

**Song divergence of chipping sparrows in mixed forest and open habitats: testing the
Acoustic Adaptation Hypothesis**

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ABSTRACT

The Acoustic Adaptation Hypothesis has been studied in the context of many different songbirds with varying results. It predicts that songbirds will alter their song frequency and trill rate to maximize transmission, with lower frequencies and faster trill rates exhibiting better sound propagation in forest habitats. In order to further test this hypothesis, we studied the song of the chipping sparrow (*Spizella passerina*) in both forest and open grassland habitats in northern Michigan. Chipping sparrow song is simplistic, enabling thorough analysis. Eight individuals were recorded at the University of Michigan Biological Station (UMBS) and five were recorded within ten miles of the station. Songs were analyzed for maximum and minimum frequency, frequency range and trill rate. Results indicate that frequency and trill rate measurements show trends inverse to those predicted by the AAH, though no values were significant. There is a variety of potential causes of the unexpected results. Small sample size could play a significant role. Habitats were also variable and thus different characterization of each recording site as forest or open habitat could produce more expected results. Though unlikely, it is also possible that forest chipping sparrows are exhibiting character displacement in the presence of pine warblers. We also must consider the possibility that chipping sparrow song does not follow the AAH.

INTRODUCTION

Habitat-dependent variation in bird song is often addressed in the context of the Acoustic Adaptation Hypothesis (AAH). First proposed by Morton in 1975, the hypothesis was not named until 1987 by Rothstein and Fleischer (Morton 1975; Rothstein and Fleischer 1987; Brown and Handford 1996). The AAH predicts that species will alter the frequency of their vocalizations in different habitats in order to maximize sound transmission. This enables males to declare their territory to males not in their direct vicinity without unnecessary energy expenditure. Evidence suggests that forest birds use lower frequencies songs to reduce excess attenuation and maximize transmission (Morton 1975). Reduction in attenuation is caused by the increased ability of lower frequencies to travel around objects instead of reflect off them (Morton 1975). It has also been shown that grassland habitats are harsh environments for sound propagation due to wind and temperature variations (Morton 1975). Thus, territorial success of grassland bird vocalization depends on audibility of the song and the rapidity of modulation, while forest birds rely on attaining optimal frequency (Morton 1975).

Since the proposal of the AAH, many case studies have obtained mixed results regarding the hypothesis. An extensive study of 120 North American oscines showed evidence that maximum frequency (highest frequency sung during song) significantly differed among habitats (Wiley 1991). The same study also showed that “minimal period of repeated units,” an indication of trill rate, is strongly associated with habitat, with slower periods predominantly found in forested habitats (Wiley 1991). A 2007 literature review of all AAH related articles concluded that maximum, minimum, peak frequency and frequency range are all significantly lower in closed habitats (Boncoraglio and Saino 2007).

However, this study concluded that habitat type would have no effect on trill rate. Both studies support the AAH hypothesis that frequency and trill rate are lower in forest habitats but they suggest that different aspects of bird songs should be altered in order to obtain maximum transmission.

The purpose of this study is to analyze the effects of closed and open habitats on the maximum frequency, minimum frequency, frequency range, and trill rate of chipping sparrow (*Spizella passerina*) songs. Chipping sparrow song is a simple trill with little individual variation (Middleton 1998). Thus, spectrographs of the songs are easy to analyze for the above parameters. The lack of individual variation increases statistical power for analyses of the parameters. Also, chipping sparrows preferentially breed in “shrubby, coniferous habitats bordering open grassy spaces” (Middleton 1998), which indicates that male territories are found both in mixed forests and in the grassy spaces bordering them. This enables us to study song transmission in different habitats. We hypothesize that chipping sparrow song will exhibit habitat divergence between the closed forests and open grasslands in accordance with the AAH, with lower maximum and minimum frequencies, a lower frequency range and lower trill rate in the closed forests.

METHODS

Song Recordings

Chipping sparrow songs differ from dawn to daytime (Liu and Kroodsma 2007); the dawn chorus songs function in territorial defense and the daytime songs are used in mate attraction. Once chipping sparrows have found mates, they no longer sing daytime songs (Liu and Kroodsma 2007). Because the timing of our study (July – August) coincided with

the end of the breeding season, we chose to analyze the dawn chorus songs to ensure availability of vocalizations and comparability across individual males. This also eliminated the need for playback stimulation.

Chipping sparrow individuals were recorded at the University of Michigan Biological Station (UMBS) and two other locations within five miles of the station. Recording sites were classified as one of two habitats: a mixed forest habitat with both deciduous and coniferous trees and an open habitat containing either cut grass or grass between a half meter and a meter in height. The open habitats contained a few scattered trees.

We recorded between five and twelve songs for eight individuals from UMBS and five individuals outside of UMBS. Songs were recorded between 0530 and 0630 EDT at approximately four feet from ground level. We recorded the songs in 48K MP3 format using a Sennheiser K6 microphone and a Marantz Professional Solid State Recorder PMD660.

Song Analysis

We analyzed all songs using Raven V 1.2.1. Song duration (seconds), frequency interval (Hz), maximum and minimum frequencies (Hz) and number of notes per song were all recorded. Trill rate (notes/sec) was calculated by counting the number of notes from the spectrograph in Raven and dividing that number by the song duration calculated in Raven.

RESULTS

Mean low frequencies for chipping sparrow males ranged between 2583 and 4205 Hz. Mean high frequencies ranged between 7200 and 9533 Hz. Mean frequencies ranges were between 2988 and 6545 Hz. Mean trill rate ranged between 8.23 and 15.6

notes/second. Mean values of the listed parameters were analyzed against habitat type using a t-Test for two situations. In the first situation (Table 1), sites were designated as forest or open based purely on whether the bird was recorded in a forest or in a field. This designation produced five individuals in forest habitats and eight in open habitats. In the second situation (Table 2), UMBS was deemed a forest habitat due to gene flow between sites, even though some birds were recorded in open fields. There were eight individuals at UMBS. The sites outside of UMBS remained designated as open habitats and had five individuals.

Variance among individuals within habitats was high, with standard deviations ranging from 7.4% to 24.7% of mean value, (Tables 1, 2). Trill rate exhibited the highest variation among individuals with standard deviations between 14.7% and 24.7% of mean value. High frequency showed the lowest variation among individuals with standard deviations between 7.4% and 10.3% of mean value.

Each of the four variables (minimum frequency, maximum frequency, frequency range and trill rate) was higher in the forested habitat than in the open habitat in both analyses. However, the T-tests showed no significant difference of parameters between habitats ($P > 0.05$ for all tests). For the non-UMBS designation, mean high frequency approached significance with a p-value of 0.085 (Figure 1a) and mean low frequency had a p-value of 0.308 (Figure 1b). Frequency range had a p-value of 0.376 (Figure 1c) and trill rate had a p-value of 0.196 (Figure 1d). For the t-test where UMBS was designated as a single habitat, mean high frequency had a p-value of 0.197 (Figure 2a) and mean low frequency had a p-value of 0.575 (Figure 2b). Frequency range had a p-value of 0.382 (Figure 2c) and trill rate had a p-value of 0.691 (Figure 2d).

DISCUSSION

Our results, though insignificant, show that male chipping sparrows in forest habitats tend to have higher-values for low frequency, high frequency, frequency range and trill rate than male chipping sparrows in open habitats. This does not corroborate the AAH, which predicts lower values in these four parameters in a forest habitat. Morton (1975) showed that frequencies between 1000 and 2500 Hz in forest habitats maximize sound transmission. Our results indicate that chipping sparrows in both habitats sing at frequencies reaching 8000 Hz. Assuming it is true that lower frequencies travel more effectively in forests, it could be interpreted that chipping sparrow dawn chorus songs are not meant to travel far and perhaps are only used to defend territories and not attract mates (Liu and Kroodsma, 2007). If this is the case, it would be interesting to perform a similar analysis of chipping sparrow daytime songs, which differ from morning songs and may have lower frequencies to maximize sound propagation through the forest.

The t-test results for the designation of UMBS as both forest and field habitats as opposed to a single habitat produced p-values closer to significant. It is possible that the strict forest/open designation is more accurate than grouping habitats in close proximity, as there is evidence that chipping sparrows song learning has no genetic basis (Liu and Kroodsma 1999). This would suggest that gene flow between territories could be disregarded when determining which habitat to classify each recording site as. Chipping sparrows learn their songs in the first spring after fledging by mimicking a neighbor (Liu and Kroodsma 2006). Thus, it could also be interpreted that the close proximity of the two habitats in UMBS allowed for song learning from a neighbor who inhabits a different habitat, which would have large effects on the differences between habitats. Movement to a

different habitat after the first spring could also mean that some males are singing songs not ideal to their environment.

One problem with our experiment that may have skewed results was small sample size. With only thirteen individuals, statistical power is low. Other case studies of the AAH used sample sizes greater than 35 males (Rothstein and Fleischer 1987; Hunter and Krebs 1979; Hylton and Godard 2001). Song variation between individuals is also very high, even within habitat. This indicates that a large sample size is necessary to distinguish true trends. However, we cannot rule out the possibility that even with a larger sample size, chipping sparrow song would still have the same trend. Their song may not follow the Acoustic Adaptation Hypothesis.

Another problem in our study was potentially inappropriate habitat classification. Five of the recordings at UMBS could arguably be classified as either forest or open, depending on characterization of habitat. The presence of scattered trees in open habitats could also affect the acoustics of bird song, and thus the frequency of vocalization. Further experiments would need more well-defined, distinguished habitats.

Chipping sparrow song variation could be further complicated due to the evidence of interactions with pine warblers in forest habitats. Visual comparison of spectrograms of both chipping sparrow song and pine warbler song (Figure 3a and 3b) show similar songs. Pine warblers have trill songs that range from 10-30 notes. Though pine warblers reportedly sing between 2500 and 5700 Hz (Rodewald et al 1998), a much lower frequency than we found in chipping sparrows, it has been observed that pine warblers respond to chipping sparrow playbacks. From personal communications (Ted Anderson 2007), we also have evidence of song dueling between pine warblers and chipping sparrows. This indicates that pine

warblers interact with chipping sparrows in natural habitats. It is possible that chipping sparrows in forest habitats are exhibiting character displacement in the presence of pine warblers. Due to the confusability of their songs, forest chipping sparrows may have evolved a higher frequency song with a faster trill rate that makes the songs of the two species more easily distinguishable.

Another potential hypothesis for the higher frequency songs of chipping sparrows is that there exists a physical constraint on trill modification due to evolutionary history (Podos, 1997). To further analyze this hypothesis, experiments comparing trill rate and frequency bandwidth, as well as anatomical study of chipping sparrows, would demonstrate the presence or absence of evolutionary constraints.

It is evident that there are many possible reasons for the high frequency and fast trill rate of the chipping sparrow. Further experimentation to compliment this study would include a lab study of the effects of pine warbler tutors on song learning in chipping sparrows. Increasing sample size and number of recording sites would add greatly to this study as well. While it is hard to draw any definite conclusions from this study, it is clear that chipping sparrows sing at frequency rates much higher than the predicted 1000 to 2500 Hz. There is also a slight tendency for even higher frequencies in males in forested habitats. Trill rates exhibit the highest variance and show little significant difference between habitats. Thus, it can be concluded that further study of trill rates is less important than further frequency studies.

Our study does not corroborate the Acoustic Adaptation Hypothesis, nor does it provide enough evidence to refute the hypothesis. However, we have discovered that the acoustic tendencies of chipping sparrows provide many avenues of study, all of which can

be combined with other selection factors to better understand the behaviors of the chipping sparrow.

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TABLE LEGENDS

Table 1: Means \pm standard deviation, t-values and p-values of parameters when sites were designated as strictly forest or open habitat, disregarding proximity within UMBS campus

Table 2: Means \pm standard deviation, t-values and p-values of parameters when UMBS sites were designated as forest habitats and off-campus sites as open habitats

FIGURE LEGENDS

Figure 1a: A comparison of mean high frequency between forest and open habitat. T-test gave a p-value of 0.085.

Figure 1b: A comparison of mean low frequency between forest and open habitat. T-test gave a p-value 0.308.

Figure 1c: A comparison of mean frequency range between forest and open habitat. T-test gave a p-value of 0.376.

Figure 1d: A comparison of mean trill rate between forest and open habitat. T-test gave a p-value of 0.196.

Figure 2a: A comparison of mean high frequency between UMBS forest and Non-UMBS open habitats. T-test gave a p-value 0.197.

Figure 2b: A comparison of mean low frequency between UMBS forest and Non-UMBS open habitats. T-test gave a p-value 0.575.

Figure 2c: A comparison of mean frequency range between UMBS forest and Non-UMBS open habitats. T-test gave a p-value 0.382.

Figure 2d: A comparison of mean trill rate between UMBS forest and Non-UMBS open habitats. T-test gave a p-value 0.691.

Figure 3a: Example chipping sparrow spectrogram, with frequency (Hz) on the y-axis and time of recording (s) on x-axis.

Figure 3b: Example of pine warbler spectrogram, with frequency (kHz) on the y-axis and time of recording (s) on x-axis. Image courtesy of Rodewald et al (1998).

Table 1:

	Mean \pm Std. Dev.		t-Test	
	Forest	Open	t	p
Low Frequency (Hz)	3533 \pm 579	3215 \pm 332	1.12	0.308
High Frequency (Hz)	8392 \pm 864	7647 \pm 566	1.28	0.085
Frequency Range (Hz)	4858 \pm 959	4432 \pm 713	0.92	0.376
Trill Rate (songs/sec)	11.7 \pm 2.9	10.1 \pm 1.5	1.38	0.196

Table 2:

	Mean \pm Std. Dev.		t-Test	
	UMBS Forest	Open	t	p
Low Frequency (Hz)	3396 \pm 481	3243 \pm 428	0.577	0.575
High Frequency (Hz)	8154 \pm 775	7580 \pm 653	1.372	0.197
Frequency Range (Hz)	4759 \pm 765	4337 \pm 888	0.911	0.382
Trill Rate (songs/sec)	10.9 \pm 1.6	10.4 \pm 1.5	0.408	0.691

Figure 1a:

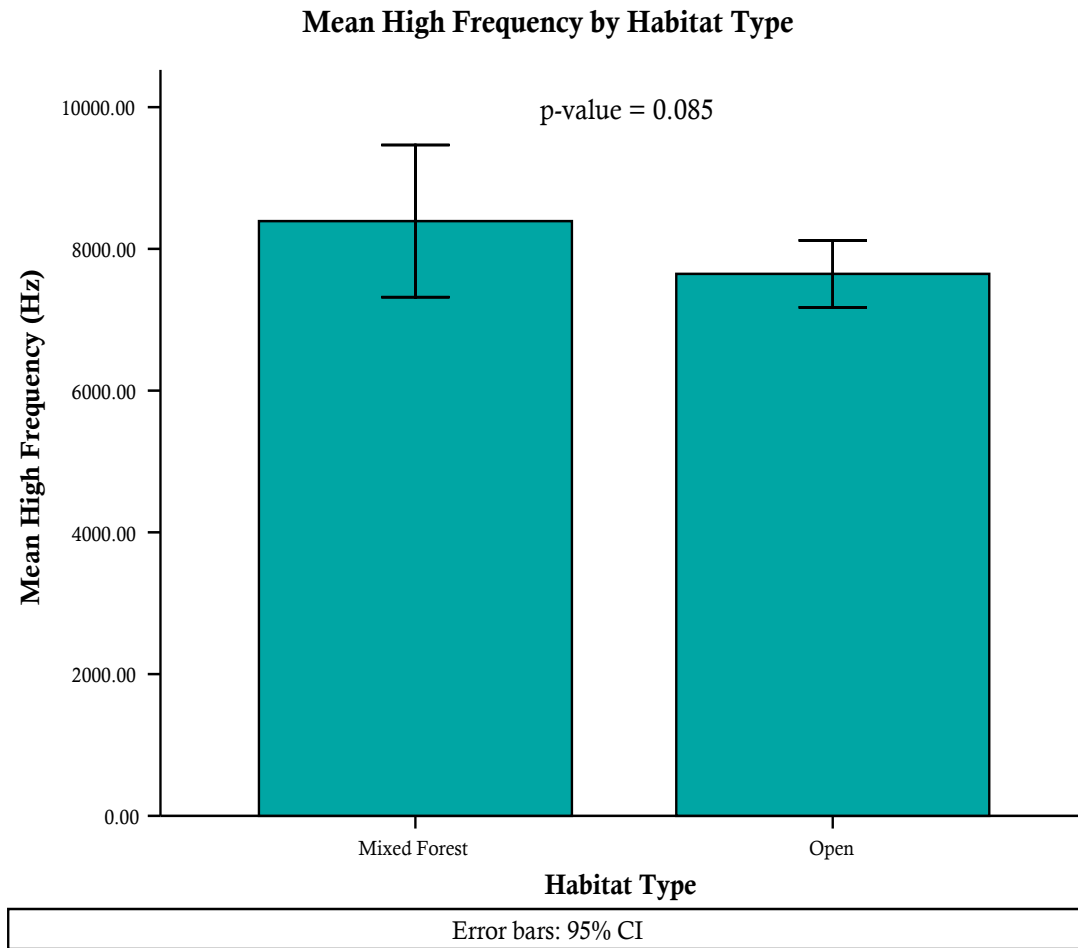


Figure 1b:

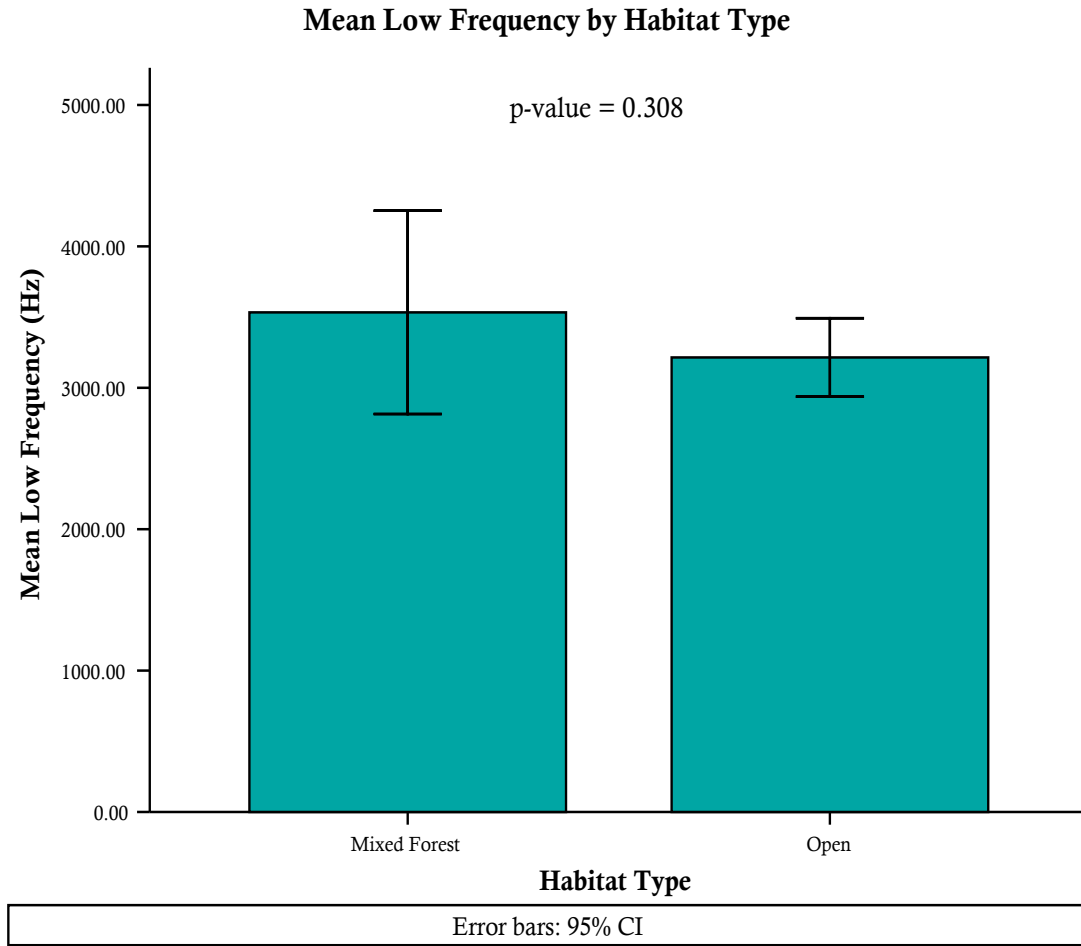


Figure 1c:

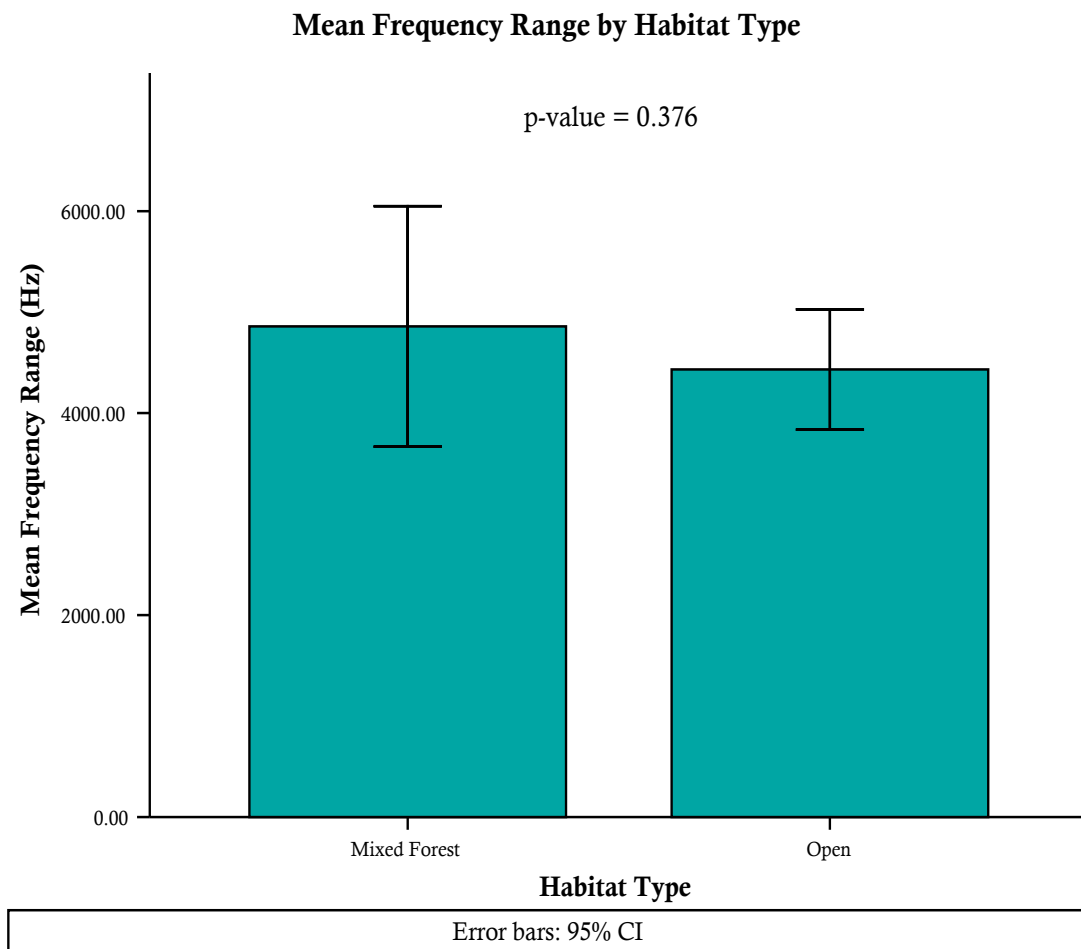


Figure 1d:

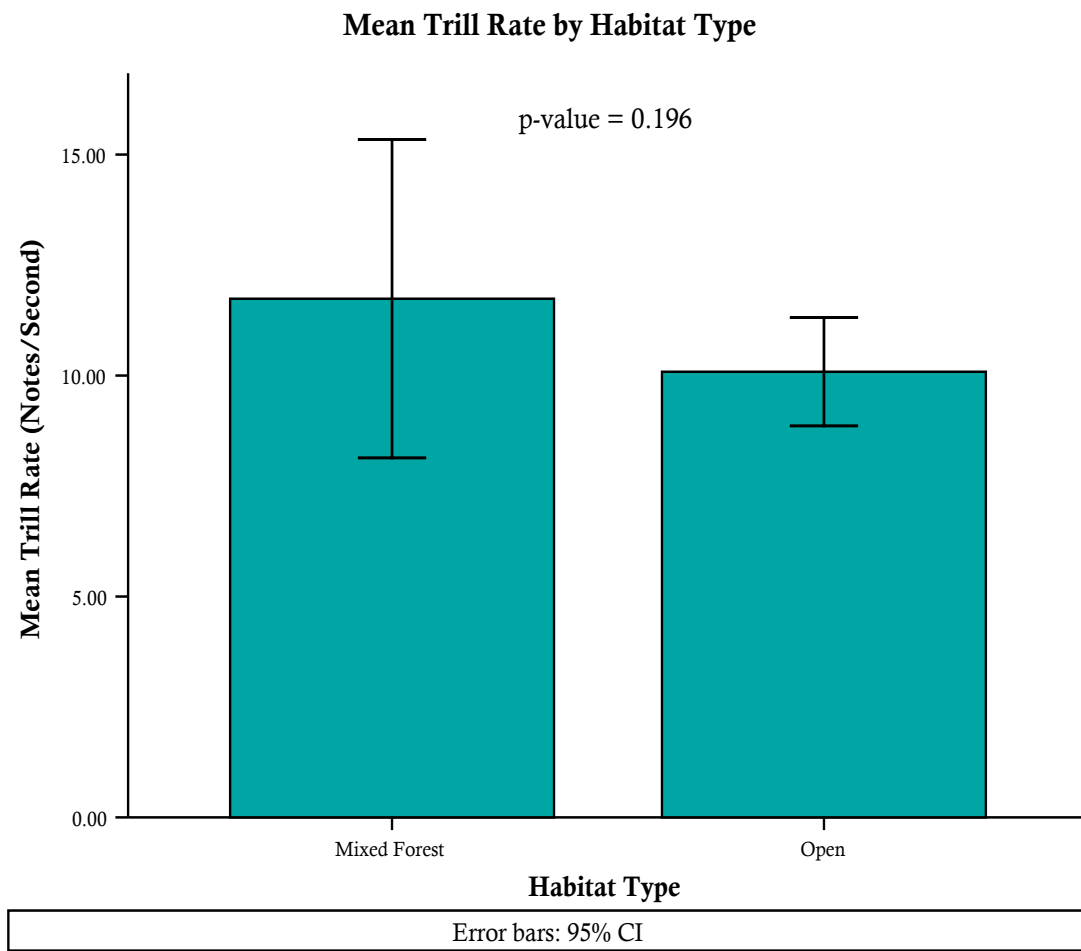


Figure 2a:

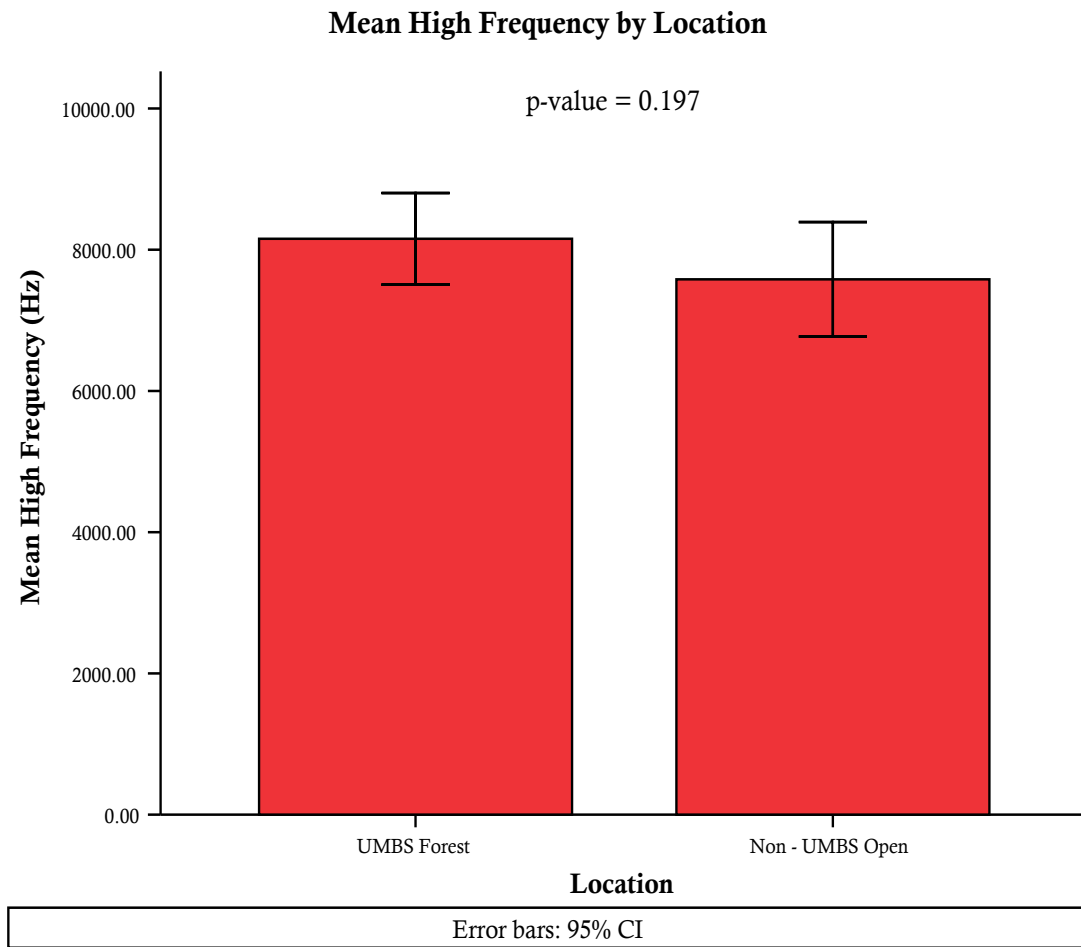


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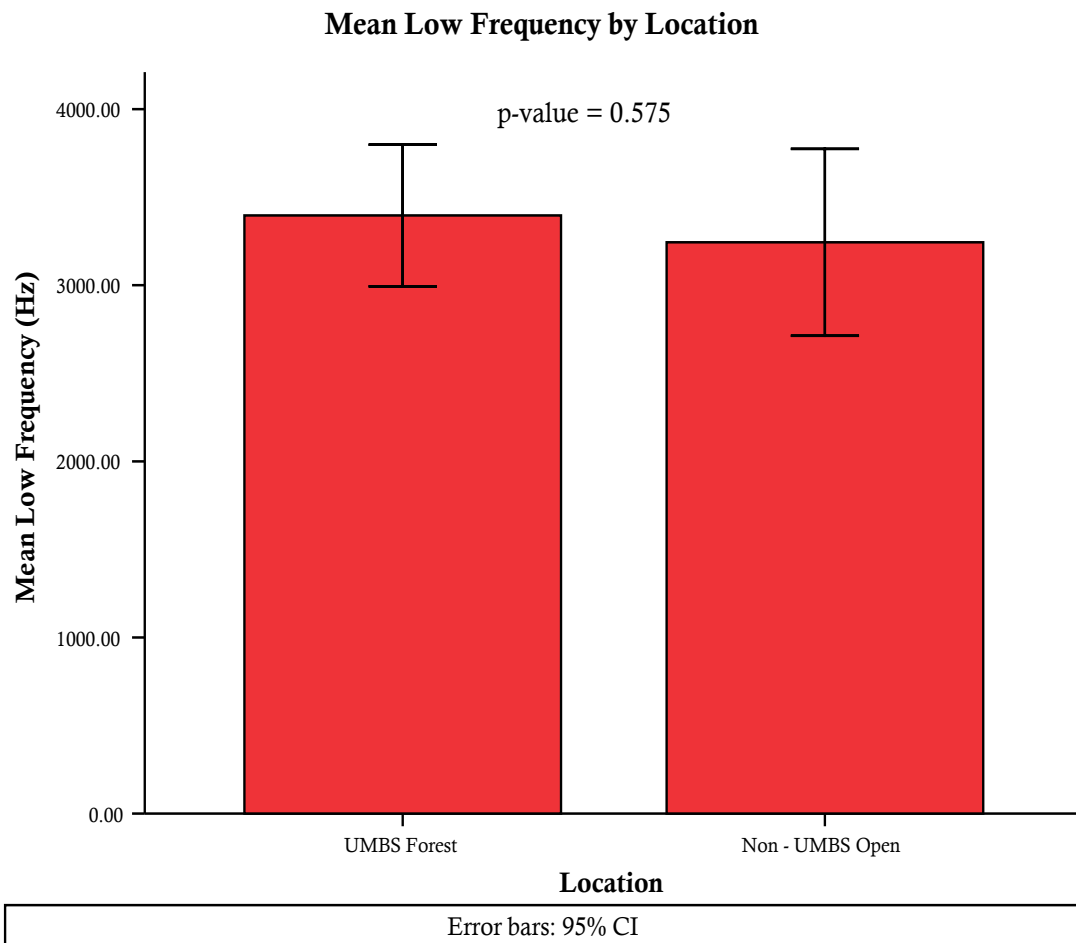


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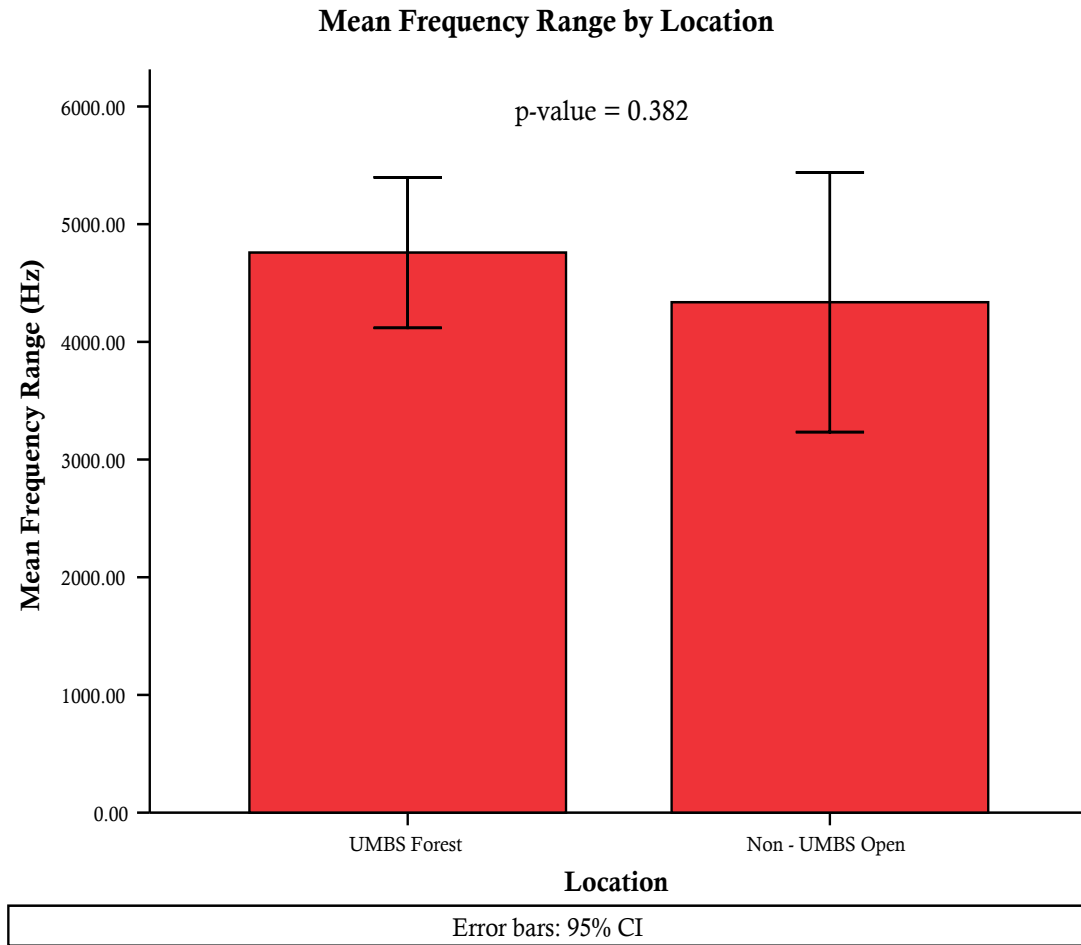


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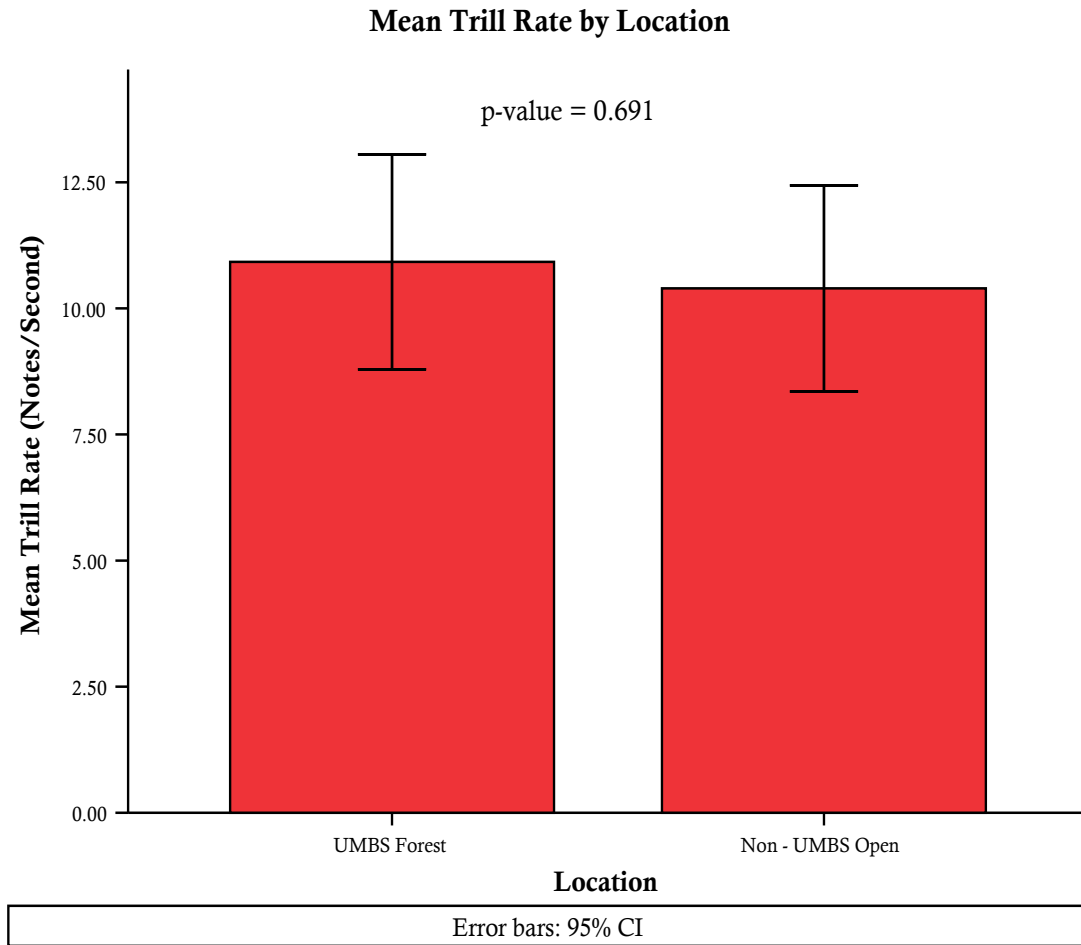


Figure 3a:

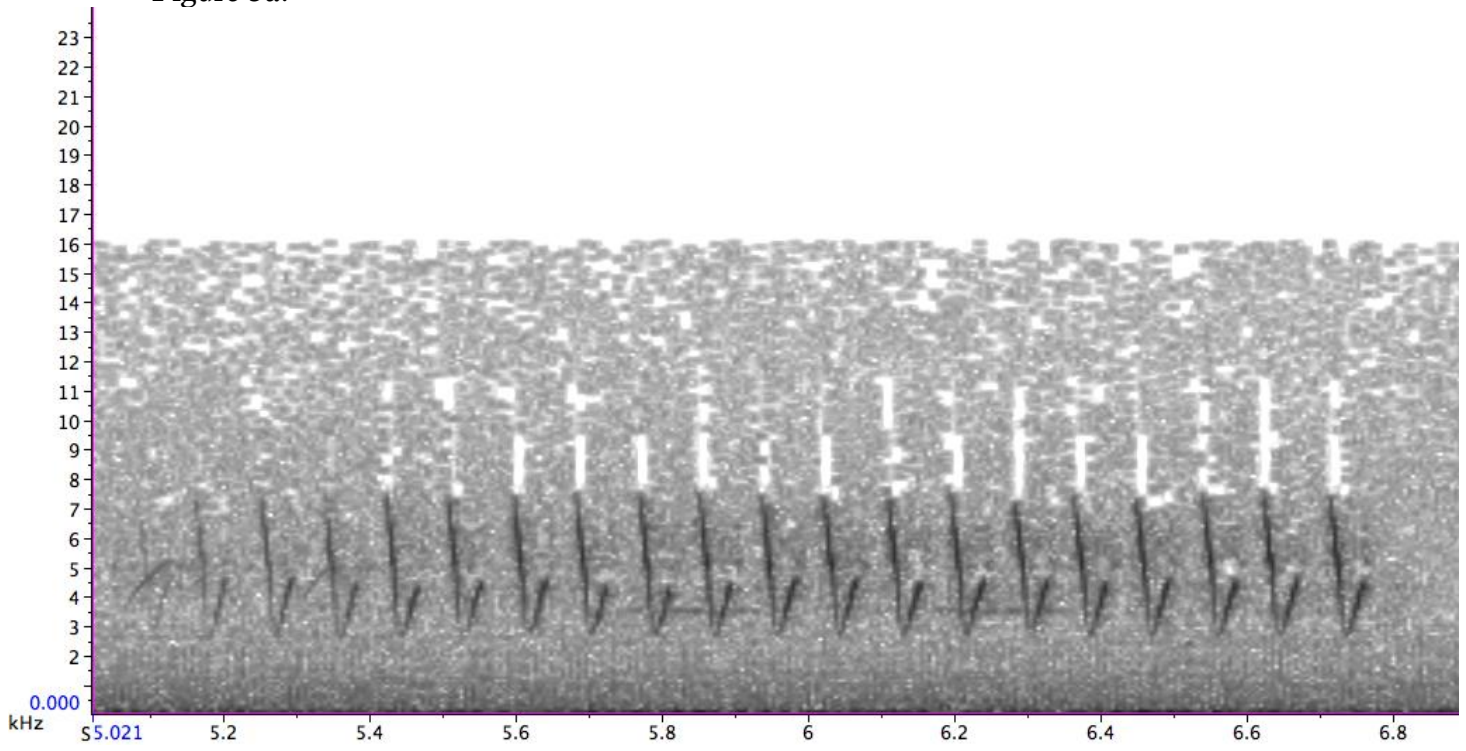


Figure 3b:

