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Recommended Citation

Danci, Ioana, "Variation in the Calling Song of the Cricket *Gryllus pennsylvanicus* Across Geographic Longitudinal Change" (2013). *Honors Theses*. 67.

<https://dx.doi.org/10.32597/honors/67/>

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Honors Thesis

Variation in the calling song of the cricket *Gryllus pennsylvanicus* across geographic
longitudinal change

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April 1, 2013

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Department: _____

ABSTRACT

Variation of cricket calling songs can be attributed to environmental factors, including temperature, humidity, vegetation, season, solar elevation, and geographic location. Recent studies found that latitudinal position affects the calling song of male *Gryllus pennsylvanicus*. My project evaluates whether longitudinal position influences the calling song of *G. pennsylvanicus*. Using the predicted values of 4 song features based on a mathematical model (Burden 2009), I evaluated data from 6 locations along a longitudinal axis. I calculated R^2 values to determine how well the model predicted the values in my sample populations. The model was found to be a poor predictor.

INTRODUCTION

Individuals within a species undeniably exhibit variation. How much variation exists within a species, and how that variation changes with habitat is of keen interest to biologists. Variability in sexual signals between populations of the same species has been documented in animals, such as fruit flies and marine mammals (Colbeck et al. 2010). In a study on treehoppers, a great amount of adaptive plasticity was observed for both the male's call and the female's responsiveness and selectivity (Fowler-Finn and Rodriguez 2012). Plasticity in mate selection determinates, such as the chirp of a cricket or the amount of plumage displayed by a bird, leaves the given determinate vulnerable to selective pressures (Simmons et al. 2001). It has been noted that distance enhances the likelihood of genetic changes that can lead to speciation (Noor and Feder 2006). Crickets provide a good model for speciation studies as they are abundant and have clear species-isolating signals that can be easily recorded and evaluated.

Burden (2009) studied variability in spectral and temporal features of the male's calling for two species of cricket, *Gryllus veletis* and *Gryllus pennsylvanicus*. Several factors influence the degree of variability in the calling song features, including temperature (Jang and Gerhardt 2006; Van Putten 2012), humidity, solar elevation, and season (Burden 2009). Furthermore, in a 2011 study of Polynesian crickets, researchers found that variation in the temporal structure of the mating calls correlates with geographical distance between each cricket. (Tinghitella et al. 2011). Change in body size is also correlated with latitudinal variation (Masaki 1967), yet there is little information on variations between populations of a species due to longitudinal differences.

While Kim (2007) found significant variation in calling song parameters for *G. pennsylvanicus* when studying how they change latitudinally, Magsipoc (2008) did not find

significant differences for *G. veletis*. Atkins et al. (2012) found significant variation in all of the spectral and temporal features of the calling song for both species with respect to changes in latitude. My research project assesses whether there are differences in spectral and/or temporal features of the male's calling song due to longitudinal differences for *G. pennsylvanicus*.

METHODOLOGY

Dr. Atkins recorded the calling songs of *G. pennsylvanicus* from six locations across the North American continent including Washington, Wyoming, South Dakota, and Ontario (Figure 1; Table 1) using a parabolic microphone and saved the recordings digitally as MP3 files. Twenty-five to thirty-five individual crickets were recorded at each location, which are approximately 500 miles apart. I evaluated the carrier frequency analysis using Fourier spectrum analysis. The purpose of the analysis was to determine whether or not the carrier frequency exhibited any variation with longitudinal changes. I evaluated the temporal features of the calling songs using the sound analysis software Raven Pro. I measured eleven consecutive chirps from each recording. From each chirp, I measured the number of syllables per chirp, the duration of each syllable, the syllable periods between syllables, the relative amplitude of each syllable, the chirp duration and period, and the carrier frequency. I then tabulated the measurements of the individual elements and averaged the information from ten chirps for each individual.

Burden (2009) investigated how environmental factors affected the variation in male calling song features. To do so, she used gamma regression because 1) regression allows one to study the effect of multiple independent factors on a dependent variable and 2) the gamma distribution limits the range of the dependent variable from $(0, \infty)$, which is the range expected for the calling song features. Burden (2009) used the general mathematical model:

$$\ln(E(Y)) = \beta_0 + \beta_1 S\# + \beta_2 \#S + \beta_3 \text{DAY} + \beta_4 \text{SOLAR} + \beta_5 \text{TEMP} + \beta_6 \text{HUMID} + \beta_7 \text{VEGHT}$$

where Y is the calling song feature, $S\#$ is the syllable placement within a chirp, $\#S$ is the number of syllables in the chirp, DAY is the day of the breeding season, SOLAR is the solar elevation in degrees, TEMP is the ambient temperature in degrees Celsius, HUMID is the

relative humidity, VEGHT is the vegetation height in inches, and the β s are parameters. She tested a suite of possible variable combinations in order to determine which variables most influenced each calling song feature. For *G. pennsylvanicus*, Burden (2009) found that four features of the calling song were significantly affected by certain environmental factors: the syllable duration of syllable 1, the syllable period of syllable 1, the chirp duration, and the chirp period (Figure 2). The syllable duration of syllable 1 was significantly affected by the number of syllables in the chirp and the ambient temperature; the syllable period of syllable 1 was significantly affected by the day of the breeding season, the solar elevation, the ambient temperature, and the vegetation height; the chirp duration was significantly affected by the day of the breeding season, the solar elevation, and ambient temperature; and the chirp period was significantly affected by the day of the breeding season, the solar elevation, the ambient temperature, and the vegetation height. Thus the best model for each of the calling song features includes only these variables and the corresponding parameter estimates. The first day of the breeding season was the 220th day of the year, or August 8. I then used the best model for each of the calling song features in order to see how well it can describe the variability in my data across geographic space.

To test how well each model explains my data, I calculated an R^2 value, which measures the goodness-of-fit of the model. R^2 is calculated by:

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2}$$

where y is the observed value for the calling song feature, \hat{y} is the predicted value produced by the model, and \bar{y} is the average of the observed values. I then compared the R^2 values for each of the locations to each other and to Burden's (2009) R^2 values. For ecological data, an R^2 value of 0.3 to 1 indicates that the model is a good predictor of the measured values. If the

calculated values are similar to Burden's (2009) values, it is likely that the longitudinal geographic variation does not affect the calling song. However, if the R^2 values decrease for progressively western populations, it is likely that longitudinal geographic variation does contribute to changes in the calling song.

RESULTS

The spectral analysis of the cricket recordings from the 6 populations showed variability, with both higher and lower frequencies, compared to Burden's (2009) base population (Figure 3). The locations with the greatest difference are Wanapum, WA with an average that is -0.0662 kHz different from the base population and Moorcroft, WY with an average that is 0.0995 kHz different from the base population. However, the variability measured between the populations was not significant (ANOVA; $p=0.370$).

The temporal analysis of the cricket recordings demonstrated variability among the populations for the 4 calling song features. After measuring the calling song features and comparing them to the predicted values from the model, the R^2 values imply that the model is a poor predictor. If the value is negative, it indicates that the average of the measured values is a better descriptor of the collected data than the RSS. For syllable length, the R^2 values ranged from 0.053 in Benton Center, MI to -4.206 in Wanapum, WA (Figure 4). For syllable period, the R^2 values ranged from 0.108 in Belleville, Ontario to -6.893 in Wanapum, WA (Figure 5). For chirp length, the R^2 values ranged from -37.67 in Benton Center, MI to -108.6 in Wanapum, WA (Figure 6). For chirp period, the R^2 values ranged from -6.666 in Naomi, MI to -60.43 in Belleville, Ontario (Figure 7). Compared to the R^2 values that Burden (2009) calculated, which are considered ecologically good, these results are not good ecological R^2 values (Table 2).

DISCUSSION

The research question of whether longitudinal change affects the calling song of the cricket *G. pennsylvanicus* cannot be answered based on the results. The negative R^2 values indicate that Burden's (2009) mathematical model does not port well over time or distance. The validation procedure used in Burden's (2009) project denotes that the mathematical model is useful for a specific place at a specific time: Benton Center, MI between the years 2006 to 2007. However, the model does not accurately provide predicted values for each of the calling song features at other locations or even for the site of parameterization 5 years after the model was parameterized.

The further east and west from the site of parameterization, the greater the decline in R^2 values for syllable length (Figure 4) and chirp length (Figure 6). However, this variation cannot be attributed to changes in longitude because the model is not predictive at Benton Center, MI. Since the model is not predictive at the site of parameterization, conclusions about the other sites cannot be drawn. The failure to validate the model outside of a certain time and place renders any conclusions drawn about the populations in this study erroneous. Thus, because the model cannot accurately predict at the site where it was created, it cannot be used to truthfully explain the variation that may occur between the populations.

While the initial research question cannot be answered at the moment, it does point out other significant discoveries and raises questions to be addressed. The study indicates that the current mathematical model is not portable across locations and year. It may be necessary to re-parameterize the model at each site and year. Lastly, a larger, more comprehensive study must be done that 1) includes more populations, 2) spans a longer period of time (i.e. 5 or 10 years), and 3) takes into account other conditions such as the harshness of the winter, precipitation

conditions, and other factors outside of the breeding season that may affect the crickets. By accounting for the conditions outside of the breeding season of the cricket, it may help explain anomalies that occur as well as provide insight to how these factors may contribute to the variation of the calling songs. This more comprehensive model may also compensate for any variation that occurs naturally within populations over a period of time. As a result, the model would be able to measure the effect of longitudinal change on calling song variation by incorporating the variable LONG into the model and the research question can be answered.

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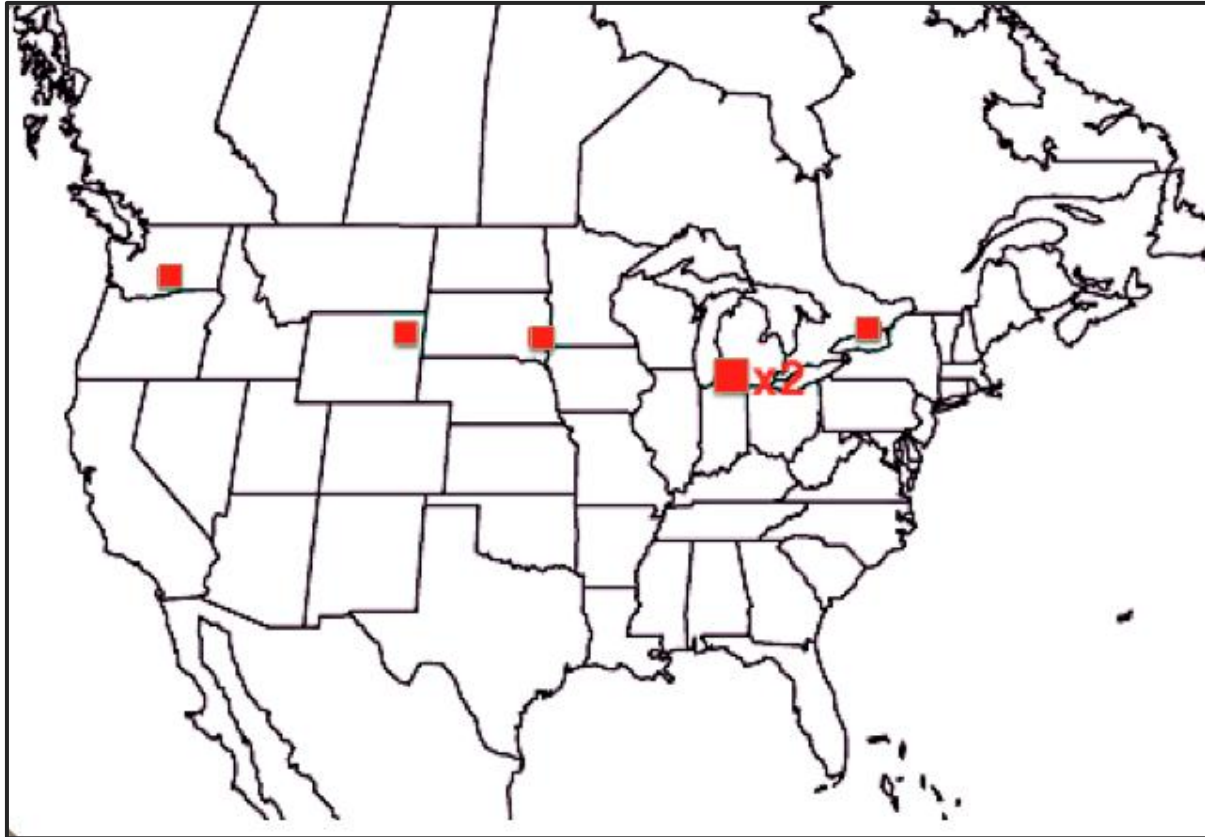


Figure 1 – The 6 sites where recordings were made for analysis. From west to east, they are Wanapum, Washington; Moorcroft, Wyoming; Sioux Falls, South Dakota; Benton Center, Michigan; Naomi, Michigan; and Belleville, Ontario.

Table 1 – The specific cities and coordinates of the locations where the recordings were made are listed below.

LOCATION	COORDINATES
Wanapum, Washington	46.901341 °N 119.991576 °W
Moorcroft, Wyoming	44.264447 °N 104.959196 °W
Sioux Falls, South Dakota	43.611213 °N 96.892117 °W
Benton Center, Michigan	42.151833 °N 86.382713 °W
Naomi, Michigan	42.045603 °N 86.280977 °W
Belleville, Ontario	44.198741 °N 77.387898 °W

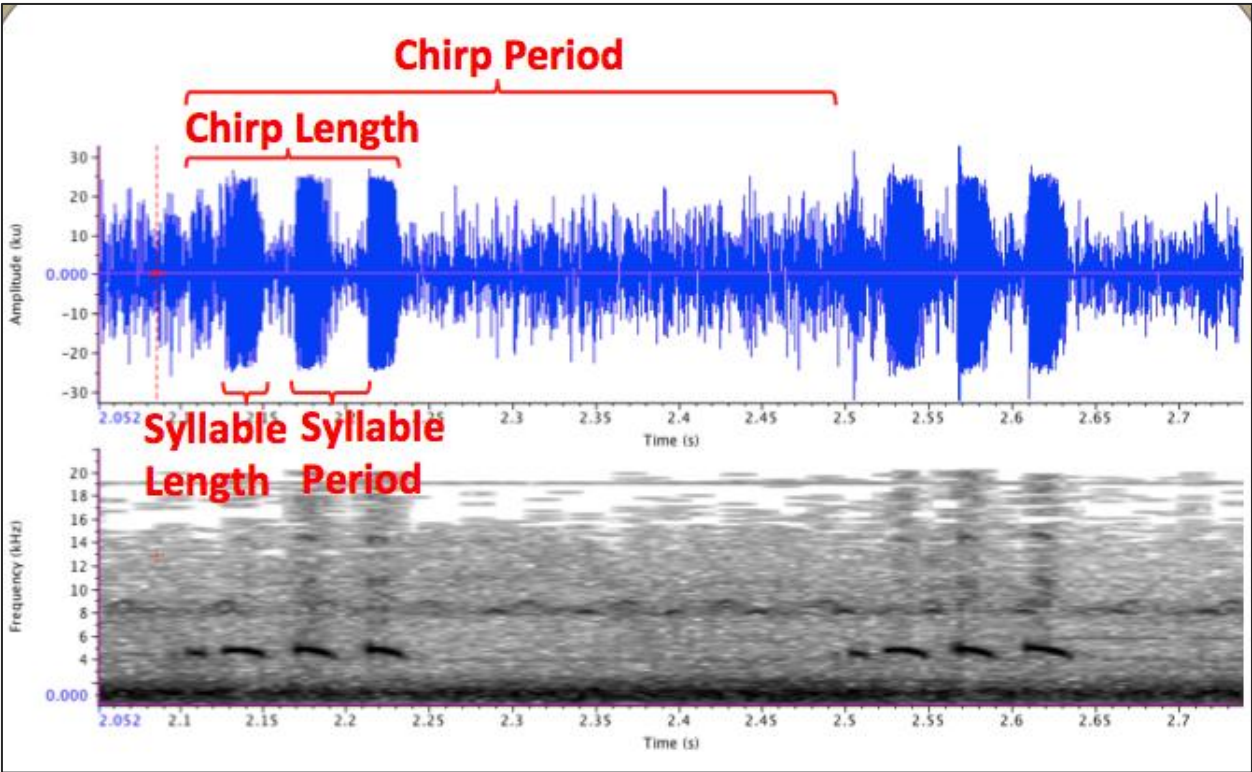


Figure 2 – The 4 calling song features that were analyzed are syllable length, syllable period, chirp length, and chirp period. The term period, such as in syllable period, refers to the amount of time it takes from the beginning of one syllable to the beginning of the next syllable.

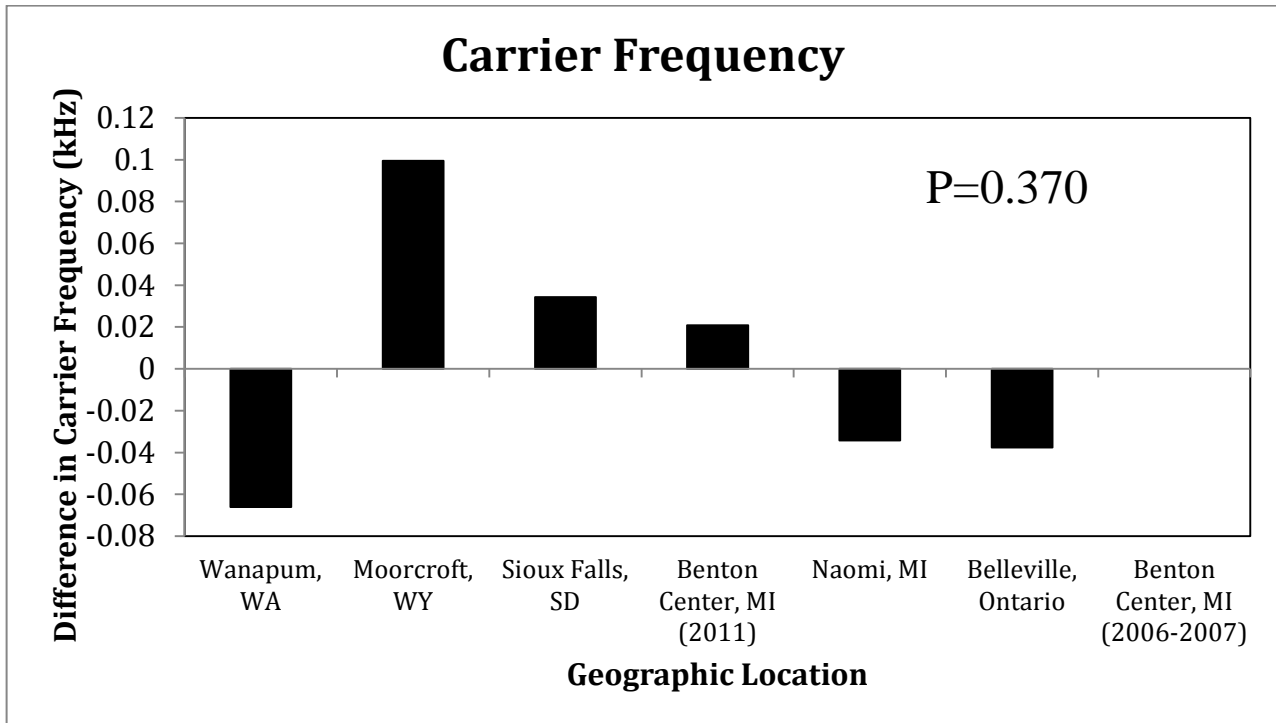


Figure 3 – This graph demonstrates the variability that occurs between the populations in reference to the fundamental carrier frequency. It is the difference between the average carrier frequency for each population compared to the base population from Burden’s (2009) study. While some variability of the fundamental carrier frequency exists, the p value indicates that the difference is not significant.

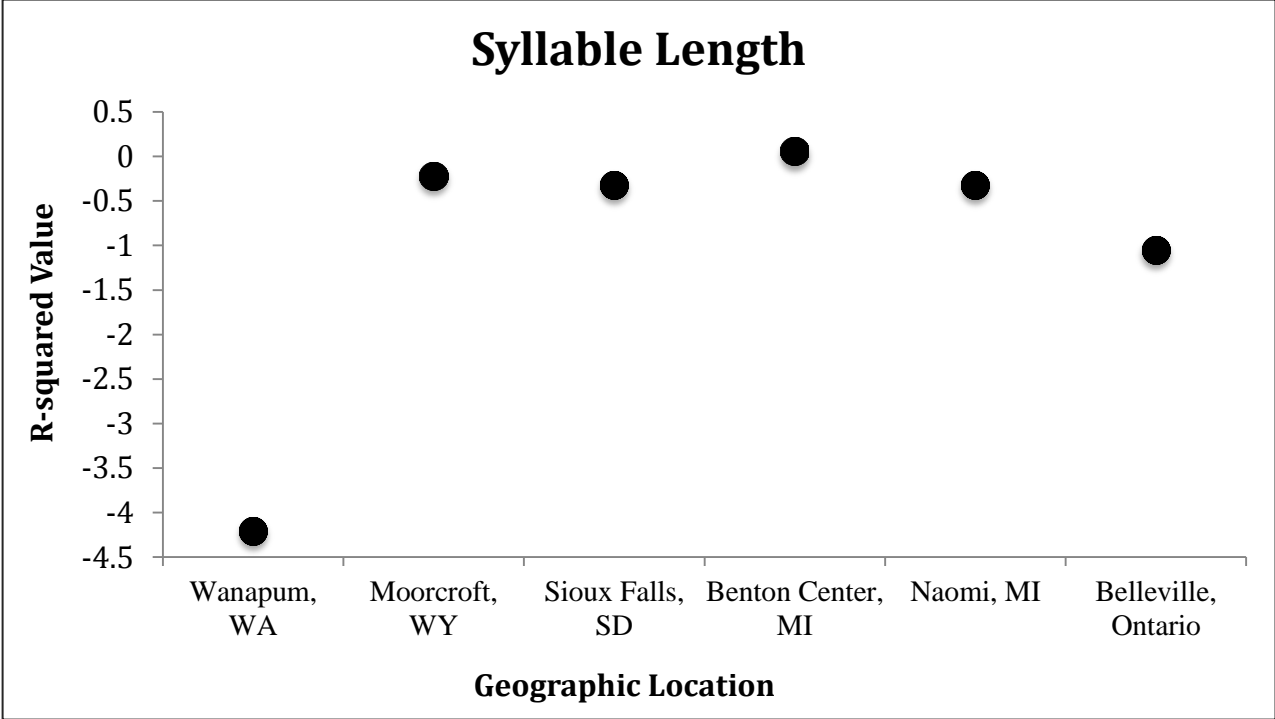


Figure 4 – This graph shows the R^2 values calculated for the syllable length. The values were found using Burden’s (2009) mathematical model and comparing the predicted values from the model with the actual values from the recorded data. Burden’s (2009) R^2 value for this feature was 0.39. The R^2 values indicate that the mathematical model is a poor predictor.

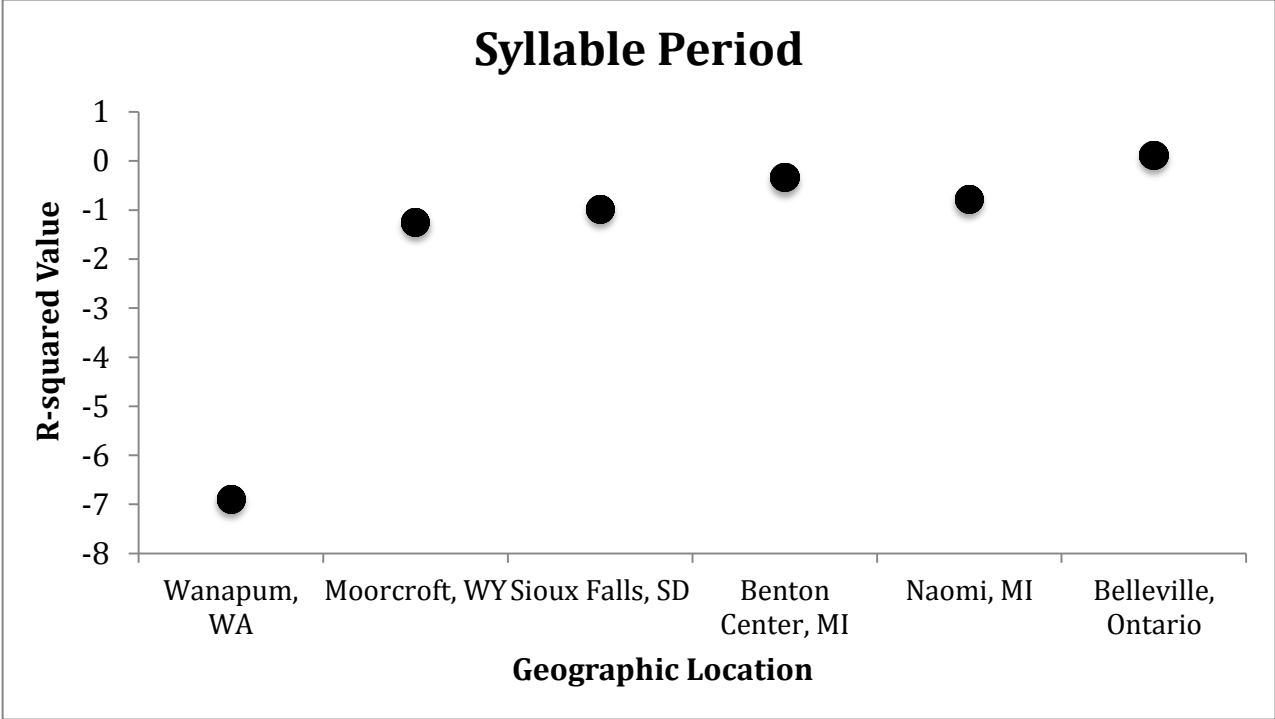


Figure 5 – This graph shows the R^2 values calculated for the syllable period. The values were found using Burden’s (2009) mathematical model and comparing the predicted values from the model with the actual values from the recorded data. Burden’s (2009) R^2 value for this feature was 0.569. The R^2 values indicate that the mathematical model is a poor predictor.

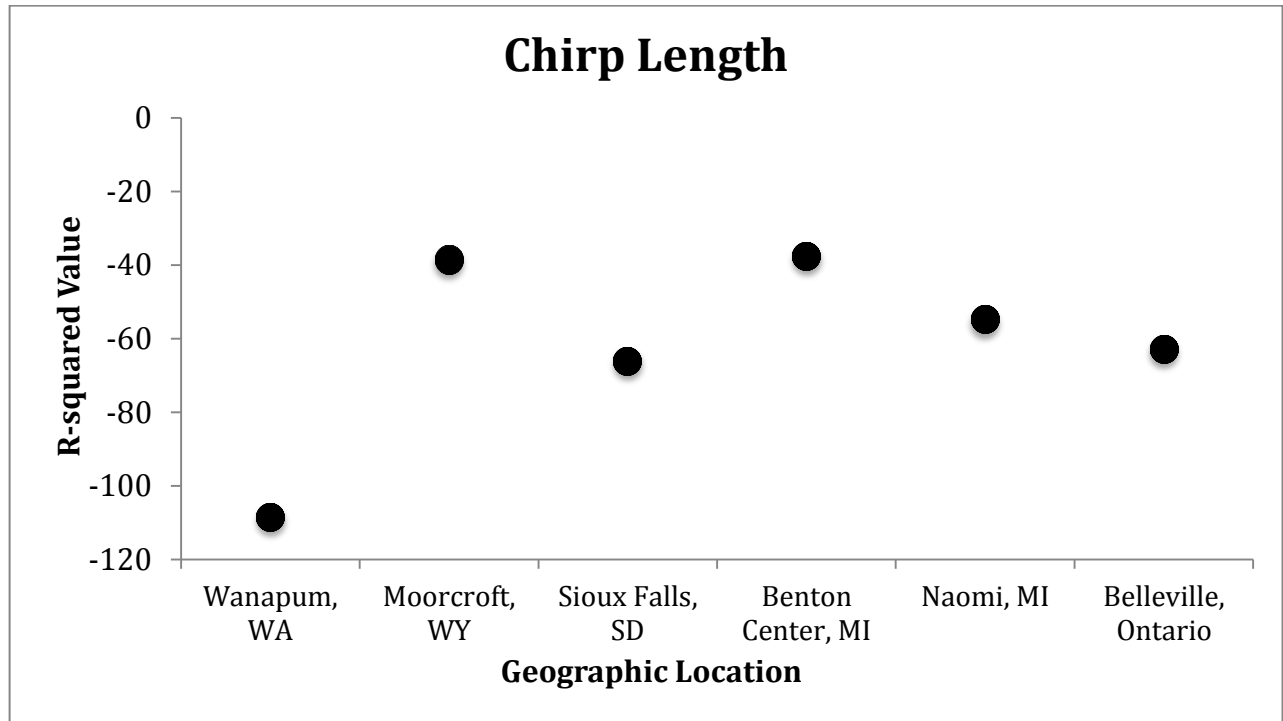


Figure 6 – This graph shows the R^2 values calculated for the chirp length. The values were found using Burden’s (2009) mathematical model and comparing the predicted values from the model with the actual values from the recorded data. Burden’s (2009) R^2 value for this feature was 0.614. The R^2 values indicate that the mathematical model is a poor predictor.

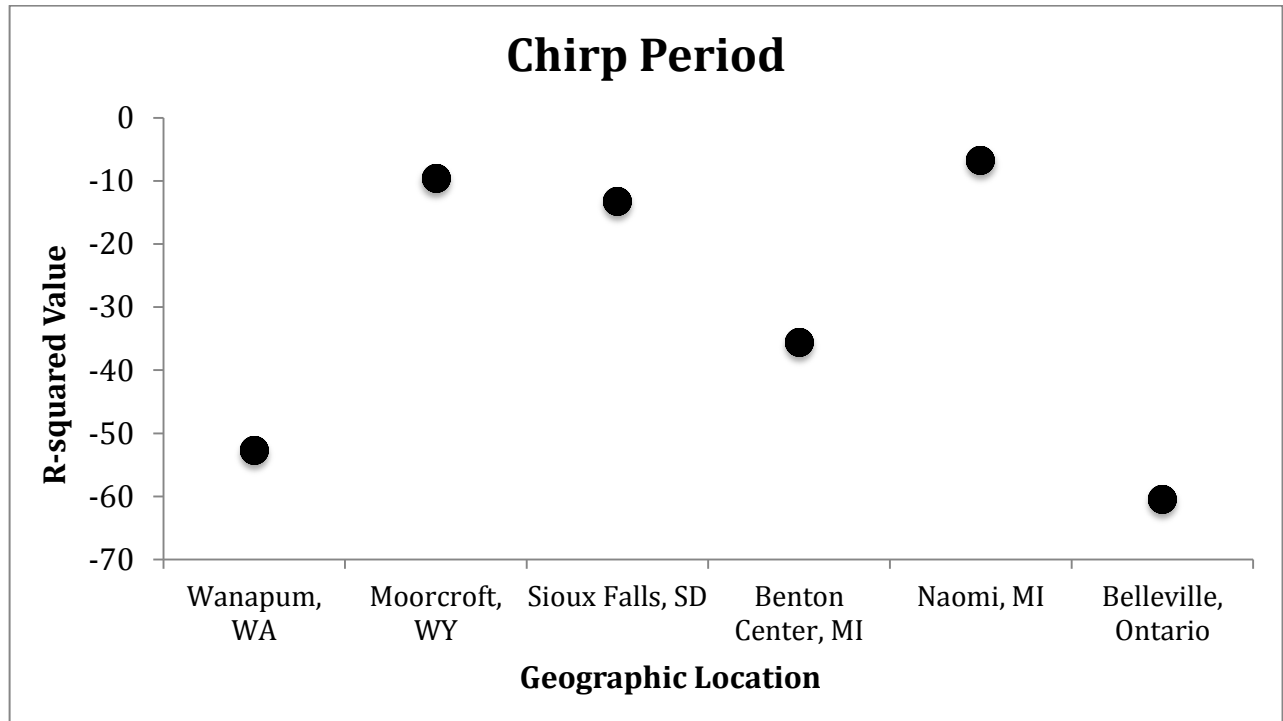


Figure 7 – This graph shows the R^2 values calculated for the chirp period. The values were found using Burden’s (2009) mathematical model and comparing the predicted values from the model with the actual values from the recorded data. Burden’s (2009) R^2 value for this feature was 0.607. The R^2 values indicate that the mathematical model is a poor predictor.

Table 2 – This table shows my R^2 values compared to Burden’s (2009) R^2 values. These are the 4 calling song features for *G. pennsylvanicus* that are significantly affected by environmental factors. By using the mathematical model, the effect of the environmental factors was accounted for and the predicted values were calculated. The R^2 values indicate how well the model predicts the actual values measured from the recordings.

	Syllable Length	Syllable Period	Chirp Length	Chirp Period
Benton Center, MI (2006-2007)	0.390	0.569	0.614	0.607
Wanapum, WA	-4.206	-6.893	-108.6	-52.72
Moorcroft, WY	-0.221	-1.255	-38.61	-9.560
Sioux Falls, SD	-0.323	-0.977	-66.10	-13.19
Benton Center, MI (2011)	0.053	-0.338	-37.67	-35.53
Naomi, MI	-0.324	-0.781	-54.87	-6.666
Belleville, Ontario	-1.057	0.108	-62.91	-60.43