

**Behavioral responses of white-crowned sparrows (*Zonotrichia leucophrys*) to synthesized
nonlinear phenomena**

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Abstract

Fear and anxiety may be adaptive responses to life-threatening situations. Animals may communicate fear to others vocally. 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 and mobbing calls, as well as in fear screams. There are several functional hypotheses for these nonlinear phenomena, and the unpredictability hypothesis suggests that because nonlinear phenomena are somewhat unpredictable, animals are less likely to habituate to them. Animals should, therefore, have a greater 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 focuses on white-crowned sparrows (*Zonotrichia leucophrys*) and uses synthesized 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 phenomenon. Planned pair-wise comparisons between stimuli 30-60 s after the playback experiment showed that birds were less relaxed after hearing noise and abrupt frequency jumps down an octave but not abrupt frequency up an octave or a pure tone. Nonlinear phenomena may be generally arousing.

Keywords: non-linear acoustic phenomena, white-crowned sparrows, arousal, fear

Introduction

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). 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? In 1977, Morton suggested that natural selection had led to convergent evolution in the sounds animals produce in certain social situations.

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 2010). 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 chords) 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). When the oscillating objects are synchronized but at different frequencies, the result is subharmonics or biphonation; when not synchronized, the result is deterministic chaos or noise (Fitch *et al.* 2002).

There are several functional hypotheses for the production of nonlinear phenomena in animals (Fitch *et al.* 2002; Blumstein and Récapet 2009). First, the production of nonlinear phenomena could simply be a non-adaptive by-product of vocal production in animals. It is also possible, however, that nonlinear phenomena are used functionally. One 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 habituate to them easily, the calls would no longer serve a functional purpose. Since nonlinear phenomena

appear to be more variable and, consequently, more unpredictable, animals are less likely to habituate to them. This would make calls that include nonlinear phenomena especially evocative and ensure that alarm calls or infant cries are more likely to be recognized and acknowledged instead of ignored (Fitch *et al.* 2002).

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 2010). 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).

Most prior tests of the unpredictability hypothesis have been conducted on mammals; 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.* (in revision), focused on birds and used synthesized stimuli with nonlinear phenomena rather than conspecific sounds; this is the study upon which we basing 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 and expanding the knowledge of how birds specifically respond to them.

Focusing on white-crowned sparrows (*Zonotrichia leucophrys*), we broadcast stimuli with and without nonlinear phenomena to birds to see whether they respond 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 to which three different nonlinear phenomena were added.

Methods

Study Site and Species

From 19 June through 15 July 2012, a single observer (EB) 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). Playback experiments were conducted from 06:00 to 10:00 h and 18:30 to 20:30 h.

Experimental Design

We used the same five stimuli for the playback experiments—two controls and three experimental—that were used in a similar experiment conducted by Slaughter *et al.* (in revision). All playback stimuli were novel sounds, allowing us to rule out any effect of novelty and focus on the effects due to the specific acoustic attributes of a sound. The control sounds consisted of one natural sound and one synthesized sound in order to control for any possible effects due to a synthesized sound. The natural control sound consisted of one of six exemplars of an approximately 1 s tropical kingbird (*Tyrannus melancholicus*) vocalization; we rotated through multiple exemplars to ensure that a specific trait of one tropical kingbird vocalization did not trigger a response. The synthesized control was a pure tone (0.5 s, 3 kHz). We chose 3 kHz because many songbirds hear well at and around 3 kHz (Dooling *et al.* 1978; Konoshi 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. All began with 0.4 s of a 3 kHz pure tone and ended in either 0.1 s of a 1-5 kHz band of white noise, a frequency jump down an octave to a 1.5 kHz pure tone (modified from Slaughter *et al.* (in revision), which shifted down to 1 kHz), or a frequency jump up an octave to 5 kHz (Herzel *et al.* 1995).

All synthesized sounds were created using Avid ProTools HD versions 9.0.5 with the DIGIRACK Signal Generator plug-in's sine and white noise functions (Avid; Burlington, MA, USA). The synthesized nonlinear phenomena ranged between 1.5 and 5 kHz because this frequency falls within white-crowned sparrows' hearing range (Konoshi 1970; Knudsen *et al.* 2010). All sounds ramped to peak amplitude over 100 ms in order to avoid startling subjects (Götz and Janik 2011). The recordings of the tropical kingbird vocalizations were obtained from a commercial CD (Oberle 2008).

Playback experiments were conducted with at least a 40 m radius between them in an attempt to not repeat trials on any bird. Since white crowned sparrows are territorial and their range averages between 1,127-2,360 m² (18.9-27.4 m radius), this radius should have been sufficient to avoid occasional inadvertent pseudoreplication (Patterson and Petrinovich 1978). In practice, we only conducted playback experiments when we were sure they were not the same bird (average distance between birds = 475.73 m ± 131.49 SE). Experiments were conducted with a minimum of five minutes between each trial (average time between trials = 41.49 min ± 4.47 SE). The five stimuli were also played according to a predetermined script in order to further avoid possible carry-over effects.

Trials were conducted from an average of 13.7 m (± 0.22 SE) from the bird. The playback tracks were stored on an Apple iPod (Apple Inc., Cupertino, CA) in AIF format. Stimuli were broadcast from a PAL Speaker (Tivoli Audio, Boston, MA) at an amplitude of 85

dB SPL. Each treatment began with 30 s of silence in order to quantify baseline behavior. The brief stimulus was broadcast and followed by 60 s of silence, during which time the behavior of the focal individual was quantified to determine any reaction to the stimulus. During each playback experiment, all behavioral observations, based on a predetermined ethogram (Table 1), were dictated 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 observer (in m), number of conspecifics within 10 m, and number of heterospecifics within 10 m. A total of 77 playback experiments were conducted: 15 tropical kingbird, 15 pure tone, 16 noise, 15 jump down an octave, and 16 jump up an octave.

Data Analysis

We quantified and scored observations using JWatcher (v1.0 Blumstein and Daniel 2007). We calculated the proportion of time in sight for all behaviors in the ethogram, as well as behavioral groups which we defined as “relaxed behavior” (foraging, preening, singing and walking), “looking and locomotion” (standing and looking, hopping, and flying), and “heightened response” (standing and looking, hopping, flying, and chinking), as presented by Slaughter *et al.* (in revision). When all behaviors and behavioral categories were graphed, we noted that birds spent large proportions of time looking throughout the trials but that we began to see substantial variation in relaxed behaviors in the final 30 s. We calculated the difference from baseline proportion, which we subsequently used in our analysis.

We also asked if any covariates varied significantly by treatment. Both the distance to subject and the number of conspecifics within 10 m of the focal subject varied significantly by

stimulus (distance to subject: $F_{(4,72)} = 2.563$, $p = 0.045$; number of conspecifics within 10 m: $F_{(4,72)} = 3.075$, $p = 0.021$) and were therefore included as covariates in the model. The interaction between distance to subject and stimulus type and the interaction between the number of conspecifics and stimulus type were also included in the model. Although distance to subject was significant and therefore a potentially confounding factor, the effect was the opposite expected, meaning that birds were less relaxed when further from the speaker. The distance of the subject from the road did not differ significantly by stimulus ($F_{(4,72)} = 0.370$, $p = 0.829$) but was included in the model nonetheless based on findings by Dietz *et al.* (in press) and Crino *et al.* (2011) which indicate that white-crowned sparrows closer to the road had higher glucocorticoid levels. The number of heterospecific birds within 10 m and the height of the bird at the time of the playback were not included as they did not vary significantly between stimuli (number of heterospecifics: $F_{(4,72)} = 0.736$, $p = 0.553$; height: $F_{(4,72)} = 0.509$, $p = 0.729$).

Simplified models consistently gave qualitatively identical results in the planned comparisons, so despite a large number of covariates, we were comfortable with including multiple covariates in the model. Preliminary analyses also showed that the sparrows responded to the kingbird stimuli; based on this information, we decided to investigate whether any of the kingbird exemplars differed by treatment. After analysis, we found that birds were significantly less relaxed after hearing a specific exemplar. We therefore removed this exemplar from the analysis, keeping the identical model. We also ran a subsequent analysis in which we excluded all kingbird playbacks from our full model.

Our variances were not normal (Levene's test in the model with the single kingbird exemplar removed ($p = 0.038$) and the model with all kingbird playbacks excluded ($p < 0.001$)),

likely due to the kurtotic nature of our data. Transformations were unable to normalize them.
Thus, we used the robust standard error in our analyses to account for this issue.

We formally analyzed the data, with and without a variety of covariates, using a general linear model in SPSS 20.0 (IBM, New York). We subsequently analyzed the data through Stata 12 (StatCorp, College Station, TX) to calculate the robust standard errors. We calculated pair-wise comparisons between all stimulus types and then calculated Benjamini-Hochberg false discovery rates on these uncorrected pair-wise comparisons. We calculated effect sizes (Cohen's d -scores) for the difference between the pure tone control and the using marginal means and pooled standard deviations. We reported the R^2 and partial eta-square values for measures of effect sizes in the general linear models and set our alpha to 0.05. Because of the relatively small sample size in this experiment, we interpreted $0.05 < p < 0.1$ as suggestive.

Results

Regardless of stimulus broadcast, birds spend the majority of their time, both before (82.99 %) and in the first 30 seconds after the stimulus playback (81.66 %), engaged in vigilance (baseline: $F_{(4,71)} = 0.555$, $p = 0.696$; first 30 s: $F_{(4,72)} = 0.412$, $p = 0.800$; Figure 1). Over time, however, they relaxed, and we therefore focused on the final 30 s interval post playback to see if the experience of hearing a stimulus influenced the amount they relaxed in the 30 - 60 s time interval after playback.

The model with kingbird playbacks included explained 33.3 % of variation in the change in time allocated to relaxed behavior ($R^2 = 0.333$, $F_{(15,60)} = 1.88$, $p = 0.044$; Table 2). Neither stimulus type nor any of the other covariates, however, accounted for significant differences in the proportion of time (difference from baseline) allocated to relaxed behaviors (Table 2).

Planned pair-wise comparisons between the control pure tone and all other stimuli revealed that white-crowned sparrows relaxed significantly less after hearing noise ($p = 0.022$), a downward frequency jump ($p = 0.016$), or a kingbird vocalization ($p = 0.025$), but not after a frequency jump up ($p = 0.072$; Figure 2). The order of magnitude of the effect sizes between the pure tone and the other stimuli also follow the pattern seen in the marginal means (Figure 2). We also examined parameter estimates for the various covariates (Table 2). While not a significant effect ($p = 0.140$), the coefficient for the distance from road effect indicates that birds become slightly more relaxed as they were farther from the road (for every 100 m away from the roads, birds are roughly 2% more relaxed).

The model excluding the kingbird exemplars explained 37.2% of the variation in the change in time allocated to relaxed behavior ($R^2 = 0.372$, $F_{(12,49)} = 2.422$, $p = 0.015$; Table 3). While stimulus type remained a non-significant parameter, our planned pair-wise comparisons between the control pure tone and stimuli with nonlinear phenomena revealed that white-crowned sparrows relaxed significantly less after hearing either noise ($p = 0.015$) or a downward frequency jump ($p = 0.012$), but not after an upward frequency jump ($p = 0.067$; Figure 3). These results parallel those of the previous model. The order of magnitude of the effect sizes between the pure tone and the other stimuli follow the pattern seen in the marginal means, with noise and the frequency jump down having substantial effect sizes (Figure 3). We also examined parameter estimates for the various covariates (Table 3). While no variables showed significant differences, the distance to road effect became marginally significant ($p = 0.067$; Table 3).

Discussion

Based on the planned pair-wise comparisons and large d -scores of key comparisons, our results suggest that white-crowned sparrows maintain heightened responses after hearing synthetic nonlinear acoustic phenomena. The response to the kingbird control was unexpected. However, the observation that the patterns of response between the pure tone and nonlinear phenomena remained the same, with or without the inclusion of the kingbird, strengthens our confidence in the observed relationship. Although the distance to road effect is only marginally significant, it still demonstrates an interesting trend that is consistent with prior results (Crino *et al.* (2011) and Dietz *et al.* (in press)).

The high average proportion of time spent vigilant among birds was unexpected. Slaughter *et al.* (in revision) found that stimuli with nonlinear phenomena significantly increased vigilance; many other playback studies of birds do not start with such a high initial vigilance (Goodale and Kotagama 2008; Nocera *et al.* 2008; Rieucan and Giraldeau 2009). With such a high average proportion of time allocated to vigilance in baseline periods, it was not possible to look for an increase in vigilance behavior. Similarly, it was not possible to look for changes in “look and locomotion” or a “heightened response” since both of these behavioral categories included “looking” as a behavior. 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.

An unexpected result of the study was the birds’ response to one of our control stimuli: the kingbird vocalizations. We are unclear on the reason for this response; there was no such response in the Slaughter *et al.* (in revision) study. Kingbird vocalizations, however, do have many rapid (though not abrupt) frequency modulations, both up and down (see Slaughter *et al.* in

revision). White-crowned sparrows could be more sensitive to frequency shifts than the grackles used in the Slaughter *et al.* study, subsequently making them more sensitive to the modulations in the kingbird control. Even though the birds responded, however, the overall results for both of the model and the planned pair-wise comparisons follow the same patterns with and without the kingbird control. Importantly, because we did not have a within-subjects design, removing the kingbird stimulus from the model was a valid analysis.

We initially included the kingbird vocalizations as a control to ensure there were no effects due to the use of synthesized sounds. Because each synthetic stimulus began with a pure tone, we are able to isolate the response to the specific sound attribute that was added. The use of synthesized sounds, however, may make the stimuli super-normal, which could cause birds to react more strongly than they would with ordinary nonlinear phenomena (Inglis and Isaacson 1984).

Our results from the planned pair-wise comparisons in both models are consistent with Morton's (1977) motivation-structural rules. Morton suggests that convergent evolution has resulted in structural similarities in sounds used by animals in social situations. Sounds that are harsher and lower-frequency are often used in "hostile" situations, while purer tones and higher-frequency sounds are more frequently used in "friendly" contexts. White-crowned sparrows relaxed least after hearing noise and the frequency jump down an octave, both of which are nonlinear phenomena which are both 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 2010). 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; again, a finding consistent with Morton’s concept of motivation-structure rules.

That stimuli with noise and the frequency jump down are more evocative to white-crowned sparrows, also supports the unpredictability hypothesis (Fitch *et al.* 2002). Although we cannot directly assert, due to a ceiling effect in vigilance behavior, that the stimuli with noise and the frequency jump down elicited anti-predator behavior, the increased time allocated to relaxed behaviors after the pure tone parallels, in the opposite manner, the anti-predator response we expected (Blumstein and Récapet 2009; Townsend and Manser 2010).

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 2010). 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.* in revision). Importantly, they highlight a generality about 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 generality of this response.

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357 Table 1. Ethogram of behaviors recorded during playbacks; modified from Slaughter et al. (in revision).
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Behavior	Description
Stand and look	Standing individual; scored each time head moved and fixated
Forage	Each time the bird moved its head towards the ground to forage or when it already had food in its beak
Preen	Each time the bird moved its beak through its feathers
Walk	Taking steps, moving legs individually
Hop	Jumping from one location to another; each individual hop was recorded
Chink	A short chirp; an alarm call
Vocalization	Any type of singing, excluding chinking
Flight	Flying, but not out of sight
Out of sight	Bird is no longer in sight

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Table 2. Summary of results of a general linear model analysis of the proportion of relaxed behavior 30s – 60s after the stimulus was played. An asterisk (*) indicates interaction. The effect size for the overall model is the R^2 ; effect size for all other variables in the partial eta-squared. B is the coefficient for the parameter. The pure tone is the reference stimulus for all parameters.

Variable	F-value	p-value	Effect Size	Parameter Estimates		
				Parameter	B	p-value
<i>Model</i>	$F_{(15,60)} = 1.88$	0.044	0.167			
<i>Stimulus Type</i>	$F_{(4,60)} = 0.27$	0.895	0.019	Pure tone	0	-
				Noise	-0.252	0.453
				Jump Down	-0.323	0.352
				Jump Up	-0.269	0.493
				Kingbird	-0.101	0.828
<i>Distance to Subject</i>	$F_{(1,60)} = 3.73$	0.058	0.067	Distance to Subject	-0.027	0.195
<i>Distance to Subject</i> * <i>Stimulus Type</i>	$F_{(4,60)} = 0.22$	0.927	0.014	Pure tone *	0	-
				Distance to Subject		
				Noise *	0.014	0.537
				Distance to Subject		
				Jump Down *	0.019	0.415
				Distance to Subject		
				Jump Up *	0.018	0.481
				Distance to Subject		
<i># of Conspecifics</i> * <i>Stimulus Type</i>	$F_{(4,60)} = 0.83$	0.513	0.120	Kingbird *	0.006	0.853
				Distance to Subject		
				# of Conspecifics	0.167	0.248
				Pure tone *	0	-
				# of Conspecifics		
				Noise *	-0.191	0.192
				# of Conspecifics		
				Jump Down *	-0.208	0.158
<i>Distance from Road</i>	$F_{(1,60)} = 2.24$	0.140	0.055	# of Conspecifics		
				Jump Up *	-0.193	0.204
				# of Conspecifics		
				Kingbird *	-0.259	0.099
<i>Distance from Road</i>	$F_{(1,60)} = 2.24$	0.140	0.055	# of Conspecifics		
				Distance from Road	0.191 E-3	0.140

369 Table 3. Summary of results of a general linear model analysis of the proportion of relaxed behavior 30s –
370 60s after the stimulus was played, excluding the kingbirds stimulus. An asterisk (*) indicates interaction.
371 The effect size for the overall model is the R^2 ; effect size for all other variables in the partial eta-squared.
372 B is the coefficient for the parameter. The pure tone is the reference stimulus for all parameters.
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Variable	F-value	p-value	Effect Size	Parameter Estimates		
				Parameter	B	p-value
<i>Model</i>	$F_{(12,49)} = 2.14$	0.031	0.219			
<i>Stimulus Type</i>	$F_{(3,49)} = 0.32$	0.810	0.021	Pure tone	0	-
				Noise	-0.265	0.433
				Jump Down	-0.336	0.334
				Jump Up	-0.286	0.495
<i>Distance to Subject</i>	$F_{(1,49)} = 3.29$	0.076	0.060	Distance to Subject	-0.028	0.173
<i>Distance to Subject</i> <i>* Stimulus Type</i>	$F_{(3,49)} = 0.27$	0.844	0.018	Pure tone *	0	-
				Distance to Subject		
				Noise *	0.014	0.525
				Distance to Subject		
				Jump Down *	0.020	0.393
				Distance to Subject		
<i># of Conspecifics</i> <i>* Stimulus Type</i>	$F_{(3,49)} = 0.81$	0.496	0.118	Jump Up *	0.019	0.448
				Distance to Subject		
				# of Conspecifics	0.161	0.237
				Pure tone *	0	-
				# of Conspecifics		
				Noise *	-0.182	0.187
<i>Distance from Road</i>	$F_{(1,49)} = 3.50$	0.067	0.108	# of Conspecifics		
				Jump Down *	-0.204	0.142
				# of Conspecifics		
				Jump Up *	-0.190	0.186
<i>Distance from Road</i>	$F_{(1,49)} = 3.50$	0.067	0.108	# of Conspecifics		
				Distance from Road	0.251 E-3	0.067

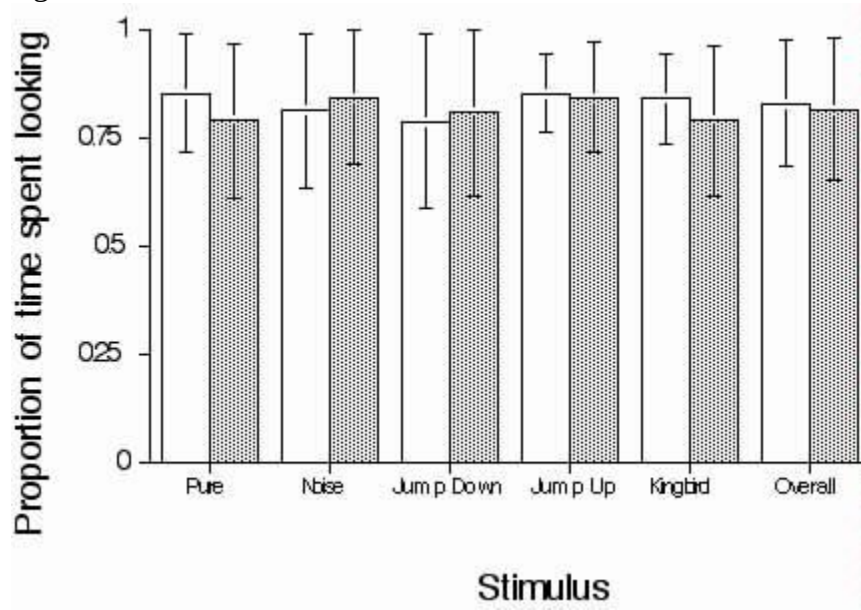
Figure Legends

Figure 1. Mean proportion of time engaged in vigilance behavior as a function of stimulus in the baseline period (unfilled columns) and the first 30 s after playback (filled columns). Error bars represent $\pm 1SD$.

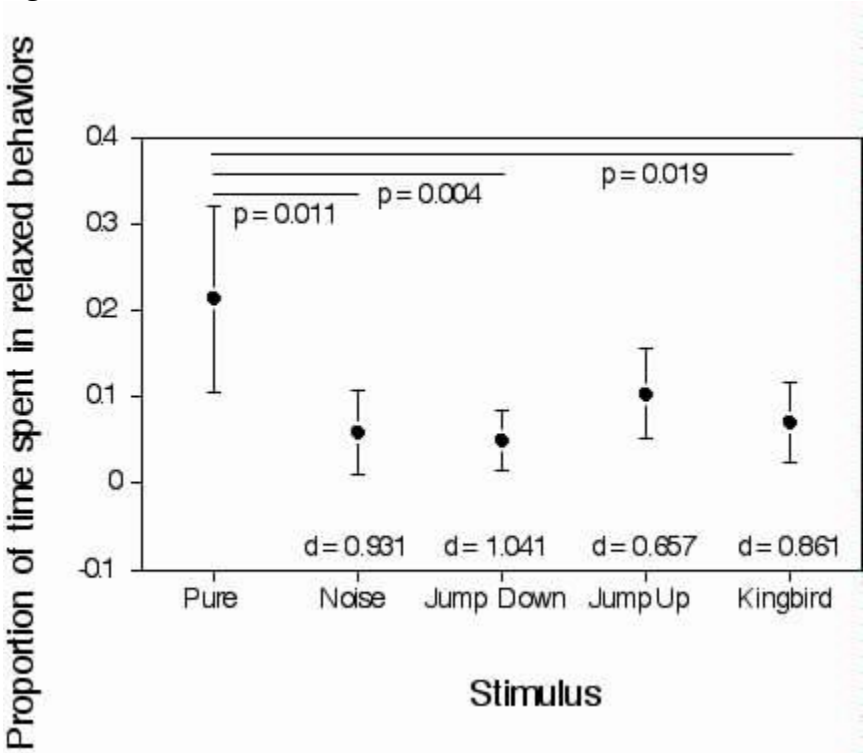
Figure 2. Marginal mean proportion of time spent engaged in relaxed behaviors (foraging, preening, walking, and singing) in the 30-60 s after the playback. Birds spent less time in relaxed behavior after hearing noise and a frequency jump down as compared to the pure tone. Error bars illustrate 95% confidence intervals. Cohen's *d*-scores were calculated from marginal means and pooled standard deviations.

Figure 3. Marginal mean proportion of time spent engaged in relaxed behaviors (foraging, preening, walking, and singing) in the 30-60 s after the playback, analyzed without the kingbird. As with the analysis including kingbirds, subjects spent less time in relaxed behavior after hearing noise and a frequency jump down as compared to the pure tone. Error bars illustrate 95% confidence intervals. Cohen's *d*-scores were calculated from marginal means and pooled standard deviations.

Figure 1

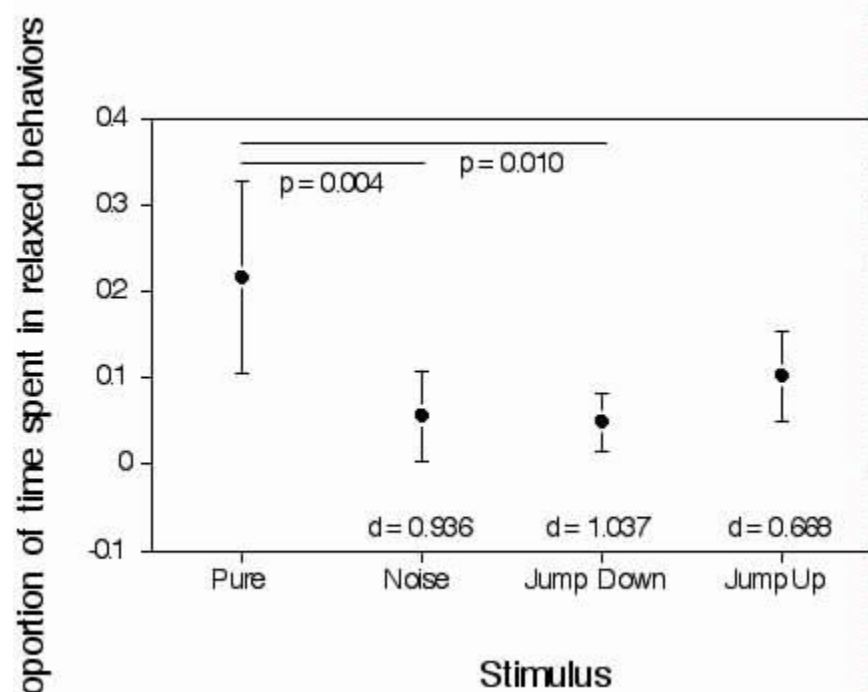


403 Figure 2



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407 Figure 3



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