

What is the sound of fear? Behavioral responses of white-crowned sparrows *Zonotrichia leucophrys* to synthesized nonlinear acoustic phenomena

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Abstract Fear and anxiety may be adaptive responses to life-threatening situations, and animals may communicate fear to others vocally. A fundamental understanding of fear inducing sounds is important for both wildlife conservation and management because it helps us understand how to design repellents and also how (and why) animals may be negatively impacted by anthropogenic sounds. Nonlinear phenomena—sounds produced by the desynchronization of vibrations in a sound production system—are commonly found in stress-induced animal vocalizations, such as in alarm calls, mobbing calls, and fear screams. There are several functional hypotheses for these nonlinear phenomena. One specific hypothesis is the unpredictability hypothesis, which suggests that because nonlinear phenomena are more variable and somewhat unpredictable, animals are less likely to habituate to them. Animals should, therefore, have a prolonged response to sounds with nonlinear phenomena than sounds without them. Most of the studies involving nonlinear phenomena have used mammalian subjects and conspecific stimuli. Our study focused on white-crowned sparrows (*Zonotrichia leucophrys* ssp. *oriantha*) and used synthesized acoustic stimuli to investigate behavioral responses to stimuli with and without nonlinear phenomena. We predicted that birds would be less relaxed after hearing a stimulus with a nonlinear component. We calculated the difference from baseline of proportion of time spent in relaxed behaviors and performed pair-wise comparisons between a pure tone control stimulus and each of three experimental stimuli, including a frequency jump up, a frequency jump down, and white noise. These comparisons showed that in the 30–60 s after the playback experiment, birds were significantly less relaxed after hearing noise or an abrupt frequency jump down an octave but not an abrupt frequency jump up an octave or a pure tone. Nonlinear phenomena, therefore, may be generally arousing to animals and may explain why these acoustic properties are commonly found in animal signals associated with fear [*Current Zoology* 60 (4): 534–541, 2014].

Keywords Nonlinear acoustic phenomena, White-crowned sparrows, Arousal, Fear, Motivation-structural rules, Entropy

Fear and anxiety may be adaptive responses to life-threatening situations (Boissy, 1995). Most of the research conducted to understand fear in animals has focused on vocalizations, such as alarm calls and fear screams (Blumstein and Récapet, 2009; Townsend and Manser, 2011). In his motivation-structural rules, Morton (1977) suggests that natural selection has led to convergent evolution in the sounds animals produce in certain social situations. Although different animals use different calls to communicate the possibility of danger, is there one specific sound or attribute of sound that might be a universal indicator of fear?

Nonlinear phenomena, which include sound attributes such as frequency modulations, frequency jumps or deterministic chaos, are commonly found in alarm

calls, fear screams and pup cries (see Gouzoules et al., 1984; Blumstein and Récapet, 2009; Townsend and Manser, 2011). When the desynchronization of sound vibrations occurs, such as when too much air is pushed through a vocal system, a relatively simple vocal system with two or more oscillating objects (i.e., vocal cords) can produce highly complex sounds. These sounds have been termed nonlinear phenomena (Wilden et al., 1998; Fitch et al., 2002; Stoeger et al., 2011). Such nonlinear phenomena can be divided into a few general categories: subharmonics and biphonation, abrupt frequency jumps, and ‘noisy’ or chaotic spectra (Fitch et al., 2002).

There are several hypotheses for the production of nonlinear phenomena in animals (Fitch et al., 2002; Blumstein and Récapet, 2009). First, the production of

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nonlinear phenomena could simply be a non-adaptive by-product of vocal production in animals. It is also possible, however, that nonlinear phenomena have a functional use. Some of the functional hypotheses that have been proposed include nonlinear acoustic phenomena being used in individual discrimination or as indicators of mate quality, body size, or dominance (Fitch et al., 2002). One specific adaptive hypothesis is the unpredictability hypothesis (Fitch et al., 2002). Especially amongst social animals, alarm calls may be heard quite frequently. If such calls are predictable and animals can, therefore, easily habituate to them, the calls would no longer serve a functional purpose. Since nonlinear phenomena appear to be more variable or more abrupt and, therefore more unpredictable, animals are less likely to habituate to them (Slaughter et al., 2013). This would make calls that include nonlinear phenomena especially evocative and ensure that alarm calls or infant cries are more frequently recognized and acknowledged by receivers instead of ignored (Fitch et al., 2002). For example, pup screams in marmots are highly individually distinctive, suggesting that they are designed to be evocative in order to garner a response from caregivers (Blumstein et al., 2008).

A corollary of the unpredictability hypothesis is that sounds that are harder to habituate to should elicit more evocative behavior from receivers (Blumstein and Récapet, 2009). In support of this, several studies have demonstrated that alarm calls that include nonlinear phenomena elicit stronger behavioral effects from subjects (Blumstein and Récapet, 2009; Townsend and Manser, 2011). This may be a consequence of nonlinear phenomena being produced under highly stressful situations, which may make them an honest indicator of an animal's situation (Fee, 2002; Fitch et al., 2002; Blumstein et al., 2008). For example, fear screams (calls made in situations of extreme stress and urgency) often contain many nonlinear acoustic phenomena (Högstedt, 1983). While some studies have shown that more stressed animals produce sounds with less entropy (e.g., Blumstein and Chi, 2012; Wilson and Evans, 2012), there nevertheless appears to be a general pattern where nonlinear acoustic phenomena are often associated with stress (e.g., Manser 2001; Blumstein and Récapet, 2009; Townsend and Manser, 2011).

Most prior tests of the unpredictability hypothesis have been conducted on mammals, and the majority of these studies used conspecific calls with nonlinear phenomena (see Blumstein and Récapet, 2009; Townsend and Manser, 2011). Only one study, Slaughter et al. (2013),

focused on birds and used synthesized stimuli with nonlinear phenomena rather than conspecific sounds; this is the study upon which we based the topic and design of our study. By expanding the Slaughter et al. study, we provide more insight into the unpredictability hypothesis of nonlinear phenomena, knowledge of how birds specifically respond to them, and the potential generality of nonlinear phenomena in signifying danger to animals.

Focusing on white-crowned sparrows (*Zonotrichia leucophrys* ssp. *oriantha*), we broadcast acoustic stimuli with and without nonlinear phenomena to birds to see whether they responded more evocatively to sounds with nonlinear phenomena. Our synthetic stimuli all began with a pure tone. This was particularly interesting in our study because the territorial song in white-crowned sparrows in our regional dialect begins with an approximately 3-kHz, 0.5 s whistle (Gilman et al., 2007). We hypothesized that sparrows would respond differently after hearing a control tone rather than the same control tone with one of three different nonlinear phenomena added.

1 Materials and Methods

1.1 Study site and species

From 19 June through 15 July 2012, one researcher (EKB) conducted playback experiments on white-crowned sparrows in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado, United States (38°57'35" N, 106°59'30" W). We conducted the playback experiments from 06:00 to 10:00 h and from 18:30 to 20:30 h.

1.2 Experimental design

We used four stimuli for the playback experiments—one control and three experimental (cf. Slaughter et al., 2013). All playback stimuli were novel sounds to control for the effect of novelty. The control stimulus was a 0.5 s pure tone at 3 kHz, chosen because many songbirds hear well at and around 3 kHz (Dooling et al., 1978; Konishi, 1970; Knudsen et al., 2010). The three experimental stimuli each presented a different computer-generated sound with acoustic discontinuities meant to simulate naturally occurring nonlinear phenomena frequently found in animal vocalization.

All experimental stimuli began with 0.4 s of a 3-kHz, pure tone and ended with one of the following: 1) a frequency jump up an octave to a 5-kHz, pure tone, 2) a frequency jump down an octave to a 1.5-kHz, pure tone [modified from Slaughter et al. (2013), which shifted down to 1 kHz], or 3) 0.1 s of a 1–5 kHz band of white noise. The synthesized nonlinear phenomena in the ex-

perimental stimuli ranged between 1.5 and 5 kHz because these frequencies fall within white-crowned sparrows' hearing range (Konishi, 1970; Knudsen et al., 2010).

We created all synthesized stimuli using Avid Pro-Tools HD versions 9.0.5 with the DIGITRACK Signal Generator plug-in's sine and white noise functions (Avid, Burlington, MA). All stimuli ramped to peak amplitude over 100 ms in order to avoid startling subjects (Götz and Janik, 2011).

Each playback trail was conducted on an individual bird. We conducted playback trials with at least a 40 m radius between focal subjects in an attempt not to repeat trials on any bird. Because white-crowned sparrows are territorial with home ranges averaging between 1,127–2,360 m² (radius of 18.9–27.4 m), a 40 m radius should have been sufficient to avoid pseudoreplication (Ralph and Pearson, 1971; Patterson and Petrinovich, 1978); in practice, the average distance between sequential focal birds was 676.67 m \pm 230.55 SE ($n = 24$). We conducted trials a minimum of five minutes apart (average time between trials = 44.83 min \pm 5.89 SE, $n = 24$). We also played the four stimuli according to a predetermined rotational script to further avoid possible carry-over effects.

We conducted trials an average of 13.8 m \pm 0.24 SE ($n = 62$) from the bird. We stored the playback tracks on an Apple iPod (Apple Inc., Cupertino, CA) in AIF format and broadcast the stimuli from a PAL Speaker (Tivoli Audio, Boston, MA) at an amplitude of 85 dB SPL at a distance of 1 m. Each treatment began with 30 s of silence during which time baseline behavior was recorded. The brief stimulus was broadcast and followed by 60 s of silence, during which time we recorded the behavior of the focal individual to determine if the subject demonstrated any reaction to the stimulus. During each playback trial, we dictated all behavioral observations, based on a predetermined ethogram (Table 1), into an audio recorder. In addition, we recorded the GPS location, wind speed (measured on the Beaufort scale; no experiments were conducted if it was above 3), percentage of cloud cover (no experiments were conducted if it was raining), distance from the observer (in meter), the number of conspecifics within 10 m, and the number of heterospecifics within 10 m.

1.3 Data analysis

We conducted a total of 62 playback experiments: 15 using the pure tone stimulus, 16 white noise, 15 octave jump down, and 16 octave jump up. We then quantified and scored observations using JWatcher (v1.0 Blums-

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

Behavior	Description
Stand and look	On ground or perching, scored each time head moved and fixated
<i>Forage</i>	<i>Moving head towards the ground to find food or having food in beak</i>
<i>Preen</i>	<i>Moving beak through feathers</i>
<i>Walk</i>	<i>Taking steps, moving legs individually</i>
Hop	Jumping from one location to another, scored by each discrete jump
Pink	Chirping, each chirp scored individually
<i>Vocalization</i>	<i>Singing or non-song vocalization, excluding pinks</i>
Flight	Gliding or flapping wings in the air while in sight
Out of sight	No longer visible to observer

Italicized behaviors were categorized as "relaxed behaviors"; the sum of the proportions of all relaxed behaviors, corrected for baseline proportions of the behaviors, was used in our statistical analyses.

tein and Daniel, 2007) and calculated the proportion of time in sight for all individual behaviors in the ethogram.

During the preliminary analysis, it became apparent that birds spent large proportions of time looking throughout the trials, showing no significant differences between treatments. Treatment groups did, however, show substantial variation in relaxed behaviors (foraging, walking, preening, vocalizing; Table 1) in the final 30 s. For this reason, we subsequently used the sum of the proportions of time spent performing each relaxed behavior, with the baseline proportion of time spent in these behaviors subtracted, as our primary indicator of relaxed behavior. Throughout the remainder of the paper, we refer to this variable simply as relaxed behavior. To account for kurtosis, we performed an arcsine transformation.

To investigate the impact of stimulus type on bird behavior, we used regression models and a general linear model in SPSS 20.0 (IBM, New York, NY). We asked if any recorded biotic or abiotic environmental factors—percentage of cloud cover, wind speed, the height of the subject, the number of heterospecific birds within 10 m, the number of conspecifics within 10 m, the distance of the subject to the observer, and the distance of the subject from the road—varied significantly by treatment. The wind speed ($F_{3,58} = 2.395$, $P = 0.058$), percentage cloud cover ($F_{3,58} = 1.288$, $P = 0.283$), the height of the bird at the time of the playback ($F_{3,58} = 0.531$, $P = 0.663$), and number of heterospecific birds within 10 m ($F_{3,58} = 0.901$, $P = 0.446$), did not vary significantly with treatment and were removed from con-

sideration. Both number of conspecifics within 10 m of the focal subject ($F_{3,58} = 3.160$, $P = 0.031$) and the distance of the subject to the observer ($F_{3,58} = 3.378$, $P = 0.024$) varied significantly by stimulus. The distance of the subject from the road ($F_{3,58} = 0.405$, $P = 0.750$) did not differ significantly by stimulus but we included this covariate in the model nonetheless based on findings by Dietz et al. (2013) and Crino et al. (2011), which indicated that white-crowned sparrows closer to the road had higher glucocorticoid levels, a type of stress hormone. Using linear regression variable selection procedures in SPSS to determine the relationship between the covariates, we determined that including distance to subject and distance to road as covariates was the best explanatory model, which we used for all further analyses. Although the number of conspecifics within 10 m varied significantly by stimulus type, it had little explanatory power in the model, not meeting the tolerance criterion of the variable selection method, and we, therefore, did not include it as a covariate.

Using a general linear model where $\alpha = 0.05$, we analyzed the effect of stimulus types on relaxed behavior. We then performed pair-wise comparisons by stimulus type using Fisher's LSD test. Using marginal means and pooled standard deviations, we calculated effect sizes (Cohen's d -scores) for the difference between the pure tone control and each other stimulus type.

2 Results

There was no significant difference among stimuli in the amount of time birds were vigilant, either before the stimulus ($F_{3,58} = 0.635$, $P = 0.596$), in the first 30 s following stimulus playback ($F_{3,58} = 0.424$, $P = 0.737$), or in the second 30 s following playback ($F_{3,58} = 1.942$, $P = 0.133$; Fig. 1). While vigilance levels remained high, the birds began to relax as the time passed after we played the stimulus. Therefore, we focused on the final 30 s interval post playback to see if hearing a particular stimulus influenced the amount they relaxed in the 30–60 s time interval after playback.

The proportion of time birds spent in relaxed behavior in the 30–60 s after the stimulus differed significantly by stimulus type ($F_{3,56} = 2.857$, $P = 0.045$), with the overall model explaining 23.4 % of variation in the change in time allocated to relaxed behavior (Table 2). Planned pair-wise comparisons between the control pure tone and each experimental stimulus revealed that white-crowned sparrows relaxed significantly less after hearing white noise ($P = 0.012$) or the downward frequency jump ($P = 0.022$) than after the pure tone (Fig. 2). Birds did not relax significantly less, however, after hearing the upward frequency jump ($P = 0.228$; Fig. 2). The increase in the Cohen's d -scores paralleled the increase in the differences in marginal means, with noise

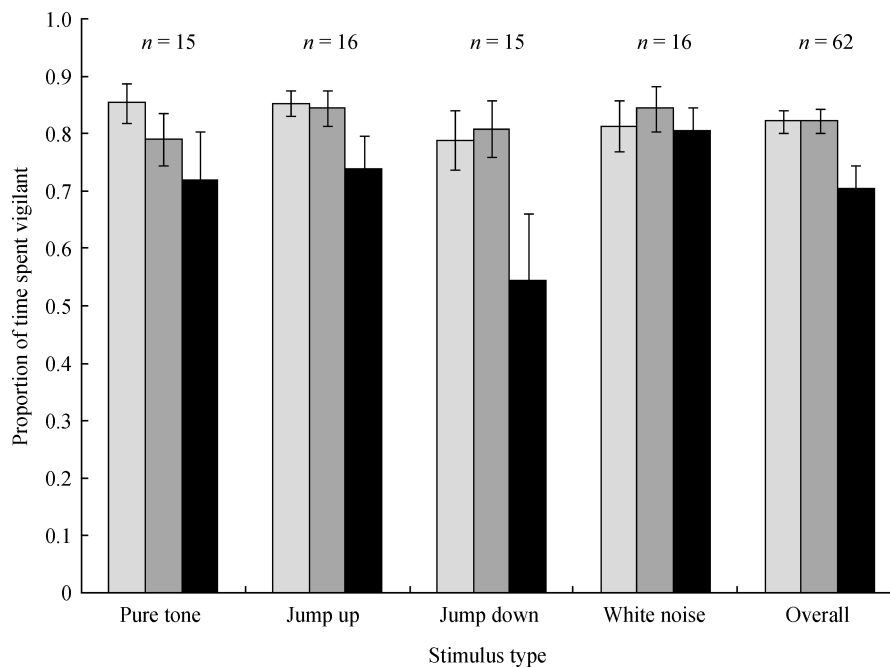


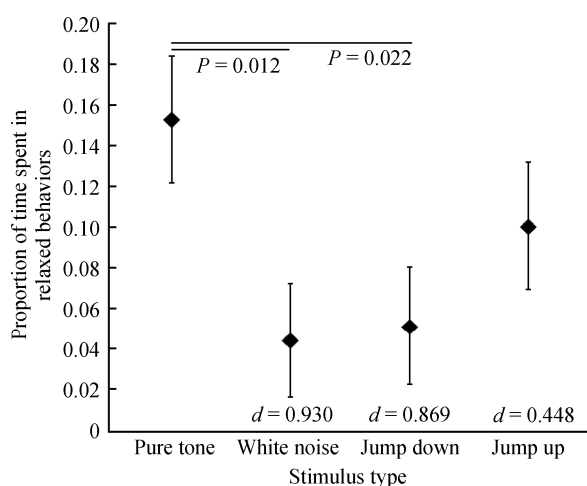
Fig. 1 Mean proportion of time engaged in vigilance behavior as a function of stimulus type before the stimulus (light gray columns), in the first 30 s after playback (dark gray columns), and in the 30–60 s after playback (black columns) showing little change across stimulus type or time period

Error bars represent $\pm 1 SE$.

Table 2 Summary of results of a general linear model analysis of relaxed behavior 30-60s after the stimulus was played

Variable	F-value	P-value	Parameter Estimates		
			Parameter	β	P-value
Model	$F_{5,56} = 3.431$	*0.009			
Stimulus Type (with pure tone as reference)	$F_{3,56} = 2.857$	*0.045	Noise	-0.108	*0.012
			Jump Down	-0.101	*0.022
			Jump Up	-0.052	0.228
Distance of Subject to Observer	$F_{1,56} = 3.159$	0.081		-0.014	
Distance of Subject to Road	$F_{1,56} = 6.801$	*0.012		0.273E-3	

Relaxed behavior was calculated as the sum of the proportions of time spent of each relaxed behavior, corrected by subtracting baseline proportions of each behavior. Stimulus type and distance from the road both had significant effects on variation. The pure tone is the reference stimulus for all parameters. An (*) indicates significance.

**Fig. 2** Marginal mean proportion of time spent engaged in relaxed behavior in the 30–60 s time interval after the stimulus

Pairwise comparisons between the pure tone control and each experimental stimulus demonstrate that birds relaxed significantly less after hearing white noise or a frequency jump down than after hearing a pure tone. Error bars represent ± 1 SE in time corrected for by subtracting baseline proportions, and d values represent Cohen's d -scores.

and the frequency jump down having large effect sizes (Fig. 2).

The distance of the focal subject from the observer did not have a significant effect on variation ($F_{1,56} = 3.159$, $P = 0.081$). In fact, the coefficient suggests a trend that birds tended to be less relaxed the further they were from the observer, which is counter to what we would have expected. The distance of the focal subject from the road also had a significant effect on variation ($F_{1,56} = 6.801$, $P = 0.012$), with the coefficient indicating that birds further from the road were slightly more relaxed than those near the road (approximately 2.7% more relaxed for every 100 m away from the road; Table 2).

3 Discussion

The results of our pair-wise comparisons support our hypothesis that white-crowned sparrows maintain a heightened behavioral response to certain synthesized nonlinear acoustic phenomena, specifically white noise and an octave frequency jump down. Our results are also consistent with Morton's (1977) motivation-structural rules. Morton suggests that convergent evolution has resulted in structural similarities in sounds used by animals in certain social situations. Animals often use sounds that are harsher and lower-frequency in "hostile" situations, while they use purer tones, harmonics, and higher-frequency sounds more frequently in "friendly" contexts. White-crowned sparrows relaxed least after hearing noise and the frequency jump down an octave, both of which are nonlinear phenomena indicative of more "hostile" situations, as might be found in alarm calls or fear screams (see Gouzoules et al., 1984; Blumstein and Récapet, 2009; Townsend and Manser, 2011). On the other hand, while birds still remained vigilant after hearing the frequency jump up an octave, most commonly associated with "friendlier" situations, they relaxed more than after the more "hostile" stimuli; this finding is, again, consistent with Morton's concept of motivation-structure rules.

We initially included a natural stimulus in our experiment: a 1 s clip of a tropical kingbird *Tyrannus melancholicus* song obtained from a commercially produced CD (Oberle, 2008). While Slaughter et al. (2013) used this natural control stimulus and saw no response, we found that the kingbird control was not neutral in our study. Because our study did not have a within-subjects design, meaning each bird only heard one stimulus and therefore stimulus order was not important, we were able to remove the kingbird playback trials

from our initial analyses.

Although we are unclear about the reason for the white-crowned sparrows' response to the tropical kingbird vocalizations, there are a few possible explanations to consider. Kingbird vocalizations have many rapid (though not abrupt) frequency modulations, both up and down (Slaughter et al., 2013). Although Slaughter et al. (2013) demonstrate that abrupt frequency jumps become less evocative with decreased abruptness in the frequency change, the frequency jumps in the tropical kingbird songs could still be acting as nonlinear acoustic phenomena. Because white-crowned sparrows learn multiple songs and then parse down their breeding song through selective attrition (Nelson and Marler, 1994), white-crowned sparrows could be more sensitive to frequency shifts than the grackles studied by Slaughter et al. (2013). Thus, sparrows could be more sensitive to the modulations in the kingbird control. Additionally, the *oriantha* subspecies of white-crowned sparrows is migratory, wintering in southern California or Mexico (Nelson et al., 1995). We do not know where our specific population of sparrow winters, but given their migratory range, it is possible that their winter range overlaps with the range of tropical kingbirds (Stouffer and Chesser, 1998). Tropical kingbirds are known to be aggressive towards other species (Stouffer and Chesser, 1998); if our population of sparrows does winter in an area with tropical kingbirds, they could perceive the kingbird song as threatening, making the kingbird stimulus a non-neutral control stimulus and causing our sparrows to decrease relaxed behavior. Even though the birds responded, however, the overall results for both the models and the planned pair-wise comparisons follow the same patterns with and without the kingbird control, so we felt comfortable proceeding with our analyses without including the kingbird playback trials.

We initially included the kingbird vocalizations as a control to ensure there were no effects due to synthesized sounds. Because each synthetic stimulus began with a pure tone, we are still able to isolate the response to the specific added sound attribute. The use of synthesized sounds, however, may make the stimuli super-normal, or more accurate and intense than found in nature (Tinbergen, 1948; Staddon, 1975), causing birds to react more strongly to the synthesized stimuli than they would to ordinary nonlinear phenomena.

We did not expect to record such a high average proportion of time spent vigilant among the birds. Using the same or slightly modified stimuli, Slaughter et al. (2013) did not experience a ceiling effect in vigilance

rates, instead finding that stimuli with synthesized nonlinear acoustic phenomena significantly increased vigilance. This may be because grackles tend to be bolder around humans than white-crowned sparrows (pers. obs.) or because the grackles were studied on an isolated island (potentially with few predators) while the sparrows were studied in an area with a reasonably intact predator community. With an average proportion of time allocated to vigilance in baseline periods at roughly 80 percent, looking for an increase in vigilance behavior was not feasible in our study. Therefore, the difference from baseline in the proportion of time spent in 'relaxed behaviors' was a more appropriate measure of changes in behavior in our analysis.

The majority of studies looking at the anti-predator responses to nonlinear phenomena have either used conspecific calls with naturally occurring nonlinear phenomena or conspecific calls with synthetic nonlinear phenomena added (see Blumstein et al., 2008; Blumstein and Récapet, 2009; Townsend and Manser, 2011). Since we used synthesized sounds, however, our results indicate that the response to nonlinear phenomena is not limited to species-specific calls (Slaughter et al., 2013). Importantly, they highlight a generality in the evocativeness of nonlinear phenomena.

Our results show that white-crowned sparrows can distinguish between different types of nonlinear phenomena. Future studies looking at different types of nonlinear phenomena, such as subharmonics and biphonations, are needed to further understand the behavioral responses to nonlinear phenomena. Experiments in additional systems will be needed to understand the extent of the generality of this response.

More broadly, nonlinear acoustic phenomena may play a role in conservation biology. The number of studies focusing on the effects of anthropogenic sounds in nature have exploded in recent years, such as the effects of the constant noise emanating from large machines on wildlife, of roads on nearby animal populations, and of the increase of urban noise on bird communication (Rabin et al., 2006; Mockford and Marshall, 2009; Parris et al., 2009; Nemeth and Brumm, 2010; Shier et al., 2012). In our study, the significant effect of distance from the road is consistent with results from previous studies on white-crowned sparrows, as well the general trend that roads are disruptive to birds and other wildlife (Crino et al., 2011; Dietz et al., 2013). Both studies found that white-crowned sparrows (*oriantha* subspecies) were more stressed closer to the road. In their study conducted on the same white-crowned sparrow population

in and around the Rocky Mountain Biological Laboratory, Dietz et al. (2013) found that male birds closer to the road had significantly higher levels of corticosterone, a stress hormone, than males 20 m from the road. Similarly, Crino et al. (2011) found that *oriantha* nestlings in a California population had higher levels of corticosterone and experienced a higher rate of predation the closer they were to a highly trafficked road.

Despite the bulk of literature about the effects of anthropogenic sounds on wildlife, there is substantially less literature on the specific acoustic qualities of anthropogenic sounds. There tends to be a general consensus that most anthropogenic sounds are low-frequency sounds (Gage et al., 2001; Napoletano, 2004; Qi et al., 2008; Joo, 2009; Joo et al., 2011, Pijanowski et al., 2011). Beyond often occurring at lower frequencies than most biological sounds, however, few other characteristics have been documented. While one may assume that many anthropogenic sounds, such as car horns and screeching tires, include nonlinear acoustic phenomena, a thorough investigation of the literature of anthropogenic sounds reveals no studies either testing or asserting this claim, especially in a biological context; if these studies exist, they do not use the terms nonlinear or nonlinearity. This appears to be a serious gap in the literature that, especially for the purposes of conservation application, should be rectified.

Despite the lack of clarity in whether anthropogenic sounds do, in fact, contain nonlinear acoustic phenomena, many studies have demonstrated negative effects of anthropogenic, specifically urban, noise on animals. Noise levels have been found to increase levels of stress hormones, decrease metabolism, increase fluctuating asymmetry (a measure of developmental stability) in offspring, decrease reproductive success, and affect communication (Kight and Swaddle, 2010). Acoustic masking, or the hindrance of acoustic communication due to excess noise, can affect territorial messages, reproductive signals, and alarm calls, among others (Barber et al., 2009).

The effects that anthropogenic sounds have on species can have important conservation implications. Chan et al. (2010) found support for the hypothesis that, in some situations, anthropogenic noise affects risk assessment in animals by causing additional distractions rather than by masking important cues: this has been referred to as “the distracted prey hypothesis” (Chan et al., 2010; Chan and Blumstein, 2011). If anthropogenic sounds include nonlinear acoustic phenomena and the unpredictability hypothesis does play a role in the sys-

tem—meaning that animals do not easily habituate to these sounds—the effects of the anthropogenic sounds could be compounded by the assertions put forth in the distracted prey hypothesis. More research is needed to determine, specifically, whether certain anthropogenic sounds do, in fact, include nonlinear acoustic phenomena, and the full implications of the unpredictability hypothesis.

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