Experimental trials of species-specific bat flight responses to an ultrasonic deterrent (#86150)

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Experimental trials of species-specific bat flight responses to an ultrasonic deterrent

Sarah Rebecah Fritts Corresp., [1], **Emma Elizabeth Guest** [1,2], **Sara Patricia Weaver** [2], **Amanda Marie Hale** [3,4], **Brogan Page Morton** [5], **Cris Daniel Hine** [6]

[1] Department of Biology, Texas State University, San Marcos, Texas, United States

[2] Bowman, San Marcos, Texas, United States

[3] Department of Biology, Texas Christian University, Fort Worth, Texas, United States

[4] Western EcoSystems Technology, Inc., Cheyenne, Wyoming, United States

[5] Wildlife Imaging Systems, Hinesburg, Vermont, United States

[6] National Renewable Energy Laboratory, Arvada, Colorado, United States

Corresponding Author: Sarah Rebecah Fritts
Email address: fritts.sarah@txstate.edu

Unintended consequences of increasing wind energy production include bat mortalities from wind turbine blade strikes. Ultrasonic deterrents (UDs) have been developed to reduce bat mortalities at wind turbines. Our goal was to experimentally assess the species-specific effectiveness of three emission treatments from the UD developed by NRG Systems for five bat species. We conducted trials in a flight cage measuring approximately 60 m x 10 m x 4.4 m (length x width x height) from July 2020 to May 2021 in San Marcos, Texas, USA. Trials focused on a red bat species group (*Lasiurus borealis* and *Lasiurus blossevillii*; n = 46) and four species: cave myotis (*Myotis velifer*; n = 57), Brazilian free-tailed bats (*Tadarida brasiliensis;* n = 73), evening bats (*Nycteceius humeralis;* n = 53), and tricolored bats (*Perimyotis subflavus;* n = 17). The trials occurred during three treatment emissions: low (emissions from subarrays at 20, 26, and 32 kHz), high (emissions from subarrays at 38, 44, and 50 kHz), and combined (all six emission frequencies). We placed one wild-captured bat into the flight cage for each trial, which consisted of an acclimation period, a control period with the UD powered off, and the three emission treatments, each interspersed with a control period. We tracked bat flight using four thermal cameras placed outside the flight cage. We quantified the effectiveness of each treatment by comparing the distances each bat flew from the UD during each treatment versus the control period using quantile regression focused on the 10th, 25th, 50th, 75th, and 90th percentiles. Additionally, we compared differences between sex and season and sex within season using analysis of variance. Broadly, UDs were effective at altering the bats' flight paths as they flew farther from the UD during treatments than during controls; however, results varied by species, sex, season, and sex within season.

For the red bat group, bats flew farther from the UD during all treatments than during the control period at all percentiles ($p < 0.001$), and treatments were comparable in effectiveness. For cave myotis, all percentile distances were farther from the UD during each of the treatments than during the control, except the 90th percentile distance during the high treatment. The low treatment was most effective for cave myotis. For evening bats and Brazilian free-tailed bats, results were inconsistent, but the high and low treatments were most effective, respectively. For tricolored bats, the combined and low treatments were significant at the 10^{th}–75^{th} percentiles, and the high treatment was significant at all percentiles. The combined treatment most effective. Results suggest UDs may be an effective means of reducing bat mortalities due to wind turbine blade strikes. We recommend that continued research on UDs focus on low emission treatments, which have decreased sound attenuation and demonstrated effectiveness across the bat species evaluated in this study.

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Sarah Rebecah Fritts[1], Brittany Fantasia Stamps[1], Emma Elizabeth Guest[1], Sara Patricia Weaver[2], Amanda Marie Hale[3,4], Brogan Page Morton[5], Cris Daniel Hein[6]

[1] Department of Biology, Texas State University, San Marcos, Texas USA
[2] Bowman, 133 West San Antonio Street #500, San Marcos, Texas USA
[3] Department of Biology, Texas Christian University, Fort Worth, Texas USA
[4] Western EcoSystems Technology, Inc., Cheyenne, Wyoming, USA
[5] Wildlife Imaging Systems, 328 Mechanicsville Road, Hinesburg, Vermont, USA
[6] National Renewable Energy Laboratory; Arvada, Colorado, USA

Corresponding Author:
Sarah Fritts[1]
601 University Drive, San Marcos, Texas, 78666, USA
Email address:fritts.sarah@txstate.edu

Abstract

Unintended consequences of increasing wind energy production include bat mortalities from wind turbine blade strikes. Ultrasonic deterrents (UDs) have been developed to reduce bat mortalities at wind turbines. Our goal was to experimentally assess the species-specific effectiveness of three emission treatments from the UD developed by NRG Systems for five bat species. We conducted trials in a flight cage measuring approximately 60 m x 10 m x 4.4 m (length x width x height) from July 2020 to May 2021 in San Marcos, Texas, USA. A single UD was placed at either end of the flight cage, and we randomly selected one for each night of field trials. Trials focused on a red bat species group (*Lasiurus borealis* and *Lasiurus blossevillii*; n = 46) and four species: cave myotis (*Myotis velifer*; n = 57), Brazilian free-tailed bats (*Tadarida brasiliensis;* n = 73), evening bats (*Nycteceius humeralis;* n = 53), and tricolored bats (*Perimyotis subflavus;* n = 17). The trials occurred during three treatment emissions: low (emissions from subarrays at 20, 26, and 32 kHz), high (emissions from subarrays at 38, 44, and 50 kHz), and combined (all six emission frequencies). We placed one wild-captured bat into the flight cage for each trial, which consisted of an acclimation period, a control period with the UD powered off, and the three emission treatments (order randomly selected), each interspersed with a control period. We tracked bat flight using four thermal cameras placed outside the flight cage. We quantified the effectiveness of each treatment by comparing the distances each bat flew from the UD during each treatment versus the control period using quantile regression focused on the 10th, 25th, 50th, 75th, and 90th percentiles. Additionally, we compared differences between sex and season (fall versus spring) and sex within season using analysis of variance. Broadly, UDs were effective at altering the bats' flight paths as they flew farther from the UD during treatments than during controls; however, results varied by species, sex, season, and sex within season. For the red bat group, bats flew farther from the UD during all treatments than during the control period at all percentiles ($p < 0.001$), and treatments were comparable in effectiveness. For cave myotis, all percentile distances were farther from the UD during each of the treatments than during the control, except the 90th percentile distance during the high treatment. The low treatment was most effective for cave myotis. For evening bats and Brazilian free-tailed bats, results were inconsistent, but the high and low treatments were most effective, respectively. For tricolored bats, the combined and low treatments were significant at the 10^{th}–75^{th} percentiles, and the high treatment was significant at all percentiles. The combined treatment most effective. Results suggest UDs may be an effective means of reducing bat mortalities due to wind turbine blade strikes. We recommend that continued research on UDs focus on low emission treatments, which have decreased sound attenuation and demonstrated effectiveness across the bat species evaluated in this study.

Introduction

Wind energy is rapidly increasing throughout the world in an effort to reduce carbon emissions as a climate change mitigation measure; however, wind energy has unintended consequences, including bat mortalities resulting from wind turbine blade strikes (Allison et al., 2019). Collision mortalities have been documented at wind energy facilities worldwide (Rydell et al., 2010; Arnett and Baerwald, 2013; Arnett et al., 2016; Zimmerling and Francis, 2016; Agudelo et al., 2021). These impacts are of concern because of their potential population-level effects on certain bat species (Frick et al., 2017; Friedenberg and Frick, 2021) that have relatively low reproductive rates compared to mammals of similar size (Barclay et al., 2003). Moreover, several species impacted by wind turbines also suffer from other natural and human stressors, including white-nose syndrome, pesticides, and land-use changes (Erickson et al., 2016; O'Shea et al., 2016; Frick et al., 2020). With these synergistic effects threatening bat populations, there is high concern among regulators, conservationists, researchers, wildlife managers, and private industry about the risk wind turbines pose to bats. Although bat mortalities have been documented at wind energy facilities for about 40 years, there are limited minimization strategies that can be widely implemented, and the need for technological solutions continues to grow (Hein and Hale, 2019; Friedenberg and Frick, 2021). Long-distance migratory bat species are of particular concern in North America as mortalities of these species occur across the continent (Arnett et al., 2005; Zimmerling and Francis, 2016; Choi et al., 2020; American Wind Wildlife Institute, 2021), and it has been projected that at least one species, the hoary bat (*Aeorestes [Lasiurus] cinereus*), could experience population declines by up to 90% from wind energy alone (Frick et al., 2017; Friedenberg and Frick, 2021). Thus, these species often are targets of impact minimization strategies, such as curtailment (Adams et al., 2021; Whitby et al., 2021), deterrents (Arnett et al., 2013; Romano et al., 2019; Weaver et al., 2020), or a combination of the two (Good et al., 2022).

Investigations related to the influence of weather on bat mortalities at wind turbines reported significantly greater mortalities during nights with low wind speeds (Arnett et al., 2005; Baerwald et al., 2009; Arnett et al., 2013); thus, feathering turbine blades during periods of low wind speed was suggested as a viable curtailment strategy, also known as blanket curtailment. Blanket curtailment has been documented to reduce total bat mortalities by 54%–69%, hoary bat mortalities by 24%–64%, eastern red bat (*L. borealis*) mortalities by 42%–74%, and silver-haired bat (*Lasionycteris noctivagans*) mortalities by 30%–66% (Whitby et al., 2001). Another meta-analysis suggested a 63% decrease in total bat mortalities during operational minimization (Adams et al., 2021). Nonetheless, this minimization strategy results in a loss of annual energy production that may not be financially sustainable for some wind energy facilities. To reduce the loss in annual energy production, curtailment strategies have advanced to incorporate additional weather variables (e.g., temperature) and acoustic bat activity (Martin et al., 2017; Hayes et al., 2019; Peterson et al., 2021; Rabie et al., 2022).

An alternative approach to curtailment is the use of ultrasonic deterrents (UDs), which attempt to create a disruptive airspace to prevent bats from entering the rotor-swept area of a wind turbine. Echolocating bats emit ultrasound and perceive their surroundings by listening to the reflected echoes (Griffin, 1958). This sense allows bats to orient, capture prey, communicate, and avoid obstacles in complete darkness. Because bats are sensitive to ultrasound and can be influenced by biological noises (e.g., "clicks") emitted by moths (Hristov and Conner, 2005; Corcoran et al., 2011), it was hypothesized that broadcasting high-frequency transmissions from wind turbines may create a disorienting airspace, thus "jamming" a bat's ability to perceive its own echoes (Szewczak and Arnett, 2007). Various UD technologies have been studied at wind energy facilities, with results varying among species at a given location or within species across different locations and times (Arnett et al., 2013; Romano et al., 2019; Weaver et al., 2020). The reasons for species-specific variability in effectiveness are unknown, but it may be related to variation in species' echolocation characteristics, ultrasound attenuation (Arnett et al., 2013; Weaver et al., 2020), and deterrent configuration (Romano et al., 2019). For example, a UD developed by NRG Systems deployed at a wind farm in Texas (USA) reduced bat mortalities for hoary bats and Brazilian free-tailed bats (*Tadarida brasiliensis*) by 78% and 54%, respectively, but no reductions in mortalities for other species in the genus *Lasiurus* were observed (Weaver et al., 2020). The GE Renewable Energy UD tested in Illinois (USA) reduced overall bat mortalities by 29%, but annual deterrent effectiveness varied for eastern red and silver-haired bats (Romano et al., 2019). The observational data required to answer why differences exist among species is lacking. Improving the effectiveness of UDs across a wider range of species requires more controlled testing that allows for observations of individual bat flight paths and echolocation responses to various ultrasound configurations (Romano et al., 2019).

The objective of this study was to experimentally assess species-specific bat responses, including from those that echolocate at both high and low frequencies, to the NRG Systems UD (hereafter UD) using a large outdoor flight cage. We examined flight responses of five species of bats to different UD signals and hypothesized that deterrent signals with low-frequency sound would have a greater effect on low-frequency echolocating bats (i.e., those with characteristic frequency <35 kHz), whereas deterrent signals with high-frequency sound would have a greater effect on high-frequency echolocating bats (i.e., those with characteristic frequency ≥35 kHz). In addition, we examined potential differences within each species between sex, season (fall versus spring), and the interactive effects of sex and season. Understanding why and how bats interact with wind turbines continues to be an active area of research (e.g., Richardson et al., 2021; Guest et al., 2022), and we hypothesized that responses of bats to UD signals could vary based on internal motivational states related to the timing of reproduction or migration.

Materials & Methods

To test the responses of individual, wild-captured bats of known species to the UD, we conducted a study at the Freeman Center, a 1,400-ha property owned by Texas State University in Hays County, Texas (29.9390, -98.0097 WGS 84). We constructed an open-air flight cage specifically designed to test bat responses to UDs (Figure 1). The open-air flight cage was approximately 60 m x 10 m x 4.4 m (length x width x height) and was surrounded by 6.4-mm, lightweight, plastic netting (Industrial Netting, Minneapolis, Minnesota, USA). The dimensions of the flight cage were selected based on the precise goals of this project and the requirements for maintaining local bat species in enclosures. Height and width were based on insectivorous bat care standards from Bat World Sanctuary (2010) and recommendations from staff at Austin Bat Refuge (Austin, Texas). The length was designed to accommodate the blade length of most modern land-based wind turbines produced prior to late 2019 (Figure 1).

The two UDs used in this study consisted of a waterproof box with six subarrays. Each subarray emitted a continuous sound at one of the following predetermined frequencies: 20, 26, 32, 38, 44, and 50 kHz. This frequency range was selected because it encompasses the echolocation range of most bat species known to occur in the United States and Canada. On average, the signal intensity for the UD was 125 dB (measured 1 m from the source). We programmed the UDs to emit three treatments: low (emissions from subarrays at 20, 26, and 32 kHz), high (emissions from subarrays at 38, 44, and 50 kHz), and combined (emission from all six subarrays).

We mounted one UD at each end of the flight cage and randomly selected one of the two ends for each night of field trials. The UDs were powered by a generator positioned approximately 10 m away from the flight cage and shielded by plywood boards to reduce noise. We mounted four AXIS 1942-e thermal video cameras (Axis 1942-e, Axis Communications, Lund, Sweden; hereafter "cameras") on the north side of the flight cage to limit nearby city heat signatures from interfering with bat thermal visibility (Figure 2). We placed the cameras ~23 m from the cage at a height of 3.7 m so that the fields of view encompassed the entire flight cage and slightly overlapped between neighboring cameras. We programmed the cameras to record at 30 frames per second. We time-synched cameras and monitored them using a cable-connected laptop at an observer station positioned 8 m from the end of the cage with the operating UD.

During trials, we minimized observer sources of light, sound, and other potential causes of disruption.

We captured bats within two hours of the flight cage (typically within 30 minutes in Hays County, Texas, USA) on both public and private properties for which we had authorization using mist nets, harp traps, and hand captures from July 13, 2020, to May 15, 2021. We placed captured bats in cloth bags and placed cloth bags in 19-L buckets to transport in climate-controlled field vehicles. We fed bats meal worms (*Tenebrio molitor*) ad libidum. Once transported to the flight cage, we recorded the species and sex of each bat. A bat trial period was 24 min and consisted of an acclimation period followed by a control period, then three randomly ordered UD emission treatments interspersed with control periods (Figure 3). The three treatments were low (20–32 kHz), high (38–50 kHz), and combined (20–50 kHz) frequencies. We only subjected bats to experimental trials if they flew during the acclimation period. If at any point during the trial the bat stopped flying, we noted the occurrence and continued the trial. We omitted bats that used ≤50% of the flight cage during the entire trial. We typically held bats between 2–6 hours and never overnight. All bats were transported back to the site of capture for release. The project was conducted under both a Texas Parks and Wildlife Department state permit (SPR-1217-243), which included protocols specific to the SARS-CoV-2 virus, and a Texas State University Institutional Animal Care and Use Committee permit (#6224). Additionally, we followed the National White-nose Syndrome Decontamination Protocol Version 10.14.2020 (U.S. Fish and Wildlife Service, 2020). No bats were harmed or euthanized; however, protocols approved cervical dislocation and secondary chest compressions had euthanasia been needed due to a severely injured bat. Due to our close proximity to Austin Bat Refuge, we also had approval to take injured bats to their facility if needed.

In 2021, we observed variation in pelage coloration among the red bats that we had presumed were eastern red bats based on known locality data. We speculated that some of these individuals were western red bats; therefore, we used the methods of Korstian et al. (2015) to confirm species identification for a subset of these bats (n = 12) using DNA extracted from fecal pellets that had been collected during the study. All of the sampled bats were western red bats (*L. blossevillii*) (unpublished data). Because our capture sites were in the known range of eastern red bats (*L. borealis*) and we did not confirm species identification for all captured red bats, we analyzed eastern and western red bats as one species group (i.e., red bats).

We analyzed the resulting thermal videos using Python and the OpenCV library. We read each video frame and applied a background subtractor to detect the movement of bats on the stationary background. We logged the coordinate (pixel location) and other feature information associated with each detection into a data frame. To eliminate erroneous detections due to noise in the video, we created a custom filter that recorded only detections that had a nearby detection, based on Euclidean distance between coordinates in adjacent frames (before or after). This allowed us to retain the detections that were part of a continuous track while omitting those detections that had no spatial or temporal neighbors nearby. Because four cameras were used to cover the full length of the flight cage, the detections from all videos were aggregated into a single data frame. To aggregate, we used the *x*-pixel coordinate for each detection to estimate the distance from the operating UD. We generated the distance estimate using a per-camera calibration relating *x*-pixel coordinates to known distances within the flight cage. Once the conversion to a global coordinate system was complete, we consolidated the detection from each camera. To eliminate duplicate detections between cameras, we acquired the minimum distance values for each camera and restricted the adjacent camera detections to prevent detections from exceeding the next camera's minimum.

To assess differences in distance that each bat flew from the UD between the first control period and each UD emission treatment, we used quantile regression in R package *quantreg* (Koenker, 2022) with distance as the response variable, treatment as the categorical independent variable, and bat unique identification number as a random effect. We conducted separate models for each treatment versus control comparison due to the large sample size of distances obtained per 4-min period and focused on the 10th, 25th, 50th, 75th, and 90th percentile distances. The goal was to compare the percentile differences between each emission treatment and control period; however, the field trials included three distinct control periods. Therefore, we first tested for differences among control periods using an analysis of variance (ANOVA). We found no statistical difference among control periods; thus, we selected the first control period following the acclimation period for the pairwise comparisons to minimize differences in sample sizes that could bias results. When we found overall differences in distances between control and treatment periods to be significant, we then assessed differences in season (spring vs. fall), sex, and the interaction between sex and season using the difference in flight distance from the UD between the UD emission treatment and control period at each percentile as the response variable using separate ANOVAs. We conducted all statistical analyses in R (R Core Team 2021) with $\alpha = 0.05$.

Results

We conducted successful trials and analyses on 46 red bats, 57 cave myotis, 73 Brazilian free-tailed bats, 53 evening bats, and 17 tricolored bats. We omitted 3, 10, 4, 6, and 0 bats from those species, respectively, for not flying during trials or having a flight path that used <50% of the flight cage during the entire 24-min trial period.

For the red bat group, bats flew farther from the UD during all treatments than during the control period at the 10th–90th percentiles ($p < 0.001$), and treatments were comparable in effectiveness as estimated by the difference in flight distance between the treatments and the control periods (Tables 1 and 2). There was a significant season effect during the combined and high treatments and an interaction between sex and season during the low treatment (fall males n = 17, spring males n = 4, fall females n = 13, spring females n = 12; Tables 3 and 4, Figure 4). The difference in distance between control and treatment periods was greater in spring than in fall during combined and high treatments. For the low treatment, the greatest distance between control and treatment was for spring males, followed by spring females, and then all fall bats combined (Figure 4).

For cave myotis, bats flew further from the UD during each treatment than controls at all percentile distances except the 90th percentile distance during the high treatment (Tables 1 and 2). For this species, the low treatment was most effective as estimated by the difference in flight distance between the treatments and the control periods (Tables 1 and 2). Because we did not capture females during the spring, we did not include the interaction between sex and season in the ANOVAs for this species. The differences between control and treatment flight distance from the UD for cave myotis males were 3.174 m ($p = 0.019$) and 3.176 m ($p = 0.015$), greater than for females during the low treatment at the 75th and 90th percentiles, respectively (fall males n = 21, spring males n = 11, fall females n = 25, spring females n = 0; Tables 3 and 4, Figure 4).

For evening bats, the results were inconsistent for the combined and low treatments, and individuals of this species flew farthest from the UD compared to the control during the high treatment (Tables 1 and 2). We did not include the interaction between sex and season in the ANOVA due to the low sample size of spring males (fall males n = 21, spring males n = 1, fall females n = 23, spring females n = 8). There were no differences in the response by sex or season for this species (Table 3, Figure 5).

For Brazilian free-tailed bats, results were inconsistent and variability was high, but the combined treatment was most effective as estimated by the difference in flight distance between the treatments and the control periods (Tables 1 and 2, Figure 6). Although the low treatment was significant at the 10th, 50th, 75th, and 90th percentiles, the difference in distances between treatment and control were low, and bats flew closer to the UD at the 90th percentile. There were some differences in distance flown by sex and an interaction between sex and season for some percentiles; however, no discernable pattern was observed for this species (fall males n = 31, spring males n = 7, fall females n = 21, spring females n = 14; Figure 6).

For tricolored bats, the combined and low treatments were significantly different from the control at the 10th–75th percentiles, whereas the high treatment was significantly different from the control at all percentiles (Tables 1 and 2). The combined treatment was most effective as estimated by the difference in flight distance between the treatments and the control periods (Tables 1 and 2). We did not include the interaction between sex and season due to the low sample size of spring females (fall males n = 7, spring males n = 4, fall females n = 5, spring females n = 1). Tricolored bats consistently flew farther from the UD compared to the control in fall than spring during the low and high treatments at all percentiles and during the combined treatment at the 25th percentile (Tables 3 and 4, Figure 7).

Discussion

Overall, the difference in distances flown between the UD emissions and control periods indicates that the acoustic signals tested were successful in shifting flight patterns of four bat species and one bat species group in experimenttal trials in a flight cage environment. Nonetheless, the apparent effectiveness of the three treatments differed among species and in some cases in ways that were not clearly interpretable. These findings are consistent with previous research that assessed effectiveness of UDs at reducing bat mortality at operational wind turbines. Previous research studies reported species-specific differences in fatality reductions at wind turbines when UDs were emitting ultrasound compared to when the devices were turned off or at wind turbines without UDs (Arnett et al., 2013; Romano et al., 2019; Schirmacher, 2020; Weaver et al., 2020). In our study, Brazilian free-tailed bats flew farthest from the UD during the combined treatment. This finding is consistent with the results of Weaver et al. (2020) in which researchers tested the same UD device and frequency emissions as this study and reported a 54.5% reduction in Brazilian free-tailed bat mortality at operational wind turbines.

The differences in effectiveness of UDs among bat species could potentially be attributed to variation in echolocation ecology. Echolocation frequency and use varies across species (Schnitzler et al., 2003; Jones and Holderied, 2007); thus, species-specific responses should not be surprising. A study in south Texas documented that the UD reduced mortalities of hoary and Brazilian free-tailed bats, both of which have lower echolocation frequencies. In contrast, mortalities of species with higher echolocation frequencies, such as the northern yellow bat (*L. intermedius*) were not significantly reduced (Weaver et al., 2020). Similar studies using other deterrent technologies have also reported varying results among species (Arnett et al., 2013; Romano et al., 2019). The effectiveness of UDs may be connected to the rapid attenuation of high-frequency sound (Griffin, 1971). Deterrent signals that include lower-frequency ultrasound travel farther from the source and may interact with species at greater distances. However, our results did not indicate a trend in effectiveness based on echolocation frequency, as Brazilian free-tailed bats were the lowest-frequency bats tested and cave myotis were the highest-frequency echolocators, and both of these species have similar flight responses during high and low treatment emissions.

Our results provided some evidence that bat species' responses can differ between the sexes, as we found to be the case for red bats and cave myotis. An accurate understanding of the potential differences in wind turbine mortalities and UD effectiveness between sexes is needed to modify and inform further deployment of UDs. Changes to the population sex ratio can greatly influence population growth, size, and risk of extinction (e.g., Donald, 2007; Lehikoinen et al., 2008; Wedekind, 2012; Ramula et al., 2018), as having too few females can limit population growth. The importance of females to population growth and stability is particularly true for bats because many species have polygamous mating systems, and females only have one litter per year and typically fewer than two pups per litter (Barclay et al., 2003; Ammerman et al., 2019). Therefore, activities that reduce the relative abundance of females are likely to lead to more dramatic population declines (Wedekind, 2012). Thus, minimization strategies that target females during periods of high risk may be more cost-effective and may provide similar population-level results as those targeting both sexes.

Our results also indicate that UD effectiveness can differ between spring and fall for some bat species. For example, tricolored bats flew farther from the UD compared to the control during fall, whereas red bats showed greater flight distances during spring. Previous studies often focused UD testing in the late summer through fall seasons (Szewczak and Arnett, 2007;

Johnson et al., 2012; Arnett et al., 2013; Romano et al., 2019; O'Neil 2020; Weaver et al., 2020) because this is when bat mortalities peak at wind energy facilities in North America (Arnett et al., 2008; Zimmerling and Francis, 2016; American Wind Wildlife Institute, 2021). A recent study by Goldenberg et al. (2021) used thermal video data to show that bats spend more time flying near wind turbines and exhibit riskier behavior in late summer and fall. It is unclear, however, why bats spend less time near wind turbines during spring and early summer (Drake et al., 2012, Kerns and Kerlinger 2004). Increasing evidence suggests that bats are attracted to wind turbines (e.g., Foo et al., 2017; Richardson et al., 2021; Guest et al., 2022), which could, in part, explain the lack of predictive relationship between indicators of risk preconstruction and estimates of bat mortality postconstruction (e.g., Lintott et al., 2016; Solick et al., 2020). A variety of explanatory hypotheses for bat attraction to wind turbines have been proposed (Cryan and Barclay, 2009; Guest et al., 2022), none of which are mutually exclusive and all of which likely vary with factors such as season, food availability, and reproductive condition. In this study, however, we can rule out any influence of attraction, as there was not a wind turbine or other large structure present in the immediate vicinity of the flight cage, and the end of the flight cage from which the UD was deployed was randomly selected each night.

There was some evidence that differences in effectiveness between seasons would have a biologically meaningful result in reducing mortalities, as male red bats were deterred >20 m farther in the spring than in fall. If a seasonal component to UD effectiveness exists, particularly with female bats, or if there is a window of time in which more females than males of a given species are being killed, then impact minimization strategies focused on that period would have a greater positive effect on population stability than strategies that were focused on time periods with greater risk to males. Much progress has been made in describing patterns of bat mortality related to wind turbines (Arnett and Baerwald, 2013; Guest et al., 2022). For example, a once widely held assumption within the wind-wildlife community was that relatively more male than female bats are killed at wind energy facilities in North America. Empirical support for this assumption came from morphological sex identification of bat carcasses collected in the field (e.g., Johnson et al., 2003; Fiedler 2004; Arnett et al., 2008). However, more recent genetic-based sex identifications indicate that morphology-based sex identifications of carcasses are inaccurate and often significantly overestimate the relative abundance of males (Korstian et al., 2013; Nelson et al., 2018; Chipps et al., 2020) because relatively more females are either misidentified or classified as unknown sex (Korstian et al., 2013; Nelson et al., 2018).

We identified several strengths and limitations in our study. This is the first study to examine species-specific differences of bats to different UD treatments in a semi-controlled environment (i.e., an outdoor flight cage). With this facility, we could visualize the responses of individual bats of known species to different acoustic treatments using statistically robust methods. With the exception of the mesh netting, the flight cage environment was as similar as possible to what the local-caught bats were experiencing just prior to the experimental trials. Other published studies on UDs have primarily focused on using bat carcasses to estimate and compare mortalities among control and treatment conditions (e.g., Arnett et al., 2013; Romano et al., 2019; Weaver et al., 2020), which does not allow researchers to incorporate behavioral observations of individual bats in the presence of UDs. A few studies have also tested the responses of free-flying bats to UDs by using thermal cameras over ponds or in riparian areas or at wind turbine towers, where species and/or sex could not be determined (Johnson et al., 2012; Lindsey, 2016; Gilmour et al., 2020). In these cases, the researches could assess how the bat community responded to the acoustic signals by using thermal or night vision cameras, but they could not make inferences to sex or individual bat species. Cameras recording flight behavior of bats at wind turbines cannot yet provide information for species identification (e.g., Horn et al., 2008).

We also recognize, however, that capturing bats and keeping them in the flight cage for even a short amount of time has the potential to alter the normal flight behavior. It also eliminates other potential factors that are associated with a wind energy facility, such as the presence of wind turbines and social interactions with other bats. We assumed the social interaction covariate was controlled for in the study, but it cannot be completely excluded due to the inability to prevent external free-flying bats from interacting with our trial subjects through the cage mesh. During the trials, we witnessed external bats interacting with a subject, specifically during control periods both during the trial in the field and in the videos. Often, the external bat(s) was detected above the cage and cropped out during the data-processing steps. Our study was also limited by the length of the flight cage. Although it is longer than the blade length of most land-based wind turbines currently deployed, it did restrict flight to within 60.2 m of the UD and cannot account for increases in blade length. Thus, the UDs may have been more effective than our results suggest, and if the flight cage were longer, it is possible that further differences among treatments could be detected. Furthermore, this study was unable to randomly select which of the UDs would be used for each treatment within a single trial. That would have required two complete setups of monitors, controllers, and cables, as well as additional field crews, for which we did not have the resources. Instead, we were limited to randomly selecting one of the two UDs to use for the entirety of each trial.

Conclusions

This study demonstrated that certain bat species respond to different ultrasonic treatments and shift activity away from the UD. Results support our hypotheses that responses will differ by species and season. We observed similar results regardless of treatment for low-frequency and high-frequency bats. However, the low or combined treatments were most effective for the combined red bat species group and for three of the four single species in the study. Furthermore, lower-frequency sounds attenuate less quickly and can cover a larger volume of airspace around a wind turbine. However, the effectiveness detected in the flight cage may not have ecologically meaningful benefits for deterrents deployed on operational wind turbines, as some differences were small (<10 m) and may not deter bats from the dangerous rotor-swept area.

For future testing, we recommend programming UDs to focus only on relatively low-frequency ultrasound (e.g., <40 kHz). This range covers other species that are vulnerable to wind energy development, such as hoary bats and silver-haired bats. We also suggest exploring the use of frequency sweeps or different sound patterns, such as randomized pulsed signals. Complex signals may further disorient bats who might adapt to constant stimuli. For future experiments using a flight cage, we suggest extending the length of the flight cage from 60 m to at least 100 m to account for longer turbine blades. We also recommend randomly assigning the UD that emits the deterrent signal among treatments.

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Figure 1. Schematic of the flight cage specifically designed to assess bat flight and echolocation behaviors during various emissions from an ultrasonic deterrent.

Figure 2. Output from one thermal camera placed outside of a flight cage in San Marcos, Texas (USA) indicating a bat's location during 30 frames per second. These distances were used to quantify the absolute distance bats were flying from an ultrasonic deterrent.

Figure 3. Bats were wild-captured and placed within the flight cage in San Marcos, Texas (USA) to undergo a 4-min acclimation period followed by a 4-min control period. We then randomly selected an ultrasonic deterrent emission treatment (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to begin the trial that consisted of all three treatments interspersed by controls.

Figure 4. Differences in flight distances (Dist) separated by sex and season of red bats (*Lasiurus borealis* and *Lasiurus blossevillii*) during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions. Trials were conducted in a flight cage

from July 2020 to May 2021 in San Marcos, Texas (USA). We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Figure 5. Differences in flight distances (Dist) separated by sex and season of cave myotis bats (*Myotis velifer*) during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions. Trials were conducted in a flight cage from July 2020 to May 2021 in San Marcos, Texas (USA). We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Figure 6. Differences in flight distances (Dist) separated by sex and season of Brazilian free-tailed bats (*Tadarida brasiliensis*) during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions. Trials were conducted in a flight cage from July 2020 to May 2021 in San Marcos, Texas (USA). We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Figure 7. Differences in flight distances (Dist) separated by sex and season of evening bats (*Nycteceius humeralis*) during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions. Trials were conducted in a flight cage from July 2020 to May 2021 in San Marcos, Texas (USA). We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Figure 8. Differences in flight distances separated by sex and season of tricolored bats (*Perimyotis subflavus*) during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions. Trials were conducted in a flight cage from July 2020 to May 2021 in San Marcos, Texas (USA). We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Table 1(on next page)

Results from quantile regression.

Beta values, standard errors (SE), t-values, and p-values from quantile regression analyses comparing flight distance during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions for one species group, red bats (*Lasiurus borealis* and *Lasiurus blossevillii*), and four bat species cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*). Trials were conducted in a flight cage from 2020 to 2021 in San Marcos, Texas, USA. We assessed differences in flight distances using quantile regression and focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles. Gray boxes indicate no significant difference in flight distance between treatment and control.

Table 1. Beta values, standard errors (SE), t-values, and p-values from quantile regression analyses comparing flight distance during three treatment emissions from the NRG Systems ultrasonic deterrent (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) to a control period of no emissions for one species group, red bats (*Lasiurus borealis* and *Lasiurus blossevillii*), and four bat species cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*). Trials were conducted in a flight cage from 2020 to 2021 in San Marcos, Texas, USA. We assessed differences in flight distances using quantile regression and focused on the 10th, 25th, 50th, 75th, and 90th percentiles. Gray boxes indicate no significant difference in flight distance between treatment and control.

Species	Treatment	Percentile	Beta	SE	t-value	P
Red bats	Combined	10th	13.21	0.22	-60.36	<0.001
		25th	19.57	0.19	-102.70	<0.001
		50th	16.07	0.21	-76.11	<0.001
		75th	7.81	0.19	-41.62	<0.001
		90th	-7.30	1.16	6.30	<0.001
	High	10th	14.59	0.20	72.70	<0.001
		25th	18.83	0.21	88.03	<0.001
		50th	15.11	0.23	65.87	<0.001
		75th	7.32	0.19	38.42	<0.001
		90th	-12.16	1.14	-10.63	<0.001
	Low	10th	9.01	0.25	35.69	<0.001
		25th	14.82	0.20	73.38	<0.001
		50th	13.29	0.60	22.23	<0.001
		75th	7.12	0.19	37.31	<0.001
		90th	-8.33	1.37	-6.10	<0.001
Cave myotis	Combined	10th	1.43	0.33	-4.30	<0.001
		25th	3.69	0.41	-9.02	<0.001
		50th	-23.85	0.76	31.28	<0.001
		75th	-1.00	0.31	3.22	<0.001
		90th	-0.33	0.15	2.13	<0.001
	High	10th	10.02	0.40	24.8	<0.001
		25th	12.64	0.61	20.70	<0.001
		50th	3.24	0.85	3.80	<0.001
		75th	0.63	0.20	3.09	<0.001
		90th	0.00	0.14	0.00	1.00
	Low	10th	1.01	0.45	2.25	0.02
		25th	12.13	1.96	6.18	<0.001
		50th	9.24	0.72	12.8	<0.001
		75th	1.77	0.18	9.62	<0.001
		90th	0.92	0.12	7.43	<0.001

Table 1 cont.

Species	Treatment	Percentile	Beta	SE	t-value	P
Evening bat	Combined	10th	2.75	1.52	-1.81	0.07
		25th	1.64	1.07	-1.53	0.13
		50th	1.41	0.99	-1.42	0.16
		75th	5.29	2.16	-2.45	0.01
		90th	2.01	1.49	-1.35	0.18
	High	10th	2.43	2.11	1.15	0.25
		25th	3.87	1.05	3.69	<0.001
		50th	10.29	1.15	8.93	<0.001
		75th	14.27	1.29	11.09	<0.001
		90th	6.53	1.42	4.60	<0.001
	Low	10th	-1.02	1.04	-0.98	0.33
		25th	-7.65	2.17	-3.53	<0.001
		50th	1.72	1.55	1.11	0.27
		75th	7.51	1.72	4.36	<0.001
		90th	1.41	1.57	0.90	0.37
Brazilian free-tailed bat	Combined	10th	-1.10	0.61	-1.80	0.07
		25th	-0.97	0.68	-1.44	0.15
		50th	-4.15	1.55	-2.68	0.01
		75th	0.23	4.24	0.05	0.96
		90th	3.19	3.12	1.02	0.31
	High	10th	-5.13	0.62	-8.23	<0.001
		25th	-1.99	1.27	-1.57	0.12
		50th	0.30	2.35	0.13	0.9
		75th	4.60	6.45	0.71	0.48
		90th	9.63	6.36	1.52	0.13
	Low	10th	-3.52	0.51	-6.95	<0.001
		25th	-1.20	0.75	-1.60	0.11
		50th	17.08	1.98	8.60	<0.001
		75th	18.19	2.86	6.35	<0.001
		90th	13.16	2.65	4.96	<0.001

Table 1. Cont.

Species	Treatment	Percentile	Beta	SE	t-value	P
Tricolored bat	Combined	10th	-41.58	0.79	52.35	<0.001
		25th	-43.18	0.75	57.76	<0.001
		50th	-34.97	2.89	12.11	<0.001
		75th	-8.51	1.59	5.35	<0.001
		90th	-0.37	0.82	0.45	0.65
	High	10th	-39.11	1.28	-30.57	<0.001
		25th	-32.36	3.49	-9.27	<0.001
		50th	-22.07	2.42	-9.13	<0.001
		75th	-5.71	2.11	-2.71	<0.001
		90th	-1.14	0.84	-1.36	0.17
	Low	10th	-43.81	0.72	-60.43	<0.001
		25th	-46.12	0.62	-74.49	<0.001
		50th	-46.01	0.66	-69.82	<0.001
		75th	-41.42	1.14	-36.35	<0.001
		90th	-23.33	1.69	-13.78	<0.001

Table 2(on next page)

Mean distances flown by bats during ultrasonic emissions and controls.

Mean (±SD) difference in distances flown during three treatment emissions from the NRG Systems ultrasonic deterrent (UD) (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) compared to a control period of no emissions for one species group, red bats (*Lasiurus borealis* and *Lasiurus blossevillii*), and four bat species cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*). Trials were conducted in a flight cage from 2020–2021 in San Marcos, Texas, USA. Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10th, 25th, 50th, 75th, and 90th percentiles.

Table 2. Mean (±SD) difference in distances flown during three treatment emissions from the NRG Systems ultrasonic deterrent (UD) (Low: 20, 26, and 32 kHz; High: 38, 44, and 50 kHz; Combined: 20, 26, 32, 38, 44, and 50 kHz) compared to a control period of no emissions for one species group, red bats (*Lasiurus borealis* and *Lasiurus blossevillii*), and four bat species cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*). Trials were conducted in a flight cage from 2020–2021 in San Marcos, Texas, USA. Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10th, 25th, 50th, 75th, and 90th percentiles.

Species	Treatment	10th	25th	50th	75th	90th
Red bats	Combined	13.21±15.60	19.57±22.2	16.07±21.27	7.81±16.6	3.57±12.29
	High	14.59±15.77	18.83±16.58	15.11±15.47	7.32±13.02	3.72±8.79
	Low	9.01±15.75	14.82±18.63	13.29±18.22	7.12±15.43	3.14±9.57
Cave myotis	Combined	11.71±12.99	14.43±15.45	9.75±18.21	3.08±8.64	0.86±2.54
	High	7.28±10.12	12.12±15.27	8.71±19.90	2.74±8.34	0.89±2.44
	Low	13.22±15.14	16.66±17.11	11.77±16.10	2.70±9.42	0.64±3.58
Evening bat	Combined	2.06±11.53	3.24±16.89	4.23±20.49	1.24±17.65	-1.48±13.19
	High	12.28±15.96	13.59±18.13	9.62±18.00	4.97±16.35	0.46±11.68
	Low	4.19±14.66	6.30±19.24	3.36±21.37	0.62±18.73	-2.63±15.34
Brazilian free-tailed bat	Combined	6.82±14.28	9.05±16.84	7.42±14.87	3.89±10.19	1.90±4.57
	High	6.96±14.16	7.78±17.16	5.88±15.97	2.00±12.40	-0.23±9.21
	Low	6.04±16.01	5.97±18.76	5.32±17.45	1.70±13.80	-0.16±10.39
Tricolored bats	Combined	10.34±27.58	13.69±30.08	12.8±24.84	8.51±17.88	1.61±10.43
	High	5.94±17.47	7.83±19.89	10.92±19.80	6.54±15.72	-0.34±11.48
	Low	5.72±20.12	11.40±26.59	11.53±25.63	7.63±21.26	0.97±10.21

Table 3(on next page)

Results from analysis of variance assessments.

Results from the analysis of variance assessments for pairwise comparisons of flight distance between the NRG System ultrasonic deterrent emissions and the control period of no emissions by sex, season, and sex within season for each bat species group (red bats (*Lasiurus borealis* and *Lasiurus blossevillii*)), or bat species (cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*)). Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles. “df” = degrees of freedom.

Table 3. Results from the analysis of variance assessments for pairwise comparisons of flight distance between the NRG System ultrasonic deterrent emissions and the control period of no emissions by sex, season, and sex within season for each bat species group (red bats (*Lasiurus borealis* and *Lasiurus blossevillii*)), or bat species (cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*)). Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10th, 25th, 50th, 75th, and 90th percentiles. "df" = degrees of freedom.

Species	Treatment	Percentile	Sex	Season	Sex:Season
Red bats (n = 46; sex df = 1; season df = 1; sex:season df = 1; residual df = 321)					
	Combined	10th	0.061	<0.001	0.436
		25th	0.064	<0.001	0.388
		50th	0.020	<0.001	0.348
		75th	0.026	<0.001	0.075
		90th	0.024	<0.001	0.480
	Low	10th	0.395	<0.001	0.002
		25th	0.534	<0.001	0.009
		50th	0.448	<0.001	0.003
		75th	0.492	<0.001	<0.001
		90th	0.597	<0.001	0.001
	High	10th	0.423	<0.001	0.082
		25th	0.512	<0.001	0.136
		50th	0.418	<0.001	0.139
		75th	0.556	<0.001	0.022
		90th	0.593	<0.001	0.261
Cave myotis (n = 57; sex df = 1; season df = 1; residual df = 396)					
	Combined	10th	0.668	0.792	
		25th	0.856	0.861	
		50th	0.894	0.991	
		75th	0.887	0.867	
		90th	0.560	0.983	
	Low	10th	0.086	0.553	
		25th	0.042	0.762	
		50th	0.068	0.508	
		75th	0.019	0.315	
		90th	0.015	0.413	
	High	10th	0.933	0.852	
		25th	0.737	0.857	
		50th	0.606	0.805	

		75th	0.824	0.669	
		90th	0.997	0.880	

Table 3 cont.

Species	Treatment	Percentile	Sex	Season	Sex:Season
Evening bat (n = ; sex df = 1; season df = 1; residual df = 368)					
	Combined	10th	0.754	0.420	
		25th	0.917	0.479	
		50th	0.820	0.493	
		75th	0.903	0.344	
		90th	0.806	0.459	
	Low	10th	0.396	0.347	
		25th	0.298	0.758	
		50th	0.306	0.521	
		75th	0.663	0.688	
		90th	0.827	0.456	
	High	10th	0.177	0.108	
		25th	0.199	0.095	
		50th	0.130	0.162	
		75th	0.223	0.074	
		90th	0.309	0.103	
Brazilian free-tailed bats (n = 73; sex df = 1; season df = 1; sex:season df = 499)					
	Combined	10th	0.243	0.659	<0.001
		25th	0.315	0.208	<0.001
		50th	0.326	0.259	<0.001
		75th	0.882	0.277	<0.001
		90th	0.659	0.333	<0.001
	Low	10th	0.036	0.452	0.078
		25th	0.039	0.100	0.025
		50th	0.056	0.095	0.032
		75th	0.112	0.162	0.145
		90th	0.128	0.208	0.220
	High	10th	0.065	0.641	0.023
		25th	0.073	0.696	0.007
		50th	0.074	0.464	0.004
		75th	0.192	0.400	0.022
		90th	0.365	0.699	0.084

Table 3 cont.

Species	Treatment	Percentile	Sex	Season	Sex:Season
Tricolored bats (n = 17; sex df = 1; season df = 1; residuals df = 116)					
	Combined	10th	0.839	0.119	
	Combined	25th	0.709	0.041	
	Combined	50th	0.698	0.059	
	Combined	75th	0.931	0.057	
	Combined	90th	0.724	0.066	
	Low	10th	0.151	0.009	
	Low	25th	0.163	0.008	
	Low	50th	0.152	0.009	
	Low	75th	0.187	0.001	
	Low	90th	0.312	<0.001	
	High	10th	0.638	0.004	
	High	25th	0.435	0.003	
	High	50th	0.41	0.003	
	High	75th	0.553	<0.001	
	High	90th	0.953	<0.001	

Table 4(on next page)

Pairwise comparisons between sex, species, and sex within species.

Pairwise comparisons from analysis of variance of flight distance between the NRG System ultrasonic deterrent emissions and the control period of no emissions by sex, season, and sex within season for each bat species group (red bats (*Lasiurus borealis* and *Lasiurus blossevillii*)), or bat species (cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*)). Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentiles.

Table 4. Pairwise comparisons from analysis of variance of flight distance between the NRG System ultrasonic deterrent emissions and the control period of no emissions by sex, season, and sex within season for each bat species group (red bats (*Lasiurus borealis* and *Lasiurus blossevillii*)), or bat species (cave myotis (*Myotis velifer*), Brazilian free-tailed bats (*Tadarida brasiliensis*), evening bats (*Nycteceius humeralis*), and tricolored bats (*Perimyotis subflavus*)). Gray boxes indicated no significant differences between treatment and control during the quantile regression analysis that focused on the 10th, 25th, 50th, 75th, and 90th percentiles.

Species	Treatment	Percentile	Pairwise results
Red bats	Combined	10th	spring > fall 9.339 m (<0.001)
		25th	spring > fall 9.636 m (<0.001)
		50th	female > male 4.576 m; spring > fall 8.810 m (<0.001)
		75th	female > male 4.237 m (0.026); spring > fall 8.475 m (<0.001)
		90th	female > male 4.169 m (0.024); spring > fall 7.585 m (<0.001)
	Low	10th	female spring > female fall 6.948 m (0.011); male spring > female fall 17.427 m (<0.001); female spring > male fall 8.709 m (<0.001); male spring > male fall 19.188 m (0.001); male spring > female spring 10.479 m (0.009)
		25th	female spring > female fall 7.047 m (0.025); male spring > female spring 17.095 m (<0.001); female spring > male fall 8.342 m (0.003); male spring > male fall 18.390 m (<0.001); male spring > female spring 10.047 m (0.033)
		50th	male spring > female fall 16.319 m (<0.001); female spring > male fall 7.910 m (0.003); male spring > male fall 18.413 m (<0.001); male spring > female spring 10.503 m (0.017)
		75th	male spring > female fall 17.297 m (<0.001); female spring > male fall 7.190 m (0.004); male spring > male fall 20.284 m (<0.001); male spring > female spring 13.093 m (<0.001)
		90th	male spring > female fall 15.244 m (<0.001); female spring > male fall 6.641 m (0.006); male spring > male fall 16.955 m (<0.001); male spring > female spring 10.313 m (0.006)

Table 4. Cont.

Species	Treatment	Percentile	Pairwise results
Red bats	High	10th	spring > fall 7.890 m (<0.001)
		25th	spring > fall 8.481 m (<0.001)
		50th	spring > fall 7.682 m (<0.001)
		75th	male spring > female fall 12.295 m (<0.001); female spring > male fall 6.110 m (0.023); male spring > male fall 13.664 m (<0.001)
		90th	spring>fall 6.013 m (<0.001)
Cave myotis	Low	75th	males > females 3.174 m
		90th	males > females 3.176 m
Brazilian free-tailed bat	Combined	10th	female fall > female spring 5.014 m (0.028); male spring > female spring 9.609 m (<0.001)
		25th	female fall > female spring 6.746 m (0.003); male spring > female spring 10.102 m (<0.001)
		50th	female fall > female spring 6.477 m (0.003); male spring > female spring 10.045 m (<.001)
		75th	female fall > female spring 5.409 m (0.011); male spring > female spring 7.314 m (0.013)
		90th	female fall > female spring 4.745 m (0.022); male spring > female spring 5.872 m (0.05)
	Low	10th	males > females 2.862 m (0.036)
		25th	female fall > female spring 5.794 m (0.035); male fall > female spring 6.224 m (0.011); male spring > female spring 7.94 m (0.029)
		50th	female fall > female spring 5.52 m (0.039); male fall > female spring 5.810 m (0.015); male spring > female spring 7.243 m (0.045)

Table 4 (cont).

Species	Treatment	Percentile	Pairwise results
Brazilian free-tailed bat	High	10th	male spring > female spring 7.601 m (0.018)
		25th	male spring > female spring 8.688 m (0.009)
		50th	female fall > female spring 4.715 m (0.079); male spring > female spring 8.594 m (0.006)
		75th	no pairwise differences
Tricolored bat	Combined	25th	fall > spring 9.262 m (0.046)
	Low	10th	fall > spring 11.098 m (0.010)
		25th	fall> spring 11.591 m (0.010)
		50th	fall > spring 10.987 m (0.011)
		75th	fall > spring 12.430 m (0.002)
		90th	fall > spring 12.422 m (0.001)
	High	10th	fall > spring 10.929 m (0.004)
		25th	fall > spring 12.063 m (0.004)
		50th	fall > spring 11.426 m (0.004)
		75th	fall > spring 11.387 m (0.001)
		90th	fall > spring 10.97 (<0.001)

Figure 1

The flight cage used to assess species-specific responses of bats to three ultrasonic deterrent emissions.

We assessed bat flight behavior to three ultrasonic deterrent emissions in a flight cage measuring (l x w x h) 60 m x 10 m x 4.4 m using four thermal cameras with overlapping fields of view. One ultrasonic deterrent was placed at each end of the flight cage and randomly selected each night for trials. The flight cage is on Texas State University property in San Marcos, Texas, USA.

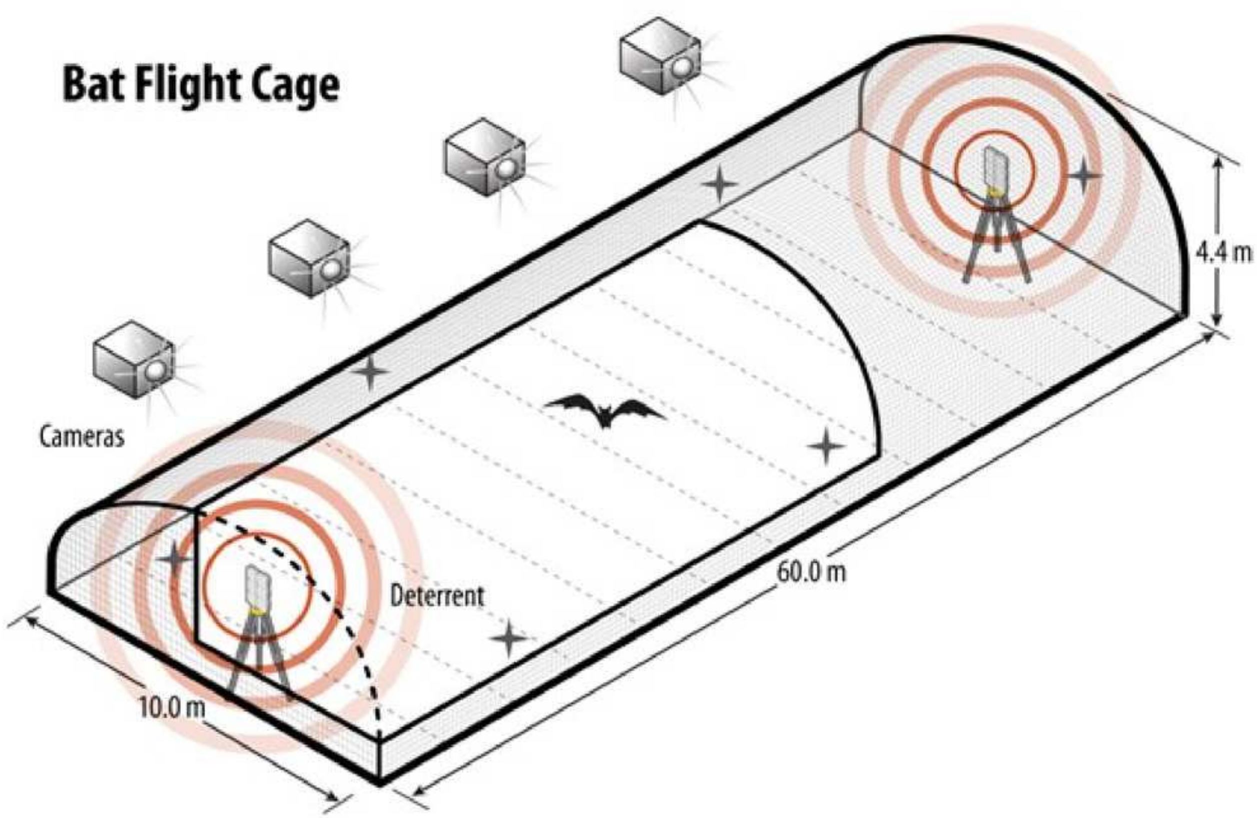

Figure 2

Example output from one thermal camera showing bat locations during each video frame that we used to calculate distance from the ultrasonic deterrent.

We used bat location during each thermal video frame to calculate the various percentile distances that bats flew from the ultrasonic deterrent during the three emission treatments versus a control period with the deterrent turned off.

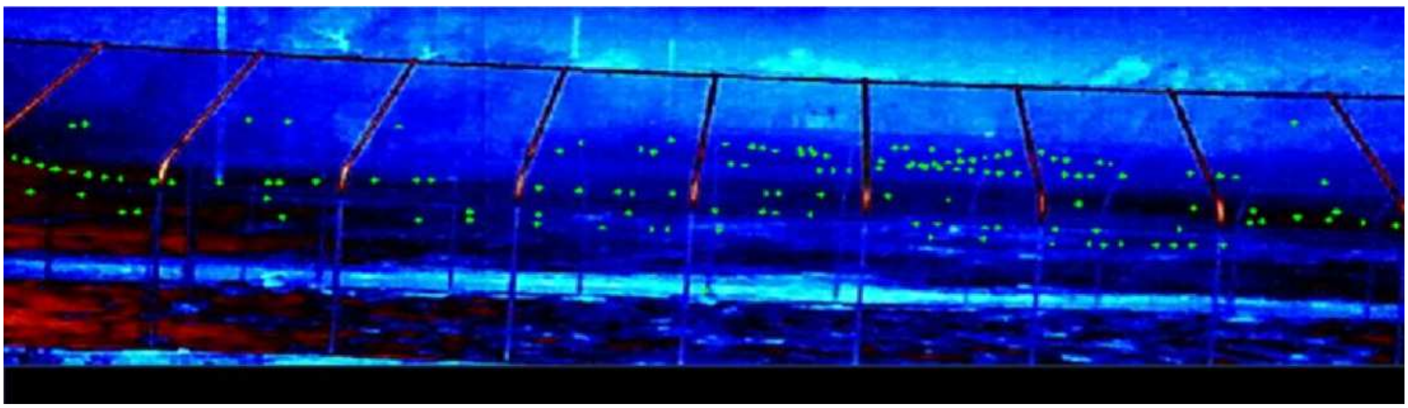

Figure 3

The experimental design consisted of releasing a bat into the flight cage followed by an acclimation period then a control period then the three emission treatments, order selected randomly, each interspersed by a control. All periods lasted 4 minutes.

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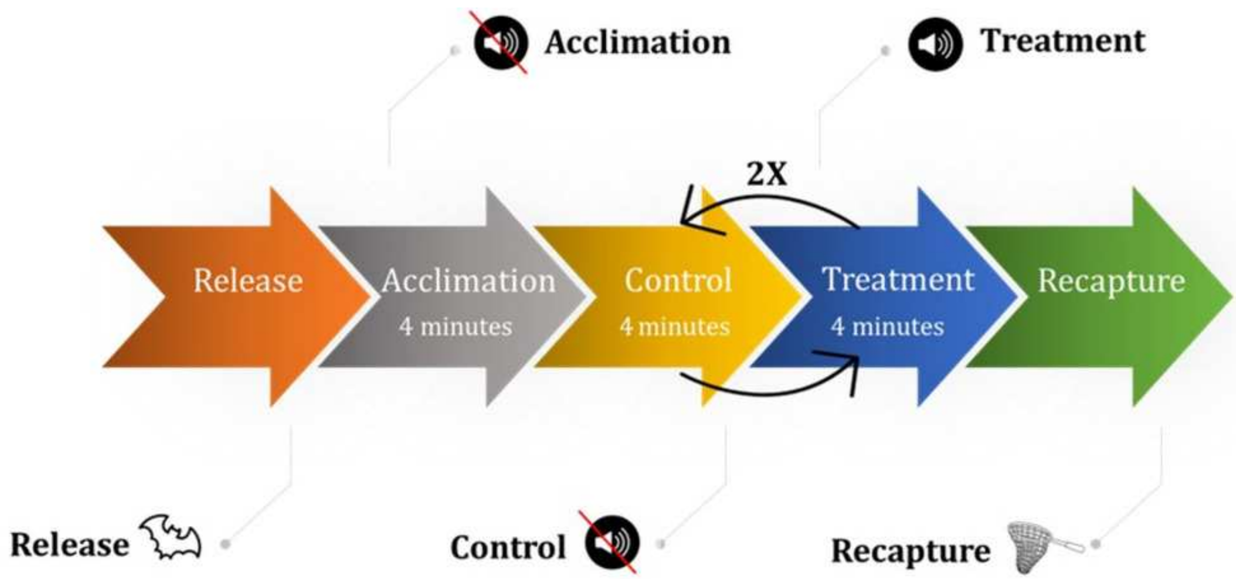

Figure 4

Differences in distances between each ultrasonic deterrent emission and control period for the red bat group.

The differences in distance (m) that the red bat group (*Lasiurus borealis* and *Lasiurus blossevillii*) flew from the ultrasonic deterrent (UD) during each emission treatment (Combined, Low, High) versus the control period with the UD powered off by sex, season, and sex within season.

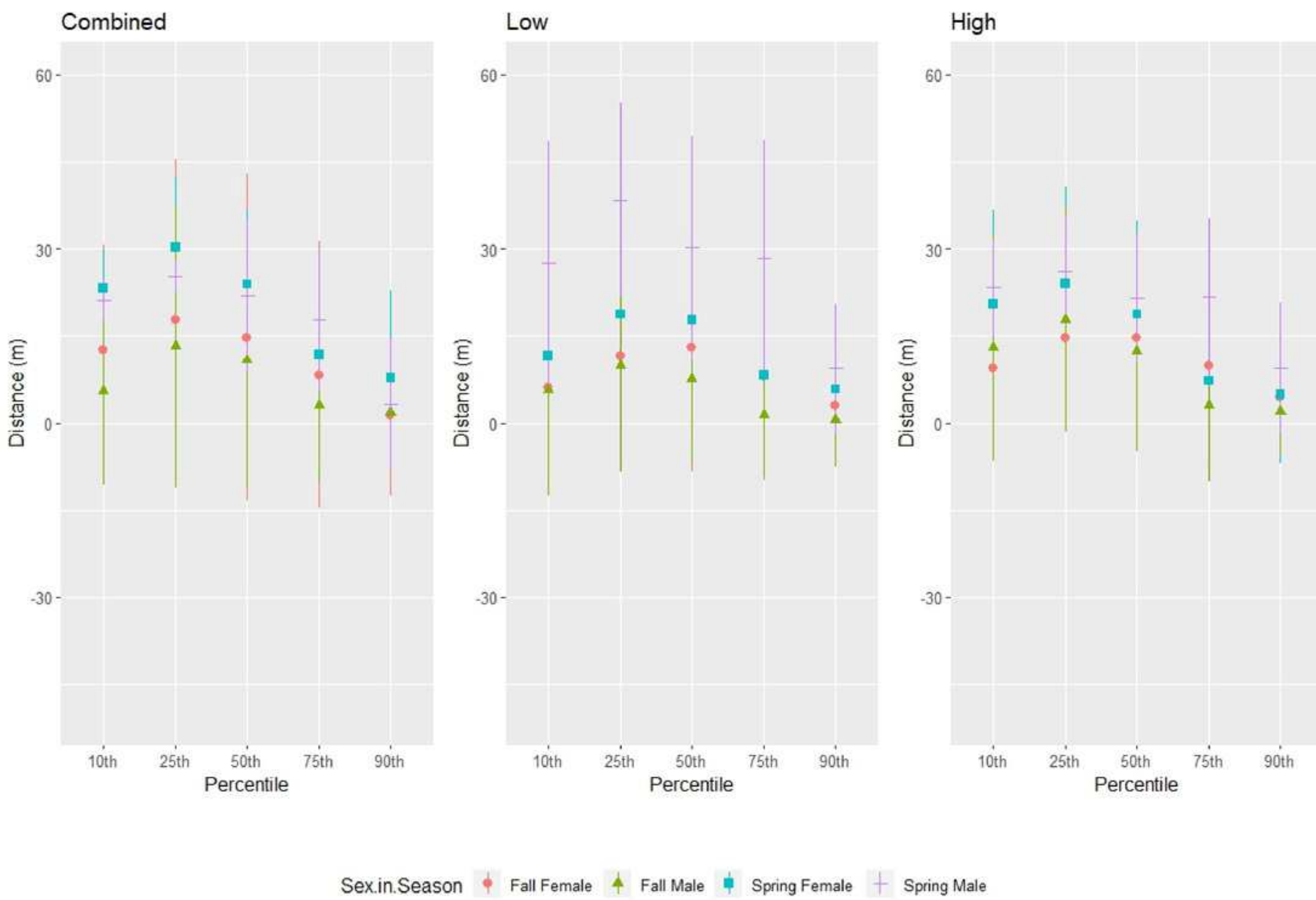

Figure 5

Differences in distances between each ultrasonic deterrent emission and control period for cave myotis.

The differences in distance (m) that cave myotis (*Myotis velifer*) flew from the ultrasonic deterrent (UD) during each emission treatment (Combined, Low, High) versus the control period with the UD powered off by sex, season, and sex within season.

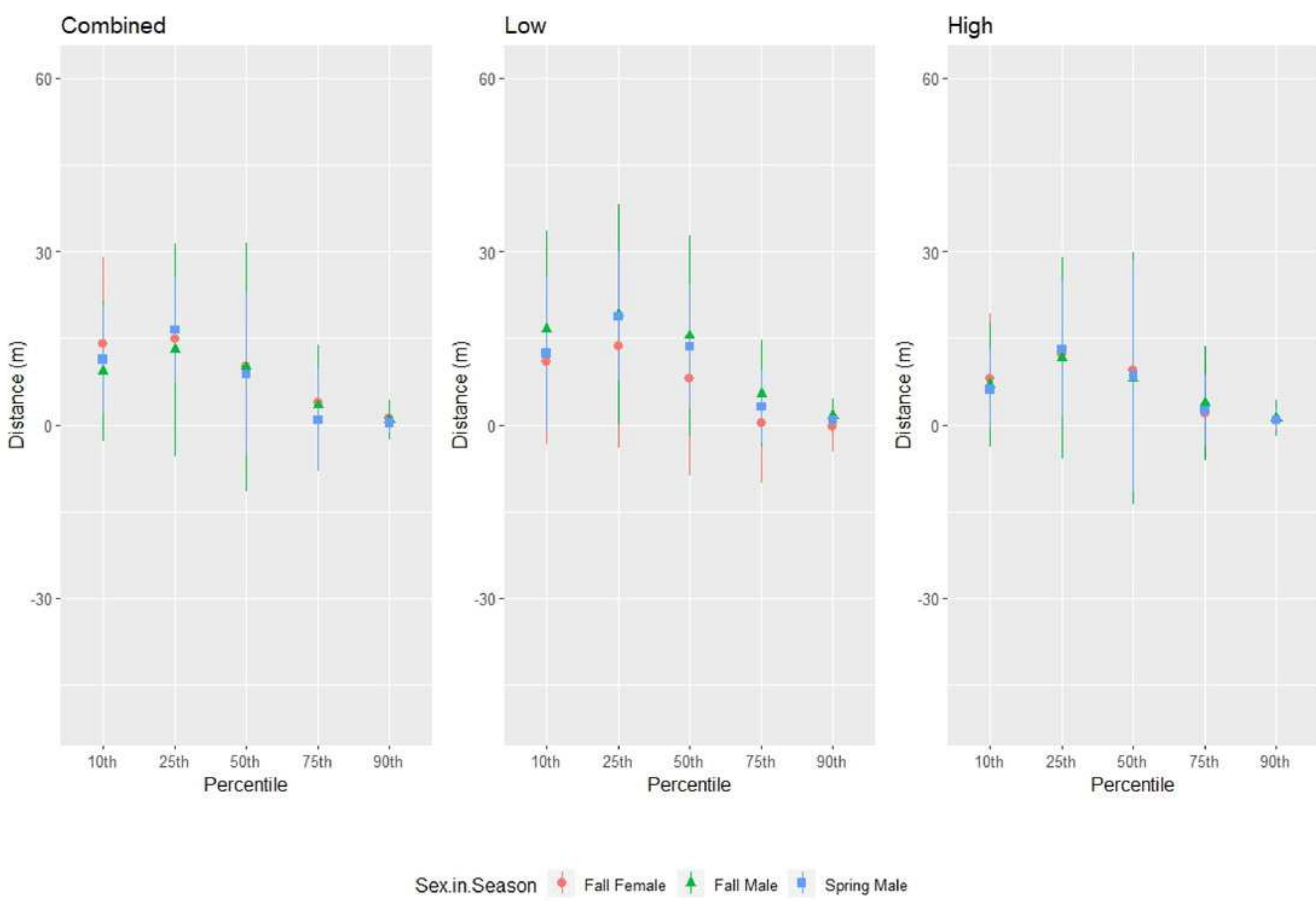

Figure 6

Differences in distances between each ultrasonic deterrent emission and control period for evening bats.

The differences in distance (m) that evening bats (*Nycteceius humeralis*) flew from the ultrasonic deterrent (UD) during each emission treatment (Combined, Low, High) versus the control period with the UD powered off by sex, season, and sex within season.

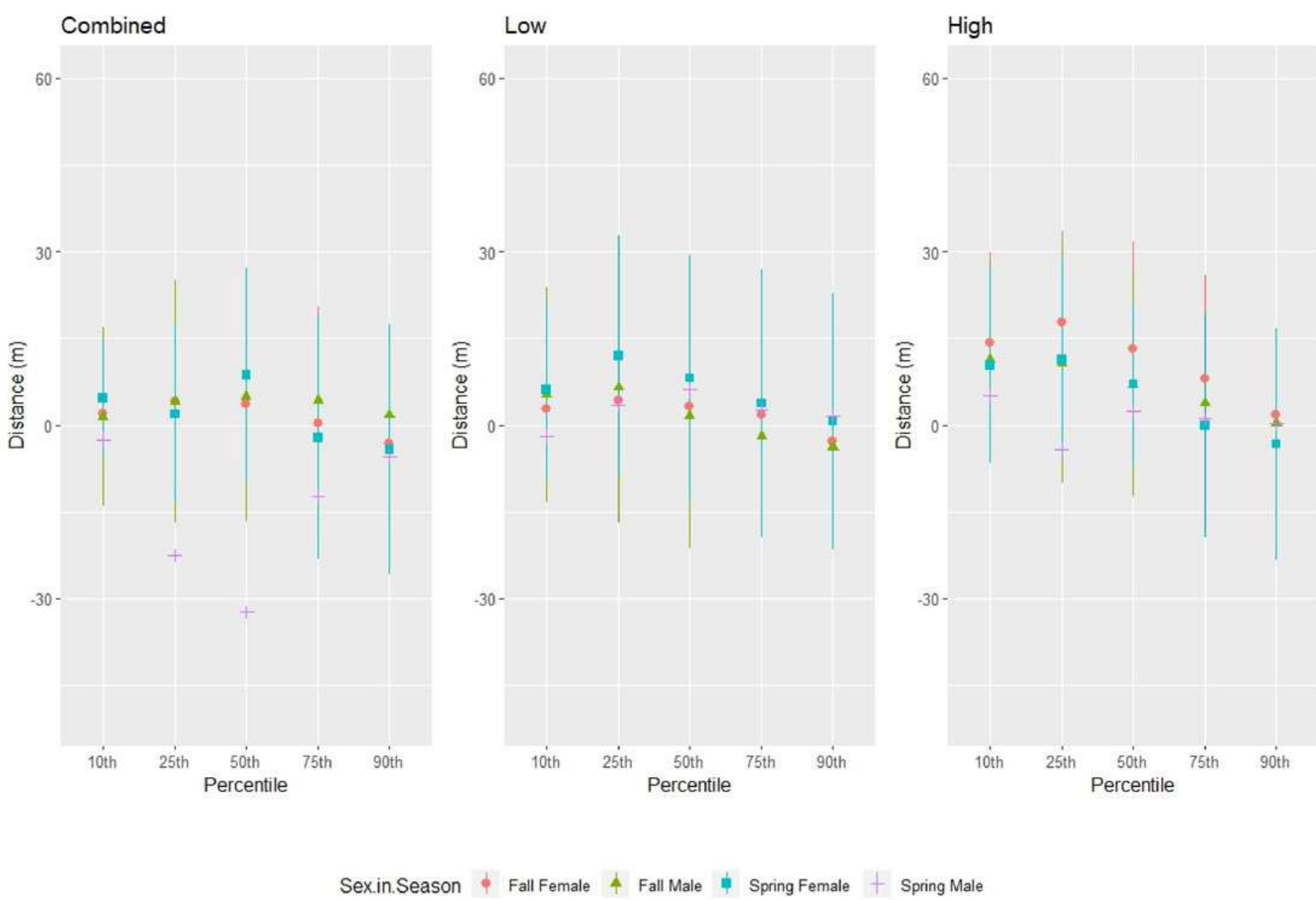

Figure 7

Differences in distances between each ultrasonic deterrent emission and control period for Brazilian free-tailed bats.

The differences in distance (m) that Brazilian free-tailed bats (*Tadarida brasiliensis)* flew from the ultrasonic deterrent (UD) during each emission treatment (Combined, Low, High) versus the control period with the UD powered off by sex, season, and sex within season.

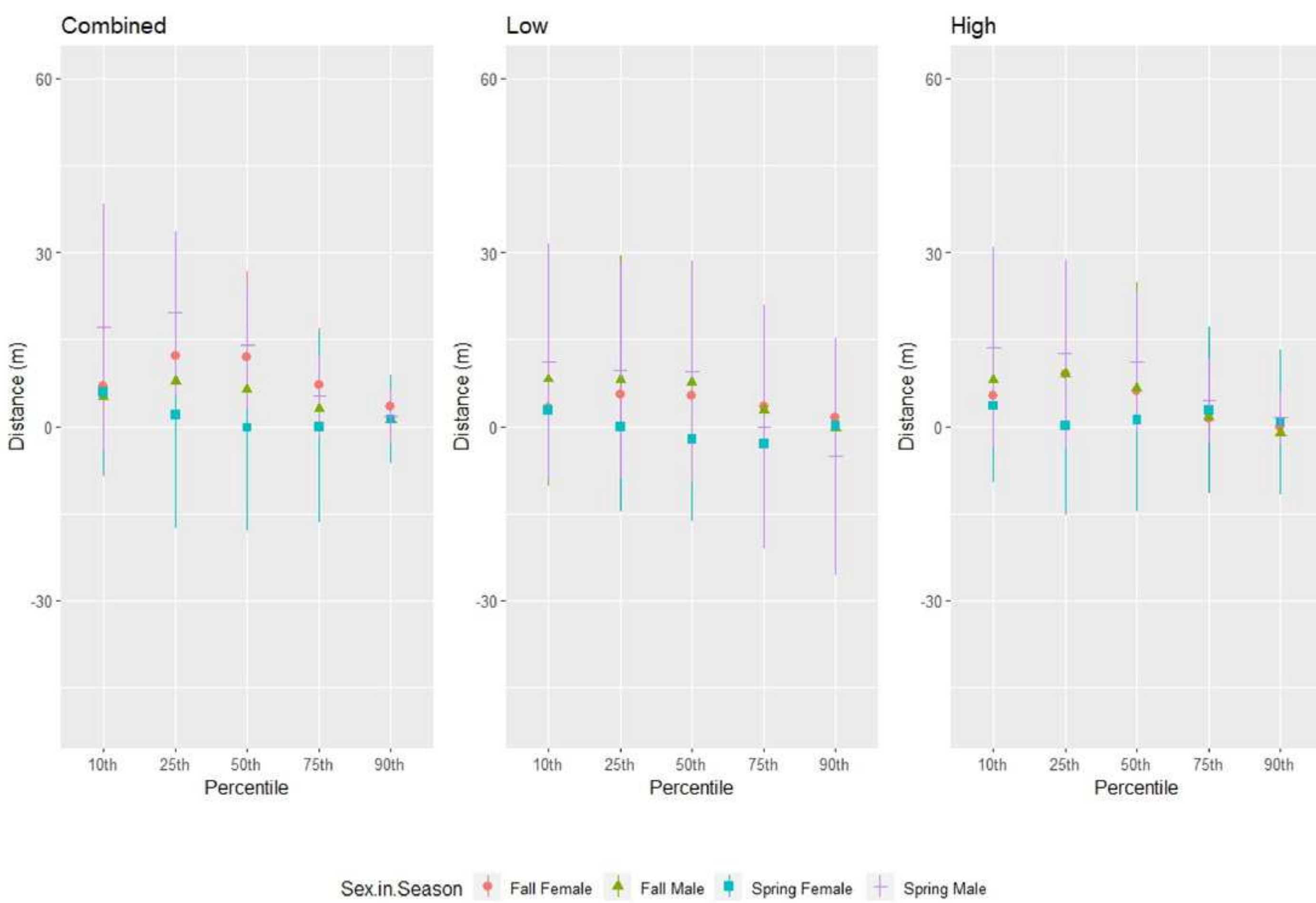

Figure 8

Differences in distances between each ultrasonic deterrent emission and control period for tricolored bats.

The differences in distance (m) that tricolored bats (*Perimyotis subflavus*) flew from the ultrasonic deterrent (UD) during each emission treatment (Combined, Low, High) versus the control period with the UD powered off by sex, season, and sex within season.