2013). While some studies have used recorded nonlinear vocalizations to study signal functions (Karp, Manser, Wiley, & Townsend, 2014), others have used short sequences of white noise to simulate vocalizations containing nonlinear phenomena (Blesdoe & Blumstein, 2014; Slaughter et al., 2013). Nonlinear dynamics in vocal systems produce deterministic chaos, not noise (Fitch et al., 2002; Hatzikirou, Fitch, & Herzel, 2006). It is unclear whether animals can discriminate between noise and deterministic chaos and whether noise could be used interchangeably with chaos in experiments testing nonlinear sound hypotheses. While the two nonlinear phenomena have a similar harsh sound quality, they differ in signal structure. Deterministic chaos retains some periodic oscillations observable as banding in spectrograms (Fitch et al., 2002), unlike white noise that has equal energy at all frequencies. Clearly, experiments using white noise stimuli might affect behavior differently than either naturally produced chaotic vocalizations, or synthesized stimuli, so one question in this study is whether white noise can act as an adequate proxy for deterministic chaos, or whether more ecologically valid stimulus features that actually contain deterministic chaos are needed.

Deterministic chaos can be produced in many different ways and represents a diverse class of nonlinear sounds. The structure of synthetically produced deterministic chaos varies substantially due to the large parameter space available. For example, Chua's oscillator is based on an electronic circuit capable of producing nonlinear phenomena dependent on how parameters (α, β, $-\gamma$, a, b, k) are varied (Chua, 1995; Pivka, Wah Wu, & Huang, 1994). A variety of chaotic attractors have been observed in Chua circuits that may have different acoustic structures (Leonov, Vagaitsev, & Kuznetsov, 2012; Matsumoto, 1984). Another method to synthesize chaos is to use a parameter above the Hopf bifurcation ($r > 3.57$) in a logistic equation. Chua and logistic chaos are both considered deterministic chaos and are two potential models for chaos in animal vocal systems—their acoustic output structure varies considerably and their effects on listeners might differ. Slight variations in a signal might affect the way sounds are perceived and could have effects on the level of arousal incited in listeners. It is unclear whether the structural differences of noise and chaos are perceptibly different. Slight structural differences among nonlinearities may not be easily discriminated after they have degraded during transmission. With increasing distance between the signaler and receiver, degradation and attenuation of sound increases due to atmospheric absorption, ground attenuation, signal scattering, and deflection of sound by layered surfaces such as spaces between tree canopy and the ground (Wiley & Richards, 1978). These effects may (or may not) vary by habitat type. Thus, we might expect that different types of noise and chaos would be more difficult to discriminate over distance.

During the entrainment of phonation modes in oscillatory systems typical of syringeal and laryngeal dynamics, desynchronization processes can result in nonlinear phenomena such as subharmonics and chaotic motion (Fitch et al., 2002). Models of deterministic chaos that approximate such vocal phenomena should reflect the dynamics of the production systems in question. By this logic, a continuous dynamical model such as a Chua circuit is a better candidate for mimicking the coupling dynamics of syringeal vibratory regimes and source-filter feedback than one-dimensional discrete dynamical models such as a logistic map. Finally, alternative models such as white noise do not approximate the dynamics of vocal production well at all but still produce output that bears some resemblance to the noisy features of high arousal vocalizations in birds and mammals.

But to what extent do acoustic differences across these types of noisy phenomena matter for perceptual systems designed to detect important features of vocalizations related to signaling arousal and danger? Accuracy in perception is always critical in domains of danger, but managing errors through shifts in criterion can lead to selection for low thresholds in arousal detection (Johnson, Blumstein, Fowler, & Haselton, 2013). The demand for speed, combined with typical ecological contexts that contain relatively few other sound sources with similar features, could reduce the importance of nonlinear spectral details in alarm signaling.

We conducted two experiments. First, we broadcast and re-recorded white noise and two types of deterministic chaos (Chua and logistic) and studied the sounds' degradation over distance. Second, we asked whether two common birds, American robins (*Turdus migratorius*) and Warbling Vireos (*Vireo gilvus*), were able to discriminate between the three stimulus conditions. While many species can produce nonlinear phenomena, the nonlinearity and fear hypothesis is not restricted to those species that regularly produce them so, in principle, any species should be appropriate to study. American robins have a diverse vocal repertoire whose song consists of variable frequency whistles (Peshek & Blumstein, 2011), as do warbling vireos (unpublished observations). Mobbing and begging calls, however, may contain harsh nonlinear phenomena. The two types of deterministic chaos sounded different with Chua chaos exhibiting more clicks (frequency jumps) and logistic chaos lacking clicks (Figure 1).

2 | METHODS

2.1 | Study site and species

From 30 May 2013 to 8 July 2013 and 2 June 2015 to 10 July 2015, we conducted environmental sound degradation and playback experiments with American robins and Warbling Vireos near the Rocky Mountain Biological Laboratory in Gothic, Colorado (N 38.9592°, W 106.9898°). Experiments were performed from sunrise until mid-morning under calm weather conditions when the wind was ≤Beaufort scale 3.

2.2 | Sound degradation experiment

We broadcast the three experimental stimuli across representative open and forested habitats where the birds were found. Stimuli were broadcast and re-recorded with an Audix OM-3xb microphone (Audix Microphones, Wilsonville, OR, USA) and Marantz PMD 660 solid-state recorder (16 bit, 44.1 kHz sampling) 1, 10, 20, 30, 40, and 80 m from the speaker. We replicated this five times in each habitat type. Stimuli were edited to 5.5 s files and we used RAVEN 1.4 (Bioacoustics Research Program 2011) to calculate spectrogram correlation values

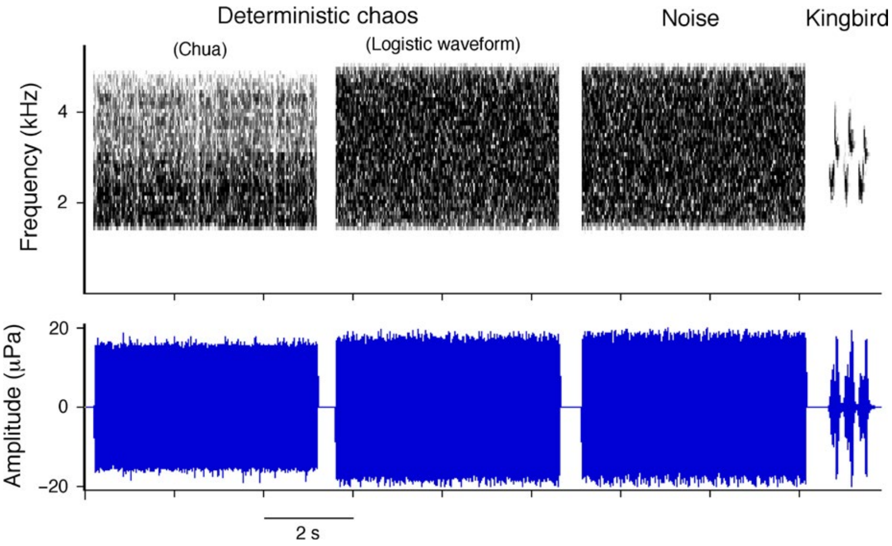

FIGURE 1 Spectrograms and waveforms of three experimental stimuli (Chua, logistic waveform, white noise) and an exemplar of the kingbird vocalization used in environmental transmission and playback experiments. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Ethogram of behaviors recorded during playbacks, modified from Slaughter et al. (2013)

Behavior	Description
Stand and look	Standing or perching, scored each time head moved and fixated
Forage	Moving head toward the ground to forage or having food in beak
Preen	Moving beak through feathers
Walk	Taking steps, moving legs individually
Hop	Jumping from one location to another, scored by each discrete hop
Other	Other behaviors such as shaking, feather ruffling, and scratching
Vocalization	Singing or non-song vocalization, excluding chinking
Flight	Flying, but not out of sight
Out of sight	No longer insight

(256 sample spectrogram with Hann window, hop size 128, 50% overlap) for each stimulus compared to other stimuli at the same distance or itself across the increasing distances. We fitted two general linear models where stimulus, distance, and habitat types were main effects (all interactions were included) to explain spectrogram correlation variation in degradation over distance. The first set of spectrogram correlation values compared each stimulus recorded at 10, 20, 40, 80 m to its 1 m value. This analysis was designed to compare the degradation of the three stimuli over distance in the two habitat types. The second compared pairs of stimuli at each distance. This analysis was designed to determine which stimuli were most distinguishable or more similar to each other with increased distance.

2.3 | Playback experiment

Four stimuli were used for the playback experiments including three experimental stimuli and one control stimulus (Figure 1). Experimental stimuli included white noise and two types of deterministic chaos (logistic wave form and a type created with the Chua oscillator). Control stimuli consisted of six tropical kingbirds (*Tyrannus melancholicus*) vocalizations not containing nonlinear acoustic attributes. The kingbird stimuli provided a novel control for comparison to the novel experimental stimuli because the species was not found locally. The amplitude on each track was RMS normalized (to 95% of peak amplitude) in Sound Studio then 1.5–5.0 kHz bandpass filtered in RAVEN 1.4 (Bioacoustics Research Program 2011). Stimuli were stored on an Apple iPod (Apple, Inc., Cupertino, CA, USA) in AIFF format for subsequent playback.

We conducted a total of, 114 playback experiments on American robins (33 for the tropical kingbird stimulus, 28 for noise, 28 for logistic waveform, and 25 for Chua chaos), and a total of 91 playback experiments on warbling vireos (20 tropical kingbird, 24 noise, 24 logistic chaos, and 23 Chua chaos).

Observers quietly positioned themselves about 10–15 m (American robin average ± *SD*: 11.6 ± 1.76; warbling vireo average ± *SD*: 12.2 ± 4.94) from a subject and waited for it to relax. Relaxed behavior was inferred if the bird was foraging, walking, or preening. Stimuli were broadcast from a PAL Speaker (Tivoli Audio, Boston, MA, USA) at a peak amplitude of 85 dB SPL (measured 1 m away, weighting A). A 30 s period of silence marked the beginning of each playback to allow baseline behavior to be recorded. Following the 30 s of silence, the brief stimulus was broadcast and followed by an additional 60 s of silence, which allowed the behavior of the focal individual to be recorded to determine whether there was any reaction to the stimulus.

We dictated, into a digital audio recorder, behavioral transitions using a standard avian ethogram (Table 1). Following playback, we recorded the GPS location, wind speed (measured on the Beaufort scale at the time of playback; no experiments conducted if above 3), percentage of cloud cover (no experiments conducted during rain), distance from observer (in m), number of conspecifics within 10 m, number of heterospecifics within 10 m, and, if obvious from plumage, the subject's age and sex. Playback trials were conducted with at least a 40 m radius between focal subjects in an attempt not to repeat trials on any bird and to ensure that the subject had not already responded to a previous playback (average ± *SD* distance between playbacks was 368 ± 471.7 m for American robins and 325 ± 263.9 m for warbling vireos). Subsequent trials were conducted a minimum of five minutes apart (American robins averaged 1 hr 5 min ± 1 hr 42 min, warbling vireos averaged 51 min ± 48 min), and the four stimuli were played according to a predetermined script to ensure a balanced number of playbacks per stimulus and to reduce any possible systematic carryover effects on subjects that might have heard a previous sound.

We explored whether any other recorded factors—distance from observer to bird, height of bird in tree, distance of the bird from the road, distance of bird from town, distance between birds, number of conspecifics within 10 m, and the number of heterospecific birds within 10 m—varied significantly by sound stimuli used for both species.

For American robins, none of our measured covariates differed significantly as a function of treatment: distance from observer to bird (GLM, $F_{3,\ 110} = 1.63$, $p = .19$); distance from bird to road (chi-square comparing <20 to ≥20 m, χ^2 (3, $N = 114$) = 1.83, $p = .61$); the number of conspecifics within 10 m (GLM, $F_{3, 110} = 0.96$, $p = .42$); the number of heterospecifics within 10 m (GLM, $F_{3, 110} = 1.25$, $p = .30$); height in trees (GLM, $F_{3, 105} = 0.82$, $p = .49$); or wind speed (chi-square comparing different Beaufort scores, χ^2 (9, $N = 114$) = 7.19, $p = .62$).

For warbling vireos, all but one of our measured covariates did not differ significantly as a function of treatment: distance from bird to road (chi-square comparing <20 to ≥20 m, χ^2 (3, $N = 91$) = 2.095, $p = .55$); the number of conspecifics within 10 m (GLM, $F_{3, 87} = 1.153$ $p = .33$); the number of heterospecifics within 10 m (GLM, $F_{3, 87} = 1.57$, $p = .20$); height in trees (GLM, $F_{3, 78} = 0.39$, $p = .76$); or wind speed (chi-square comparing different Beaufort scores, χ^2 (9, $N = 91$) = 5.19, $p = .82$). However, the distance from the observer varied significantly as a function of playback treatment (GLM, $F_{3, 87} = 3.03$, $p = .03$). Hence, we included the distance from observer in subsequent analyses.

2.4 | Data analysis

A total of 114 playback experiments were conducted on robins (33 using the tropical kingbird stimulus, 28 white noise, 28 logistic waveform chaos, and 25 Chua chaos), and a total of 91 playback experiments were conducted on warbling vireos (20 using the tropical kingbird stimulus, 24 white noise, 24 logistic waveform chaos, and 23 Chua chaos).

We used JWATCHER (Blumstein & Daniel, 2007) to calculate the proportion of time insight for all individual scored behaviors. Based on these calculations, we defined two additional collective behaviors. Relaxed behavior included time allocated to foraging, preening, and walking for robins. We noticed that warbling vireos spent much of their observed time singing so we included vocalization in "relaxed" for them. Total locomotion was defined to include hopping, flying, and walking.

Because responses were transient, we focused on the first 30 s following playback. We calculated the change in time allocated to looking, relaxed behavior, and total locomotion in the first 30 s after hearing the playback compared to the 30 s baseline time allocation by subtracting the after minus the baseline times (in no cases were baseline time allocations significantly different as a function of treatment). We then arcsine transformed these differences to normalize variation in these difference scores. We fitted general linear models in SPSS v. 21 to compare response to the treatments and to calculate the planned comparisons between the response to the kingbird and the other three treatments and to see whether noise and the two types of deterministic chaos led to similar responses. Throughout, our alpha was set to .05; we did not correct for the planned multiple comparisons. We tested for homogeneity of variance across treatments and examined residuals from models to confirm normality.

3 | RESULTS

3.1 | Sound degradation

Spectrogram correlation values compared between individual stimuli and 1 m reference distances showed significant habitat (GLM, $F_{1, 120} = 11.9$, $p = .001$, $\eta^2 = 0.090$) and distance effects (GLM, $F_{1, 120} = 54.3$, $p < .001$, $\eta^2 = 0.644$); the model explained 58.8% of the variation in spectrogram correlation values. For both forest and open habitat, decreased spectrogram correlation values indicated that sounds became less similar to 1 m reference distances with increased distance (Figure 2).

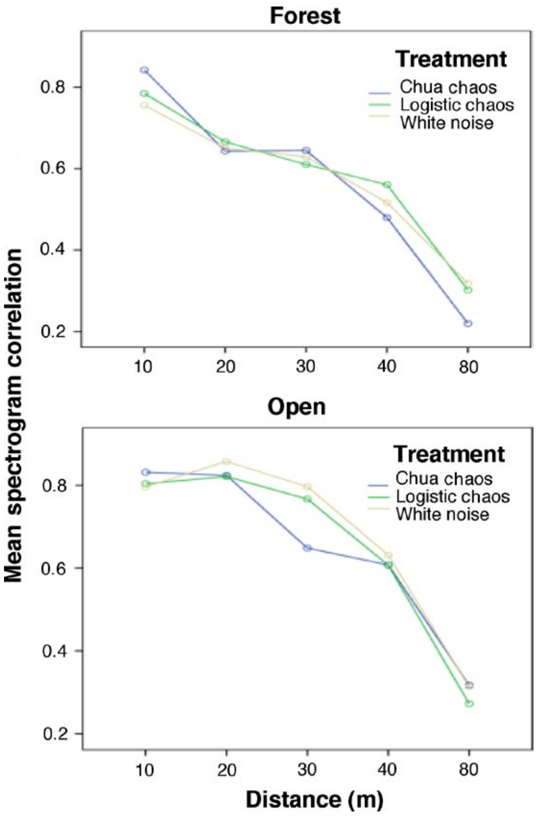

FIGURE 2 Spectrogram correlation of stimuli compared to 1 m reference distances. There were significant effects of habitat ($p = .001$) and distance ($p < .001$) on degradation. [Colour figure can be viewed at wileyonlinelibrary.com]

Spectrogram correlation values for paired comparisons at each distance showed significant pair (GLM, $F_{2, 144} = 9.5$, $p < .001$, $\eta^2 = 0.117$) and distance effects (GLM, $F_{5, 144} = 5.6$, $p < .001$, $\eta^2 = 0.164$), while there was no significant effect of habitat on correlation values (GLM, $F_{5, 144} = 3.4$, $p = .07$, $\eta^2 = 0.023$). In both forest and open habitats, individual sounds became more distinguishable from each other with increased distance (Figure 3). Noise and logistic chaos were more similar, while Chua chaos differed from them both (Figures 4 and 5).

3.2 | Playback experiments

The time robins (Figure 4) allocated to relaxed behavior was the most sensitive variable measured. While there was no highly significant effect of playback type on relaxed behavior (GLM, $F_{3, 110} = 2.3$, $p = .08$, $\eta^2 = 0.060$), pairwise analyses showed that robins engaged in significantly more relaxed behavior after hearing the kingbird treatment compared to noise ($p = .03$), Chua chaos ($p = .03$), and logistic chaos ($p = .049$). Robin time allocation to vigilance was also significantly modified as a function of the playback heard (GLM, $F_{3, 110} = 2.7$,

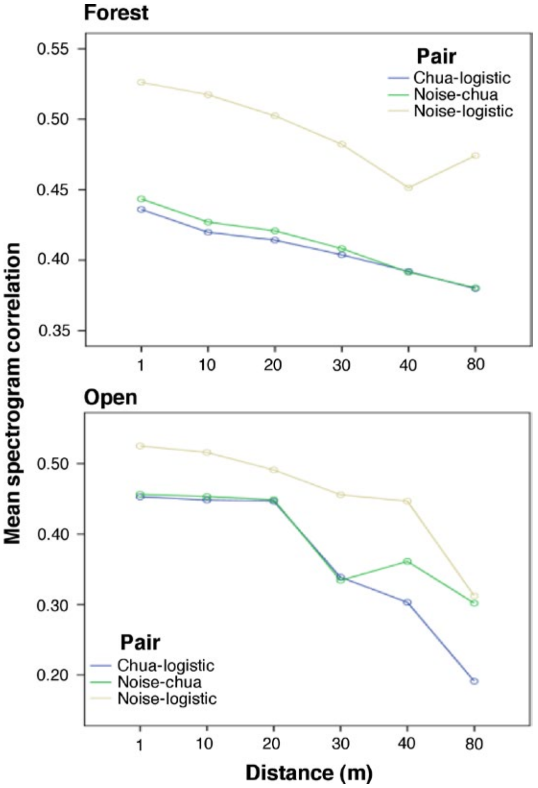

FIGURE 3 Spectrogram correlation pairs of stimuli compared over increasing distance. There were significant pair ($p < .001$) and distance effects ($p < .001$) on similarities at a distance. [Colour figure can be viewed at wileyonlinelibrary.com]

$p = .047$, $\eta^2 = 0.070$). Pairwise analyses revealed that hearing logistic chaos reduced time allocated to looking significantly more than hearing Chua chaos ($p = .001$) or noise ($p = .03$). Robin locomotion was unaffected by any playback (GLM, $F_{3,\,110} = 1.3$, $p = .29$, $\eta^2 = 0.033$).

For vireos, (Figure 5) and after controlling for variation explained by distance to speaker, playback type did not influence time allocated to relaxed behavior (GLM, $F_{3,\,86} = 1.2$, $p = .30$, $\eta^2 = 0.041$) or time allocated to looking (GLM, $F_{3,\,86} = 0.6$, $p = .63$, $\eta^2 = 0.020$). However, vireos modified the time they allocated to locomotion as a function of playback type (GLM, $F_{3,\,86} = 2.9$, $p = .040$, $\eta^2 = 0.091$). Pairwise comparisons showed that compared to the kingbird, warbling vireos increased locomotion after hearing noise ($p = .040$) and Chua chaos ($p = .008$).

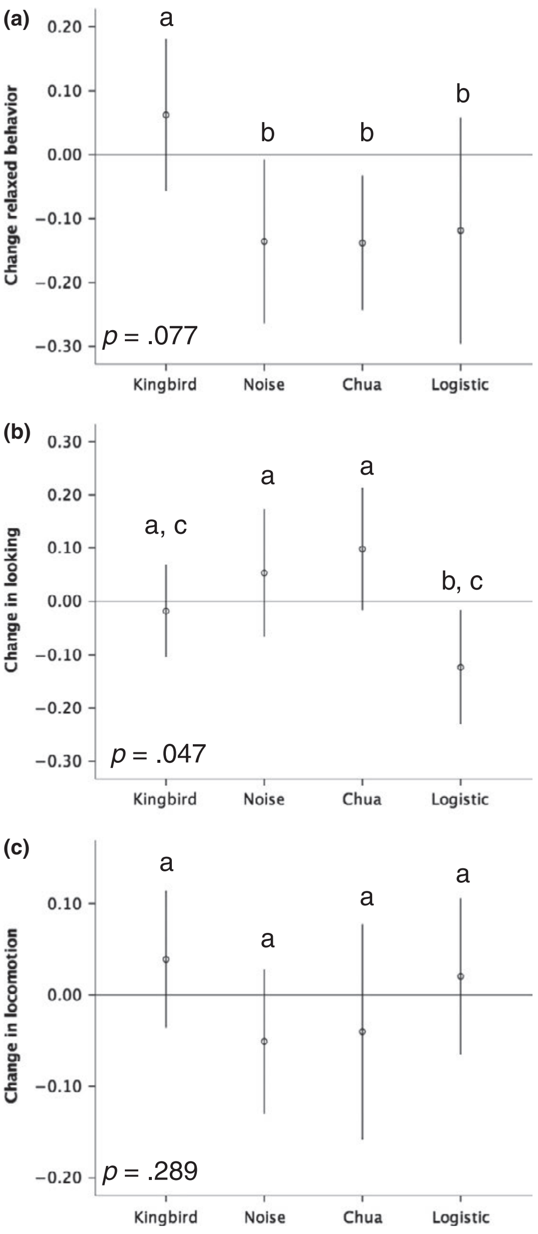

FIGURE 4 Arcsine transformed mean differences from baseline (±95% CI) in time that American robins allocated to relaxed (preen, walk, forage), looking, and locomotion (walk, hop, flight). Different letters indicate significant ($p < .05$) pairwise comparisons from GLM; *p*-values are from the GLM treatment effect

4 | DISCUSSION

Taken together, our results largely suggest that American robins and warbling vireos do not respond substantially differently after hearing white noise compared to at least two types of deterministic chaos—that created from a Chua oscillator and that created from a logistic equation. In fact, American robins responded to the nonlinear Chua chaos, logistic chaos, and noise similarly by exhibiting less relaxed behavior compared to a novel tropical kingbird stimulus that contained no nonlinear acoustic attributes although their vigilance response suggested that there may be differences between how they perceived logistic chaos which differed from Chua chaos and noise. Warbling vireos tended to increase locomotion after hearing white noise and Chua chaos compared to kingbird song and logistic chaos, but overall, there was not strong evidence that these sounds elicited different responses.

Deterministic chaos can be produced different ways and these different synthesis algorithms create stimuli that sound different. Logistic and Chua chaos differed in how they degraded when broadcast and in how birds responded to them. Specifically, Chua degraded much differently than noise and logistic chaos possibly because the stimulus we used had a lower amplitude at higher frequencies.

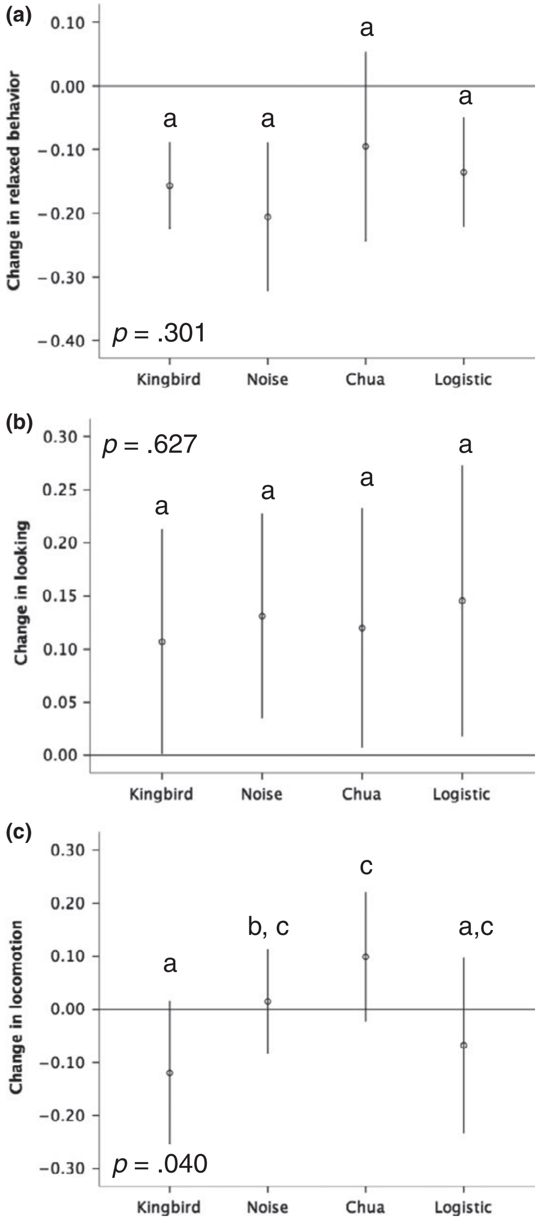

FIGURE 5 Arcsine transformed mean differences from baseline (±95% CI) in time that warbling vireos allocated to relaxed (preen, walk, forage, sing), looking, and locomotion (walk, hop, flight). Different letters indicate significant ($p < .05$) pairwise comparisons from GLM; *p*-values are from the GLM treatment effect

While Chua and logistic chaos we used differed structurally and were transmitted differently, and both were structurally different from white noise, they seemed to elicit largely similar responses in at least two species of birds. Importantly, these similar responses are not because these sounds were novel; our kingbird stimulus permitted us to control for novelty. These results suggest that white noise may be a valid surrogate with which to evaluate the nonlinearity and fear hypothesis. However, the results also suggest that deterministic chaos can be quite variable in its acoustic structure, and our results strictly hold for the specific exemplars that we used. Deterministic chaos should not be treated as a single type of nonlinear acoustic attribute, such as the presence of frequency shifts or the presence of subharmonics.

All information-processing mechanisms possess criteria for what kinds of input they will accept, both in format and in parameter space, and these evolved criteria are shaped by selection processes. Sperber (1994) called these specific criteria the "proper domain" of a given mechanism. But systems vary widely in their flexibility regarding what inputs should be processed, depending on the adaptive problem the system is designed to solve. Most mechanisms have some flexibility in what they will process, and the boundary conditions of these criteria constitute the "actual domain" of the system. For example, facial fusiform areas of the brain process a variety of stimuli containing patterns reminiscent of faces (McKone, Kanwisher, & Duchaine, 2007). One general reason that an actual domain of a system might be relatively large by design is when the cost of a false negative is systematically higher than a false positive. An example of this is the smoke detector principle (Nesse, 2001). Increases in processing flexibility for particular elements of a stimulus, such as by the use of any nonlinear feature in a vocalization as evidence of an alarm, can shift the odds of making one kind of error over another (false positive > false negative).

Given the uniqueness of nonlinear acoustic phenomena in typical environments where most birds evolved and currently live, we might expect bird alarm detection systems to err on the side of caution, and process a variety of nonlinear phenomena as functionally equivalent despite fairly substantial differences in acoustic structure. The data reported here suggest this might be the case. White noise might often function similarly to more ecologically valid kinds of manipulations in studies such as this, but given the relative ease of generating more realistic stimuli using sophisticated equations, researchers should generally opt for better stimuli. Nevertheless, previous work using white noise as a proxy for deterministic chaos has likely yielded interpretable data. Future studies could expand the focus to different nonlinear acoustic phenomena and explore how variation in species-specific (as opposed to novel) stimuli elicits behavioral responses.

ACKNOWLEDGEMENTS

We thank Arik Kershenbaum for discussions about nonlinear acoustics and providing the logistic exemplar and code, and Tecumseh Fitch for providing a Python script for a Chua oscillator. The comments of two anonymous reviewers helped improve the MS. DTB's work at the RMBL is supported by the NSF. JW was supported by NSF DBI-1226713 to the RMBL.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ORCID

Daniel T. Blumstein http://orcid.org/0000-0001-5793-9244

REFERENCES

Bioacoustics Research Program (2011). *Raven pro: Interactive sound analysis software (Version 1.4) [Computer software]*. Ithaca, NY: The Cornell Lab of Ornithology. Retrieved from http://www.birds.cornell.edu/raven

Blesdoe, E. K., & Blumstein, D. T. (2014). What is the sound of fear? Behavioral responses of white-crowned sparrows *Zonotrichia leucophrys* to synthesized nonlinear acoustic phenomena. *Current Zoology*, *60*, 534–541.

Blumstein, D. T., Bryant, G. A., & Kaye, P. (2012). The sound of arousal in music is context-dependent. *Biology Letters*, *8*, 744–747.

Blumstein, D. T. & Daniel, J. C. (2007). *Quantifying behavior the JWatcher way*. Sunderland, MA: Sinauer.

Blumstein, D. T., Davitian, R., & Kaye, P. D. (2010). Do film soundtracks contain nonlinear analogues to influence emotion? *Biology Letters*, *6*, 751–754.

Blumstein, D. T. & Recapet, C. (2009). The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology*, *115*, 1074–1081.

Blumstein, D. T., Richardson, D. T., Cooley, L., Winternitz, J., & Daniel, J. C. (2008). The structure, meaning and function of yellow-bellied marmot pup screams. *Animal Behaviour*, *76*, 1055–1064.

Charlton, B. D. (2015). The acoustic structure and information content of female koala vocal signals. *PLoS ONE*, *10*, e0138670.

Charlton, B. D., Watchorn, D. J., & Whisson, D. A. (2017). Subharmonics increase the auditory impact of female koala rejection calls. *Ethology*, *123*, 571–579.

Chua, L. O. (1995). A glimpse of nonlinear phenomena from Chua's oscillator. *Philosophical Transactions: Physical Sciences and Engineering*, *353*, 3–12.

Fee, M. S., Shraiman, B., Pesaran, B., & Mitra, P. P. (1998). The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature*, *395*, 67–71.

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, *63*, 407–418.

Hatzikirou, H., Fitch, W., & Herzel, H. (2006). Voice instabilities due to source-tract interactions. *Acta Acustica United With Acustica*, *92*, 468–475.

Johnson, D. D., Blumstein, D. T., Fowler, J. H., & Haselton, M. G. (2013). The evolution of error: Error management, cognitive constraints, and adaptive decision-making biases. *Trends in Ecology & Evolution*, *28*, 474–481.

Karp, D., Manser, M. B., Wiley, E. M., & Townsend, S. W. (2014). Nonlinearities in meerkat alarm calls prevent receivers from habituating. *Ethology*, *120*, 189–196.

Laje, R., Gardner, T. J., & Mindlin, G. B. (2002). Neuromuscular control of vocalizations in birdsong: A model. *Physical Review E*, *65*, 051921.

Larsen, O. N., & Goller, F. (1999). Role of syringeal vibrations in bird vocalizations. *Proceedings of the Royal Society Series B*, *266*, 1609–1615.

Leonov, G. A., Vagaitsev, V. I., & Kuznetsov, N. V. (2012). Hidden attractor in smooth Chua systems. *Physica D: Nonlinear Phenomena*, *241*, 1482–1486.

Matsumoto, T. (1984). A chaotic attractor from Chua's circuit. *IEEE Transactions on Circuits and Systems*, *31*, 1055–1058.

McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences*, *11*, 8–15.

Morton, E. S. (1977). Occurrence and significance of motivation structural rules in some bird and mammal sounds. *The American Naturalist*, *111*, 855–869.

Nesse, R. M. (2001). The smoke detector principle. Natural selection and the regulation of defensive responses. *Annals of the New York Academy of Science*, *935*, 75–85.

Neubauer, J., Edgerton, M., & Herzel, H. (2003). Nonlinear phenomena in contemporary vocal music. *Journal of Voice*, *18*, 1–12.

Peshek, K. R., & Blumstein, D. T. (2011). Can rarefaction be used to estimate song repertoire size in birds? *Current Zoology*, *57*, 300–306.

Pettitt, B. A., Bourne, G. R., & Bee, M. A. (2012). Quantitative acoustic analysis of the vocal repertoire of the golden rocket frog (*Anomaloglossus beebei*). *Journal of the Acoustical Society of America*, *131*, 4811–4820.

Pivka, L., Wah Wu, C., & Huang, A. (1994). Chua's oscillator: A compendium of chaotic phenomena. *Journal of the Franklin Institute*, *331*, 705–714.

Rendall, D., Notman, H., & Owren, M. (2009). Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. *Journal of the Acoustical Society of America*, *125*, 1792–1805.

Rice, A. N., Land, B. R., & Bass, A. H. (2011). Nonlinear acoustic complexity in a fish 'two-voice' system. *Proceedings of the Royal Society B*, *278*, 3762–3768.

Riede, T., Arcadi, A. C., & Owren, M. J. (2007). Nonlinear acoustics in the pant hoots of common chimpanzees (*Pan troglodytes*): Vocalizing at the edge. *Journal of the Acoustical Society of America*, *121*, 1758–1767.

Slaughter, E. I., Berlin, E. R., Bower, J. T., & Blumstein, D. T. (2013). A test of the nonlinearity hypothesis in great-tailed grackles (*Quiscalus mexicanus*). *Ethology*, *119*, 309–315.

Sperber, D. (1994). The modularity of thought and the epidemiology of representations. In L. A. Hirschfield, & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture* (pp. 39–67). Cambridge, UK: Cambridge University Press.

Stoeger, A. S., Baotic, A., Li, D., & Charlton, B. D. (2012). Acoustic features indicate arousal in infant giant panda vocalisations. *Ethology*, *118*, 896–905.

Stoeger, A., Charlton, B., Kratochvil, H., & Fitch, W. (2011). Vocal cues indicate level of arousal in infant African elephant roars. *Journal of the Acoustical Society of America*, *130*, 1700–1710.

Tkaczyszyn, M., Olbrycht, T., Makowska, A., Soboń, K., Paleczny, B., Rydlewska, A., & Jankowska, E. A. (2013). The influence of the sounds of crying baby and the sounds of violence on haemodynamic parameters and autonomic status in young, healthy adults. *International Journal of Psychophysiology*, *87*, 52–59.

Tokuda, I., Riede, T., Neubauer, J., Owren, M. J., & Herzel, H. (2002). Nonlinear analysis of irregular animal vocalizations. *Journal of the Acoustical Society of America*, *111*, 2908–2919.

Townsend, S. W., & Manser, M. B. (2011). The function of nonlinear phenomena in meerkat alarm calls. *Biology Letters*, *7*, 47–49.

Tyson, R. B., Nowacek, D. P., & Miller, P. J. O. (2007). Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America*, *122*, 1365–1373.

Wilden, I., Herzel, H., Peters, G., & Tembrock, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, *9*, 171–196.

Wiley, R. H., & Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, *3*, 69–94.

Zollinger, S. A., Riede, T., & Suthers, R. A. (2008). Two-voice complexity from a single side of the syrinx in northern mockingbird *Mimus polyglottos* vocalizations. *The Journal of Experimental Biology*, *211*, 1978–1991.

How to cite this article: Blumstein DT, Whitaker J, Kennen J, Bryant GA. Do birds differentiate between white noise and deterministic chaos? *Ethology*. 2017;123:966–973. https://doi.org/10.1111/eth.12702