

**Comparative approaches to estimating repertoires and American Robin
individuality**

Kathleen Peshek
Advanced Undergraduate Research
August 2009

Mentor: Dr. Daniel T. Blumstein

Abstract

Song repertoire size is the range of distinct syllables, phrases, and song types created by an individual or population. Variations within songs create complex repertoires, making them difficult to estimate. There are several methods to estimate repertoire size, however prior studies discovered that all but a full numerical count of song types might have substantial inaccuracies associated with them. We evaluated a new method to estimate repertoire size—rarefaction. Ecologists use rarefaction to measure species diversity on individual and population levels. Using the repertoires of American Robins (*Turdus migratorius*), we compared the common techniques of estimating repertoires to the results of a rarefaction analysis. We found that the rarefaction technique was the best alternative to a full numerical count of song types, which is the most accurate method. American robins have elaborate and unique songs with few syllables shared between individuals. This is important because it can further the understanding of robin communication. Especially in their formation of songs, such as a large repertoire suggests that robins invent their songs. Individuality of robin songs can help with the understanding evolution of complex songs because females choose males with complex songs.

Key words:

repertoire, individuality, rarefaction, behavioral accumulation curve, capture-recapture, numerical count, and syllables

Introduction

Avian communication is widely diverse amid the 4000 songbird species (Brenowitz 1997). Bird's songs vary in acoustics, composition, and repertoire size—the number of different notes, syllables, phrases, or songs produced (Williams 2004).

Repertoires differ between species and individuals (Catchpole and Slater 2008). For example, thrushes that are recognizable for their elaborate and various songs may have a repertoire of 200 different song types, while others have a single song type (Ince and Slater 1985; Brumm et al. 2009; Catchpole and Slater 2008).

Components of avian repertoires include notes, syllables, phrases, and how they are assembled into songs (Brenowitz et al. 1997). Brenowitz et al. define a note as a single sound, while syllables are a sequence of notes. At least one syllable generates a phrase and certain phrase arrangements repeat to establish song types (Brenowitz et al. 1997). Repertoire complexity relates to these components and their repetition or order (Williams 2004).

Documenting this acoustic diversity within individuals and a species is a challenge (Krebs and Kroodsma 1980; Kroodsma 1982; Catchpole and Slater 2008). Several methods have been used, and each has its set of assumptions. The comparison of these assumptions is in Table 1. For instance, the most common is to graph the number of songs recorded versus the number of song types (Wildenthal 1965; Catchpole and Slater 2008). When the curve reaches an asymptote, the maximum repertoire size has been discovered. One method for estimating repertoire sizes is a numerical count of the syllables within a song. Small repertoires are preferable for the numerical count method because it becomes difficult and impractical to directly count the syllables in larger repertoires (Kroodsma & Parker 1977; Botero et al. 2008). An ecological approach, using a capture-recapture technique, can also estimate repertoires by randomly choosing a sample of recorded songs and then "recapturing" some of those songs in succeeding samples (e.g. Garamszegi et al. 2002, 2005; Catchpole and Slater 2008). This approach assumes that repertoire sizes are fixed (Botero et al. 2008) and

that the recordings are long enough to estimate the repertoire size (Table 1). The last common technique is to use a behavioral accumulation curve equation (Dias et al. 2009). Similar to the other techniques this method assumes that the repertoire is a fixed length; other assumptions appear in Table 1. The above techniques are not perfect; they may over- and under-estimate the true repertoire size (Catchpole and Slater 2008). Prior research discovered that estimates using models produced incorrect results when compared to comprehensive numerical counts (Botero et al. 2008).

We propose a new approach that uses rarefaction techniques (Gotelli and Colwell 2001; Coddington et al. 2002; James and Wamer 1982) to estimate repertoire sizes. Rarefaction is a technique for sampling distributions within certain categories, such as individuals in a population or species in a community (James and Wamer 1982). This method is typically used for studying species diversity to estimate the predicted number of species from a sample of individuals (James and Wamer 1982). A rarefaction curve begins with a steep slope and then becomes asymptotic as fewer new species are added in each successive sample (Gotelli and Colwell 2001). Rarefaction analyses standardize the sample size, allowing accurate species richness comparisons to be made (James and Wamer 1982).

To use rarefaction to estimate song diversity, we will treat the syllables within a song as species, and the number of recorded individuals as samples. Rarefaction, like other methods, has a set of assumptions. These include; the sample size is standardized across samples, long enough recordings were made to accurately portray the repertoire size, and that the results fit the sample size but cannot be extended to larger sample sizes (Gotelli and Entsminger 2009). Assumptions for this method besides that the sample size is standardized are shared with the common techniques in

estimating repertoire sizes (Table 1). Rarefaction repertoire analysis can accurately portray the repertoire size of both individuals and populations, while using a smaller sample of recordings.

After evaluating this rarefaction technique to estimate the repertoire size of the American Robin (*Turdus migratorius*) by comparing the results of rarefaction to other techniques, we then wish to study vocal individuality. Robins are the most common thrush in North America (Sallabanks and James 1999) and thrushes are notable for their elaborate songs (Ince and Slater 1985; Brumm et al. 2009). Prior studies on song elements discovered that individual robins have at least 12 phrases that differ within an individual's repertoire (Borror 1965; Thomas 1979). However, prior studies did not find an upper limit for the species.

This large repertoire is somewhat remarkable since robins are not vocal mimics, which are known to have large repertoires because they learn songs from other species throughout their lives (Williams 2004). Therefore diverse robin repertoires may result from two reasons: robins are one of the few species that invent their songs; or that juveniles learn their songs prior to moving away from their parents (Konishi 1965; Johnson 2006), to enhance the population's diversity of their new habitat. Importantly, robins may have a large repertoire to communicate individuality if each robin has a unique repertoire. To understand this, we must quantify the percent of syllables shared, and the spatial distribution of syllable sharing. An individual with distinguishable songs may have a higher fitness if distinct songs more efficiently attract mates and help them defend their territory. Therefore to better understand the communication of American Robins it is necessary to study their repertoires and how they vary among individuals.

Methods

To compare the techniques for estimating repertoires, from May 30 until June 11, we recorded the dawn and/or dusk songs of 38 American Robins in and around the Rocky Mountain Biological Laboratory (RMBL—38° 57 46 N 106° 59 34 W). A single observer walked around recording the robins and the GPS locations of each singing robin. A GEO XT was used to map the locations of the singing birds and to record the metadata attributes of each location. We aimed to record a set of individuals on two separate occasions by returning to the same location and recording the territorial resident. Song was recorded using a Sennheiser ME67 directional microphone with a K6 power module, a Rycote windscreen, and onto a Marantz Professional Solid State Recorder PMD660. We did not record songs during rainy or windy conditions because such environmental noise reduced the quality of recordings.

Once the songs were recorded we analyzed them with Raven Pro 1.3 (Krein et al. 2003-2007, www.birds.cornell.edu/raven). The songs were viewed in a standardized window of 0-5.5 kHz and 0-0.8 seconds, while using Raven Pro 1.3. We used the 100-contrast level and two different brightness levels (70 and 75). Two syllable keys were made that matched these brightness levels to help score syllables (Appendixes 1 and 2 in pdf at RMBL website). We identified each syllable in every recording that was > 1 min.

With the set of syllables sung by each bird, we used four different methods to estimate an individual's and the population's syllable repertoire size.

First, we counted the syllables and calculated an average repertoire size. However, this method was biased because we didn't have that same number of syllables recorded for each bird. The 95% confidence interval for the individuals' repertoire of all

three data sets was calculated with SPSS 17 (SPSS Inc. 2009, Chicago, Illinois, www.spss.com).

Second, we used capture-recapture techniques to estimate the repertoire size by randomly selecting a set of syllables from all observed syllables 11 independent times. The first selection was the set of syllables that were "captured and marked"; the remaining 10 selections were the "recaptures". We applied the capture-recapture formula,

$$N(t) = N*(N/n)$$

where N is the sample size and n is the number off recaptured individuals (Catchpole and Slater 2008). This capture-recapture procedure was repeated three times with data sets containing accumulations of 50-, 100-, and 150- syllables from each individual. Therefore the data sets consisted of 800, 1400, and 750 accumulated syllables from which we randomly chose 50-, 100-, and 150- syllables. Once we had calculated the ten repertoire estimations for the population, we calculated an individual's repertoire. To accomplish this we divided the population results by the number of individuals within the data set, repeating this for all data sets. To compare these results with the other methods we averaged the ten estimations, for the individual and population estimates of every data set. We used SPSS 17 to calculate the 95% confidence intervals of the above results.

Third, we used a behavioral accumulation curve (Dias et al. 2009) to calculate the robin repertoire size. The counts of the first 50-, 100-, 150- syllables sung were placed in the behavioral accumulation curve,

$$P_{Sobs} = T_{Sobs} / (a/b)$$

Where, P_{Sobs} is the portion of observed behaviors, T_{Sobs} is the total number of observed behaviors, a is the intercept, and b is the slope (Dias et al. 2009). A quadratic equation best explained the accumulation of robin syllables in previous studies (Dziadosz 1977), and in our study; thus, we estimated these parameters from a quadratic formula. We then averaged the results from the above calculations for the 50-, 100-, and 150-syllables and calculated a 95% confidence interval with SPSS 17.

Fourth, we used EcoSim 7.72 (Gotelli and Entsminger 2009) to apply rarefaction methods for data sets that contained 50-, 100-, and 150-syllables from individuals. For each data set we created a table containing individuals and the syllables they sang. Each row in the table contained one syllable. We then entered the times an individual sang that syllable in the corresponding cell. Once this table was completed we transferred the data into EcoSim 7.72 (Gotelli and Entsminger 2009) by creating a matrix with 220 rows and 16-, 14-, and 5- columns (one for each robin in the data set). Using the species diversity function we then calculated the richness within the data sets. Using a computer simulation in EcoSim. However, without computer simulation this rarefaction formula must be used,

$$E(S_n) = S - \left(\frac{N}{n}\right)^{-1} \sum_{i=1}^S \left(\frac{N - N_i}{n}\right)$$

where $E(S_n)$ is the estimated species number, N is the total number of individuals within a sample, n is a sub-sample of randomly selected individuals, and S is the number of species (Heck et al. 1975; James and Wamer 1982). In the species diversity window of EcoSim we used the all the default settings, besides sampling the whole sample (data set) and allowing the program to use a rarefaction algorithm.

To study American Robin song individuality, we counted the number of syllables used by each bird, the percentage of shared syllables within the sample sizes of 50-,

100-, and 150- syllables, the distribution of shared syllables in each data set, and the percent of shared syllables within each data sets' population. We calculated the percentage of shared syllables for each individual by dividing a robin's amount of shared syllables by its total syllable count, and multiplying by 100. This calculation was made for each robin in every sample of an individual's first 50-, 100-, 150- syllables sung. For each data set we calculated the distribution of shared syllables by counting the syllables that were used at each percentage. We then calculated the percentage shared within the population by calculating the total count that each syllable was used within the population. That result was then divided by the total number of individuals in the population and multiplied by 100. This was performed for the 50-, 100-, and 150-syllable data sets and for every shared syllable. We then plotted the frequency of syllable sharing for the entire population to identify the most frequently shared syllables. To calculate the percentage of shared syllables within each data set, we counted the total number shared syllables and every syllable sung for each data set. We then divided the total number of shared syllables by the number of all syllables sung and multiplied by 100.

Results

Repertoire size

Of the 38-recorded individuals, nine were recorded for at least 5 minutes and another 14 for at least three minutes on separate occasions; the remainders were recorded < 1 min. Using the set of recordings > 1 min, we identified 220 distinct syllables (see Appendixes 1 and 2 in pdf at RMBL website). A comparison of the results of using different techniques for repertoire size estimation is summarized in table 2.

When we counted the first 50 syllables per individual, we estimated the average robin repertoire to be 10.79 syllables (95% CI: 7-14 syllables). The 100-syllable sample estimated the robin repertoire to be 12.86 syllables (95% CI: 9-16 syllables). The 150-syllable sample estimated the robin repertoire to be 16 syllables (95% CI: 11-21 syllables). The population repertoires for the numerical count technique do not have confidence levels. A population's average repertoire size is 166, 180, and 78 corresponding to the 50, 100, and 150 syllable samples.

Capture-recapture generated similar individual repertoire size estimates as the direct count when we used the data sets consisting of 50 (8.5 syllables, 95% CI: 7-14 syllables) and 100 syllables (15.69 syllables, 95% CI: 14-17 syllables). When we used 150 syllables, we estimated that each robin sang 45.98 syllables, (95% CI: 12-49 syllables). The population estimate for the 50-syllable sample was lower (136.04, 95%, 118-154 syllables) than that calculated from the direct count, while the results from 100-syllable (219.6 syllables, 95% CI: 202-237 syllables) and 150-syllable (229.9, 95% CI: 221-246 syllables) data sets were larger. This is the only analysis that did not count the accumulated notes, which allowed us to have confidence intervals in our results.

The behavioral accumulation analysis also estimated larger repertoires than those seen in the count analyses. The 50-syllable accumulation analysis estimated 20.03 syllables per individual (95% CI: 3-37 syllables), the 100-syllable analysis estimated 19.3 syllables (95% CI: 9-30 syllables), and the 150-sample analysis estimated 101.73 syllables (95% CI: 72-132). The results for the behavioral accumulation curve do not overlap the other confidence intervals for the 150-syllable estimates. Instead the behavioral accumulation estimates for an individual's repertoire are very large, ranging

from 72 to 132. The population repertoire estimates are 389.1, 339.8, and 508.6 syllables, respectively.

The 95% confidence levels overlap for the count and rarefaction techniques, although these intervals are larger for the rarefaction analysis. Rarefaction analysis estimated an average individual repertoire of 14.69 syllables (95% CI: 2-25) for the 50-syllable accumulated data set, 17.64 syllables (95% CI: 8-25) for the 100-syllable analysis, and 18.73 syllables (95% CI: 14-24) for the 150-syllable analysis. The population repertoire estimates for this technique were 166, 180, and 78.

Individuality

Most syllables were unique (Fig. 1). 20.33% of the syllables were shared in the 50-syllable data set (N = 246 syllables), 16% were shared in the 100-syllable data set (N = 250 syllables), and 11.96% were shared in the 150-syllable data set (N = 92 syllables). The distribution of shared syllables ranged from 12.5-43.75% in the 50-syllable data set (Fig.2), 14.9-50% in the 100-syllable data set (Fig. 3), and 40-80% in the 150-syllable data set (Fig. 4). The most commonly shared syllables for the 50 and 100 syllable data sets were syllables 44, 66, 64, 65, and 91 (Fig. 5), while syllables 64 and 65 were the most common within the 150-data set (Fig. 6).

Discussion

Methods for estimating repertoire sizes are imperfect; a full numerical count is the best method (Botero et al. 2008). However, for large repertoires, a full count may be impractical since the amount of effort is substantial.

The capture-recapture method is accurate in estimating repertoires for large sample sizes because the 95% confidence levels included those of the numerical count for the 50 and 100 syllable data sets. This technique's 100-syllable data set had a small

confidence interval, suggesting that this method may best predict the repertoires of mid-range sample sizes. However it is still a reliable method for large sample sizes.

Individual analysis of the 150-syllable data set's average was higher than the numerical method but had a confidence level that included the numerical count's interval. This method did not significantly differ from the numerical count approach but the 150-syllable data set had a very large confidence interval, indicating that this method may over estimate the repertoire size for small samples.

The behavioral accumulation curve method's individual repertoire analysis did not differ significantly from those of the numerical count and capture-recapture methods, for the 50-and 100-syllable data sets because its confidence intervals contained the intervals from the other methods. The behavioral accumulation curve method's individual repertoire analysis of the 150-syllable data set over-estimated the repertoire size. This over-estimation consists of a large confidence interval that excludes the confidence intervals of all the other methods, illustrating the inaccuracy of behavioral accumulation curves with small sample sizes. The overestimation of this method can be attributed to the assumption that syllables appear randomly within a repertoire (Botero et al. 2008), which we know to be false. Due to this over-estimation the behavioral accumulation method is most appropriate for large sample sizes.

The rarefaction confidence levels, for each individual repertoire analysis, were similar in size to those of the numerical count's, suggesting that rarefaction is accurate for all sample sizes and indicating it is the best alternative to the numerical count method. Rarefaction decreases the effort through using shorter recordings of songs. This will allow researchers to increase the sample size of individuals, for the same effort level. The variation among recorded individuals may also increase since researchers can

spend more time traveling to different habitats than using the previous techniques that required long recording samples. Increasing efficiency will also allow researchers to perform more experiments or study more aspects concerning animal communication and behavior.

Having a more accurate method for estimating avian communication repertoire size is important because prior studies using other techniques could have over- or under-estimated the repertoire size of songbirds, usually concerning small sample sizes. This is potentially problematic because research on the complexity of songs and their evolution involves repertoire analysis can create problems (Botero et al. 2008).

Repertoire rarefaction analysis can apply to any animal behavior, for example on avian communication or the social interactions in primates. Future studies should include testing the method on other animal behaviors and using larger variety of sample sizes.

American Robins have unique repertoires in which very few syllables are shared. These large distinct repertoires could be the result of sexual selection for longer repertoires (Byers and Kroodsma 2008) because females usually choose mates based on their complex songs. Through this selection for song complexity females also create natural selection for inventing songs, which would create distinct and complex songs (Konishi 1965; Johnson 2006). This connection means that further research should include experiments to test robin repertoires for invention of syllables to increase repertoire length.

Future research on robin individuality could also study how the songs of juveniles vary from their parents. This will provide insights into how robins learn songs, and

whether similar to, South American fur seals (Phillips and Stirling 2000) they are used in parent-offspring identification.

Literature Cited

- Borror, D. J. 1965. Birdsong: the anatomy of a miracle. *Audubon* 67, 159-163.
- Botero, C. A., Mudge, A. E., Koltz, A. M., Hochach, W. M., & Vehrencamp, S. L. 2008. How reliable are methods for estimating repertoire size? *Ethology* 114, 1227-1238.
- Brenowitz, E. A., Margoliash, D., & Nordeen, K. W. 1997. An introduction to Birdsong and the avian song system. *Journal of neurobiology*. 33, 495-500.
- Brenowitz, E. A. 1997. Comparative Approaches to the Avian Song System. *Journal of neurobiology*. 33, 517-531.
- Brumm, H., Lachlan, R. F., Reibel, K., & Slatet, P.J.B. 2009. On the function of song repertoires: testing the 'antiexhaustion hypothesis' in chaffinches. *Animal Behaviour* 77, 37-42.
- Byers, B.E. & Kroodsma, D.E. 2008. Female mate choice and songbird song repertoires. *Animal Behavior*. 77, 13-22.
- Catchpole, C. K. & Slater, P. J. B. 2008. Bird Song. *Biological Themes and Variations*, 2nd edn. Cambridge: Cambridge University Press.
- Dias, P. A. D., Rangel-Negrín, A., Coyohua-Fuentes, A., & Canales-Espinosa, D. 2009. Behaviour accumulation curves: a method to study the completeness of behavioural repertoires. *Animal Behaviour* 77, 1551-1553.
- Dziadosz, V. 1977. The vocalizations of the American Robin. Doctorate Dissertation, Ohio State University, Columbus, Ohio.
- Gotelli, N. J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology* 4, 379-391.
- Gotelli, N.J. & G.L. Entsminger. 2009. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465.
<http://garyentsminger.com/ecosim.htm>.
- Garamszegi, L. Z., Boulinier, T., Moller, A. P., et al. 2002. The estimation of size and composition of avian song repertoires. *Animal Behaviour*, 63, 623-30
- Garamszegi, L. Z., Balsby, T. J. S., Bell, B. D., et al. 2005. Estimating the complexity of bird song by using the capture-recapture approaches from community ecology. *Behav. Ecol. Sociobiol.*, 57, 305-17.
- Ince, S. A. & Slater, P. J. B. 1985. Versatility and continuity in the songs of thrushes *Turdus* spp. *Ibis*, 127, 355-364.

- James, F.C. & Wamer, N.O. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63, 159-171
- Johnson, Steven L., 2006. Do American Robins acquire songs by both imitating and inventing?. *The Wilson Journal of Ornithology* 118, 341-352.
- Krebs, J. R. & Kroodsma, D. E. 1980. Repertoires and geographical variation in bird song. *Adv. Study Behav.*, 11, 143-77.
- Krein, T., Hawthorne, D., Hu, D., Strickman, L., and Nelson, S. 2009. Raven Pro sound software. Bioacoustics Research Program, Cornell Lab of Ornithology.
www.birds.cornell.edu/raven
- Kroodsma, D. E. & Parker, L. D. 1977: Vocal virtuosity in the brown thrasher. *Auk* 94, 783—785.
- Kroodsma, D. E. 1982. Song repertoires: Problems in their definition and use. In: *Acoustic Communication In Birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 125-46. New York: Academic Press.
- Konishi, M. 1965. Effects of deafening on song development in American Robins and Black-headed Grosbeaks. *Zeitschrift für Tierpsychologie* 22, 584 –599.
- Longeno, J.T., Coddington, J., and Colwell, R.K. 2002. The ant fauna of tropical rain forest: estimating species richness three different ways. *Ecology* 83, 689-702.
- Phillips, A.V. & Stirling, I. 2000. Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science*. 16, 592-616.
- Sallabanks, R. & James, F. C. 1999. American Robin (*Turdus migratorius*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online:
<http://bna.birds.cornell.edu/bna/species/46> doi:10.2173/bna.462.
- Thomas, D. K. 1979. An analysis of the morning song of the American Robin (*Turdus migratorius*) throughout the breeding season. M.Sc. thesis, Bloomsburg State College, Bloomsburg, Pennsylvania.
- Wildenthal, J. L. 1965. Structure in primary song of the mockingbird (*Mimus polyglottos*). *Auk*, 82, 161-89.
- Williams, H. 2004. Birdsong and Singing Behavior. *Annals of the New York Academy of Science*. 1016, 1-30.

Table 1: Assumptions of each repertoire analysis method.

Method	Assumptions
Count	The repertoire has a explicit size With suffiecient effort it is possible to fully enumerate an individuals repertiore(Botero et al. 2008)
Capture-recapture	The repertoire has a explicit size (Botero et al. 2008) We recorded enough to accurately estimate the large repertoire size
Behavioral Accumulation	The repertoire has a explicit size (Botero et al. 2008) We recorded enough to accurately portray the large repertoire size The songs and syllables are random within a repertoire (Botero et al. 2008)
Rarefaction	The repertoire has a explicit size We recorded enough to accurately portray the large repertoire size (Gotelli and Entsminger 2009) The songs and syllables are random within a repertoire (Gotelli and Entsminger 2009) The sample size is standardized (Gotelli and Entsminger 2009) Syllables are camparable and from the same species (Gotelli and Entsminger 2009)

Table 2: Summary of each repertoire estimation method's results for the 50-, 100-, and 150-syllable data sets. For the population methods only the capture-recapture method had a confidence interval because it was not a count of the accumulated syllables but an average between several tests.

	N individuals	Avg N syllables	Median N syllables	Variance	95% Confidence Low	95% Confidence High
50 individuals						
Count	16	10.79	11	35.72	7.33	14.23
Capture-Recapture	16	8.502484813	7.81	2.36	7.4	9.6
Behavioral Accumulation	16	20.03	19.7	183.8	3.19	36.86
Rarefaction	16	14.691	15	29.21674	2	25
100 individuals						
Count	14	12.85714286	13	38.9010989	9.26	16.46
Capture-Recapture	14	15.68565271	15.53	2.96	14.45	16.92
Behavioral Accumulation	14	19.3	17.67	72.4	8.73	29.87
Rarefaction	14	17.635	17	30.06984	8	25
150 individuals						
Count	5	16	18	17.5	10.81	21.19
Capture-Recapture	5	46.68	46.64	39.1535282	11.81	49.13
Behavioral Accumulation	5	101.73	105	589.9	71.6	131.9
Rarefaction	5	18.365	19	16.31809	14	24
50 Population						
Count		166	166	0		
Capture-Recapture		136.039757	125	505.519245	118.44	153.64
Behavioral Accumulation		389.1000979				
Rarefaction		166	166	0		
100 Population						
Count		180	180	0		
Capture-Recapture		219.599138	217.391304	475.269801	202.37	236.83
Behavioral Accumulation		339.8179146				
Rarefaction		180	180	0		
150 Population						
Count		78	78			
Capture-Recapture		229.897516	229.591837	195.767641	221.19	245.67
Behavioral Accumulation		508.64		0		
Rarefaction		78	78			

Figure 1: A graph of the percentage of shared syllables within the American robin populations of the 50, 100, and 150 syllable data sets. Robins have unique repertoires with few shared syllables, each population had < 25% of syllables shared.

Figure 2: A graph of the distribution of the percent of shared syllables within the 50-syllable data set.

Figure 3: A graph of the percent distribution of shared syllables within the 100-syllable data set.

Figure 4: A graph representing the percent distribution of shared syllables in the 150-data set.

Figure 5: The most common syllables within the 50 and 100- syllable data sets. These five syllables have a distinct shape and sound.

Figure 6: The two most common syllables found in the 150-syllable data set.

Figure 1:

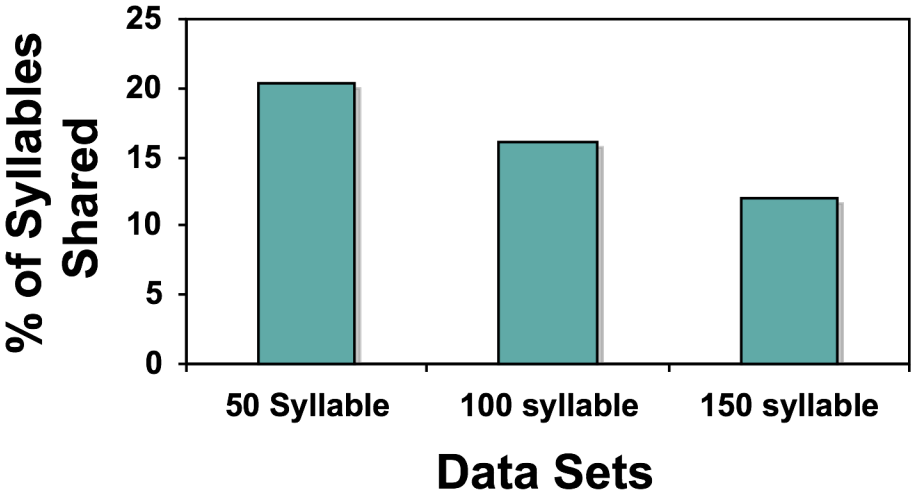


Figure 2:

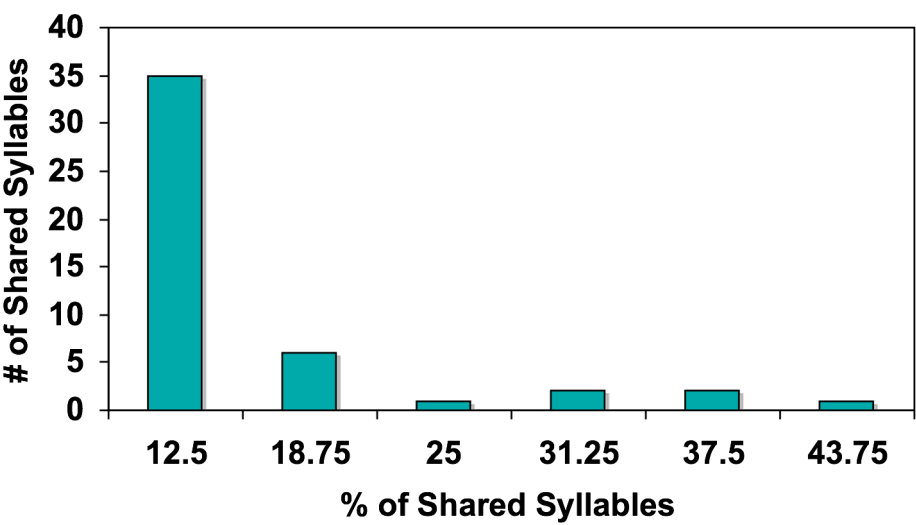


Figure 3:

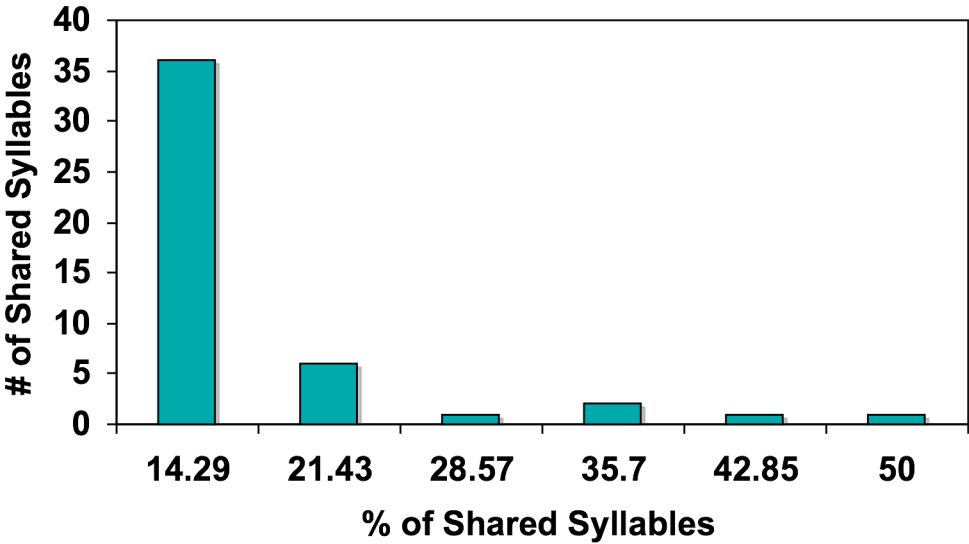


Figure 4:

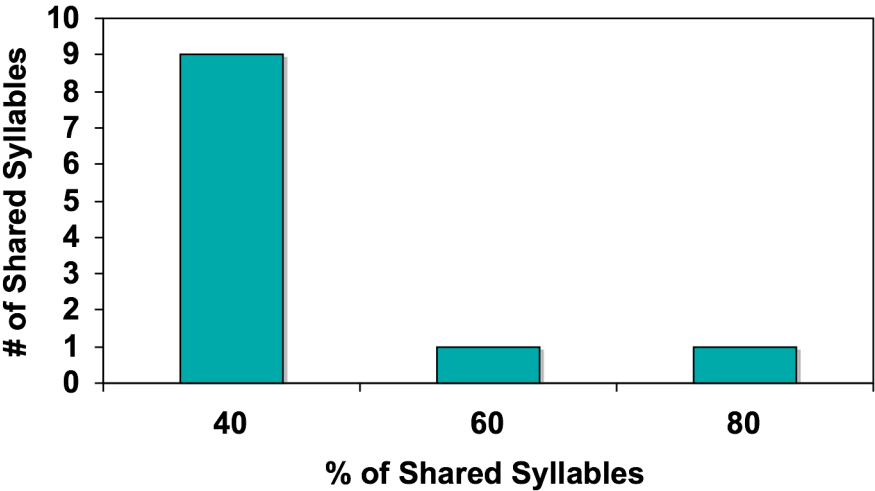


Figure 5:

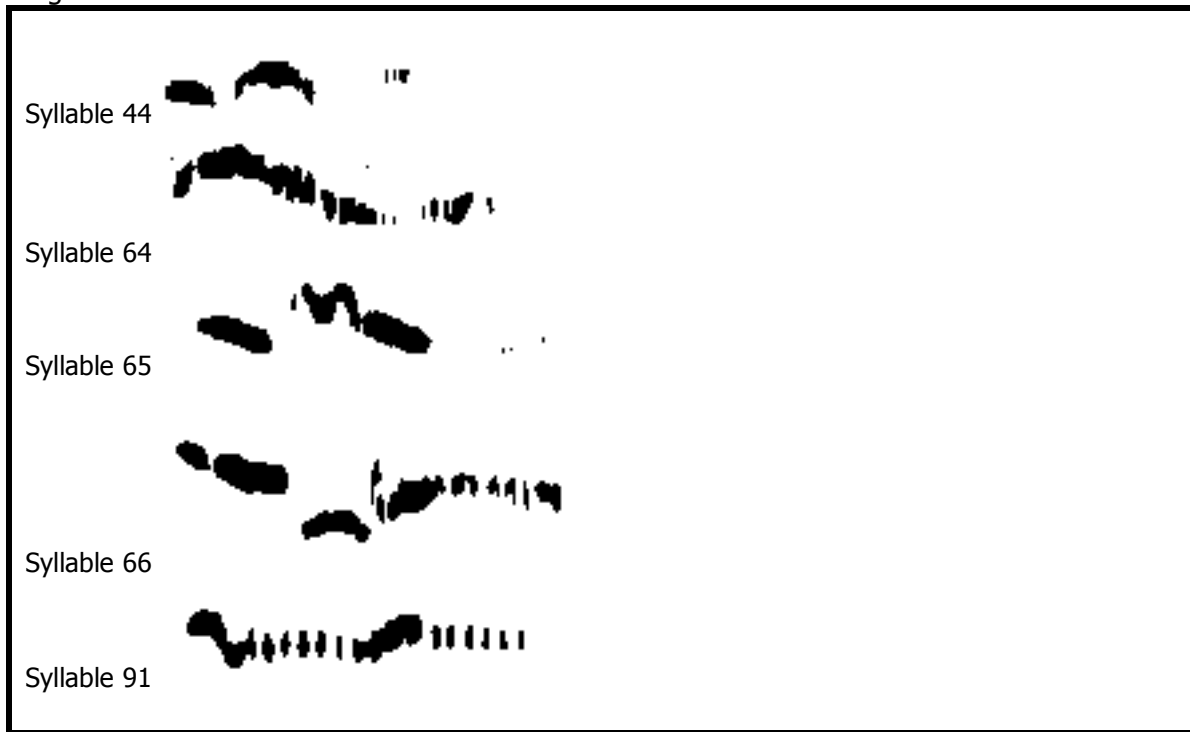
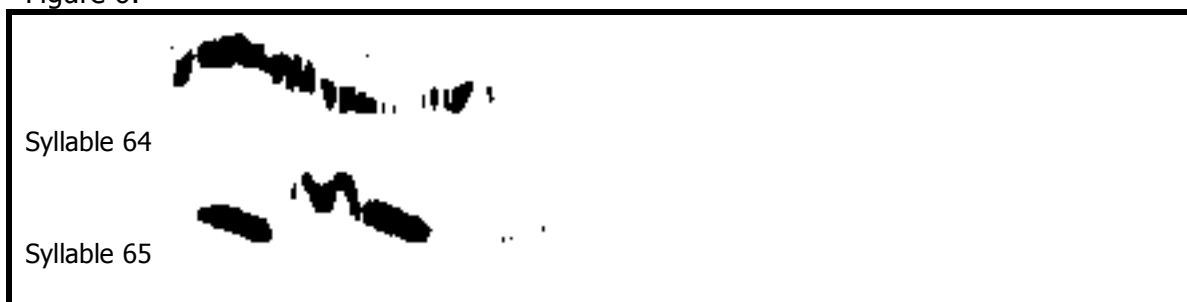


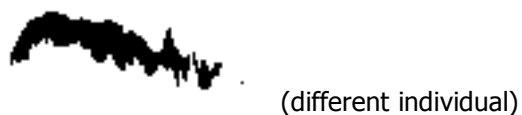
Figure 6:



Appendix 1

(Brightness:70, Contrast:100)

Curved line:



Syllable 174

Syllable 176



Syllable 71



Syllable 104



(different individual)

Syllable 209



Syllable 66



(different individual)

Syllable 117



(different individual)

Line:

Syllable 164



Syllable 166



Syllable 192



(different individual)

Syllable 188

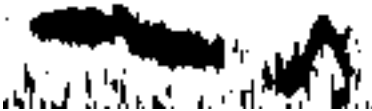


(different individual)

Syllable 37



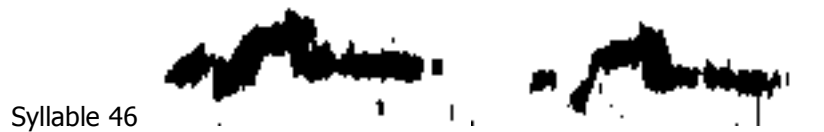
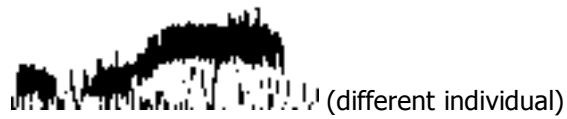
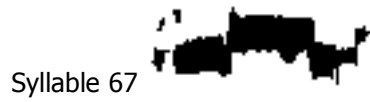
Syllable 116



Syllable 52



Box Line:



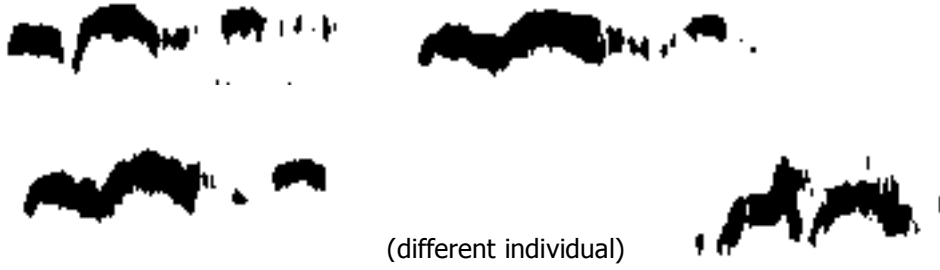
Ribbon:



Curves:



Syllable 44



Syllable 181



Syllable 208



Syllable 215



Syllable 13



Syllable 82



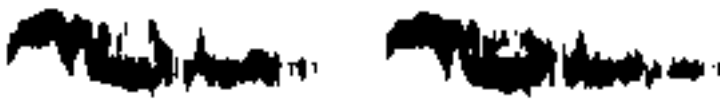
Syllable 150



Syllable 42



Syllable 73



Syllable 29

Round-headed:



Syllable 142 .



Syllable 65



Syllable 22



Syllable 168



Syllable 106



Syllable 43



Syllable 49



(different individual)

Pointed lines:



U-shaped headed lines

Syllable 47



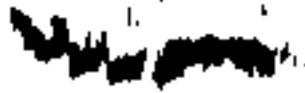
Syllable 56



Syllable 57



Syllable 21



Syllable 147



(different individual)

Syllable 55



(different individual)

Syllable 69



(different individual)

Syllable 19



Line with tail



Multi-part Line:

Syllable 202

A black and white waveform plot for Syllable 202, showing a series of peaks and troughs.

Syllable 91

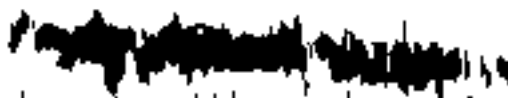
A black and white waveform plot for Syllable 91, showing a series of peaks and troughs.

(different individual)

Syllable 111

A black and white waveform plot for Syllable 111, showing a series of peaks and troughs.

Syllable 132

A black and white waveform plot for Syllable 132, showing a series of peaks and troughs.

Syllable 172

A black and white waveform plot for Syllable 172, showing a series of peaks and troughs.

Syllable 135

A black and white waveform plot for Syllable 135, showing a series of peaks and troughs.

(different individual)

Syllable 206

A black and white waveform plot for Syllable 206, showing a series of peaks and troughs.

Vertical Lines:



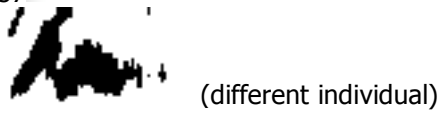
Syllable 195



Syllable 41



Syllable 157



Syllable 152



Syllable 165



Syllable 7



Syllable 81



(different individual)



Syllable 16



Syllable 77



Syllable 68



(different individual)



Syllable 131



Syllable 145



Syllable 118



Syllable 93



Syllable 31



Syllable 20

Syllable 169



Syllable 125



Syllable 107



Syllable 159



Syllable 97



Syllable 170



Syllable 162



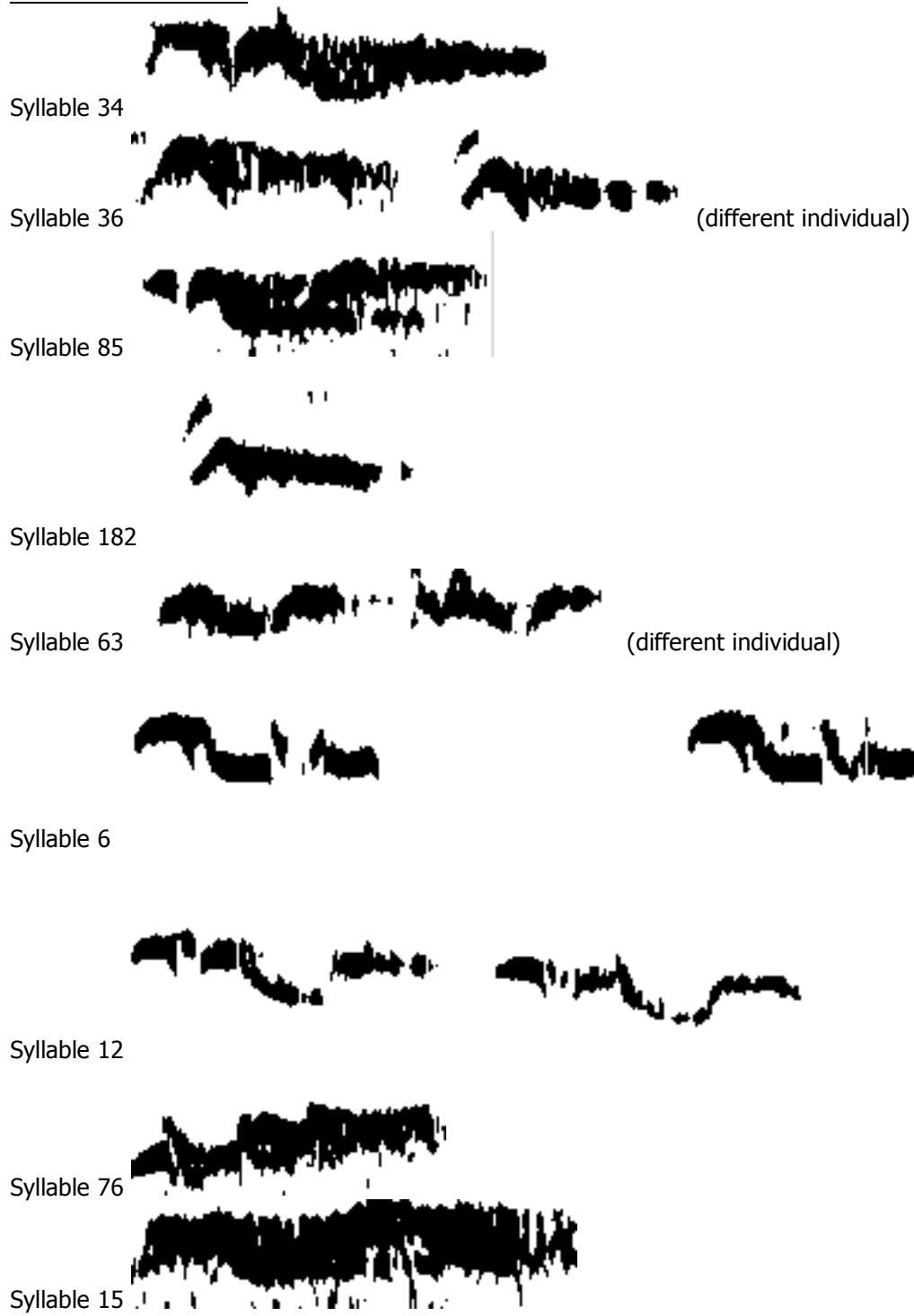
Syllable 5



Syllable 23



Curve-headed Line



Multiple parts:

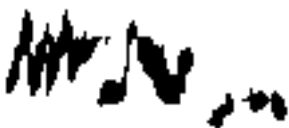
Syllable 141  (different individual)

Syllable 54 

Syllable 187 

Syllable 179 

Syllable 140 

Syllable 204 

Syllable 189  (different individual)

Syllable 79 

Syllable 212 

Syllable 110 

Syllable 51 

Syllable 17



Syllable 213



Syllable 200



Syllable 194



Syllable 70



Syllable 83



Syllable 90



Syllable 2



Syllable 137



Syllable 190



(different individual)

Syllable 158



Syllable 121

Syllable 61

Syllable 130

Syllable 62

Syllable 207

Syllable 28

Syllable 114

Syllable 178

Syllable 94

(different individual)

Syllable 119

Syllable 143

Syllable 84



Syllable 201



Syllable 198



Syllable 186



Syllable 25



Syllable 99



Syllable 112



Syllable 180



Syllable 4



Syllable 211



Syllable 96



Syllable 59



Syllable 108



Syllable 185



Syllable 89



Syllable 217



Syllable 53



Syllable 18



Syllable 86



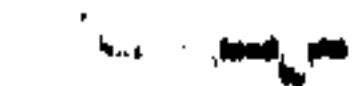
Syllable 9



Syllable 148



Syllable 120



Syllable 197



Syllable 50



Zigzags:

Syllable 123



Syllable 27



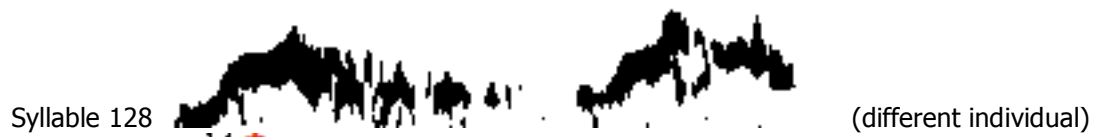
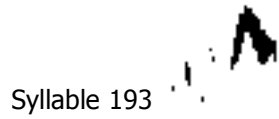
(different individual)



Roller coasters



Points:



Hooked-headed



Syllable 144



Syllable 134



(different individual)



Syllable 155

Appendix 2

(Brightness: 75 Contrast: 100)

Curved Line:

Syllable 64 (different individual)

Syllable 11

Syllable 133

Syllable 216

Syllable 101 too light

Syllable 3

Syllable 174

Syllable 176

Syllable 176

Syllable 71

Syllable 104

Syllable 104

Syllable 209

Syllable 209

Syllable 66 (different individual)



Syllable 117

Line:



Syllable 164



Syllable 166



Syllable 192



Syllable 188



Syllable 37

(different individual)



(different individual)



Syllable 116



Syllable 52

Box Line:

Syllable 95  (different individual)

Syllable 67 

Syllable 109 

Syllable 39  (different individual)
Syllable 146 too light 

Syllable 126 

Syllable 46 

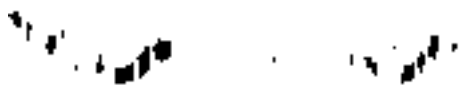
Syllable 24 

Syllable 122 

Syllable 38 

Ribbon:

Syllable 35  (different individual)

Syllable 105 

Syllable 196 

Syllable 72 

Syllable 58 

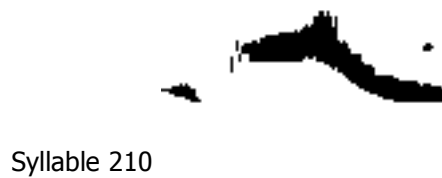
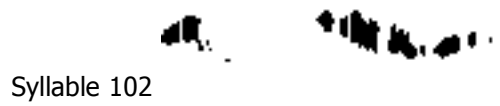
Syllable 199 

Syllable 149 

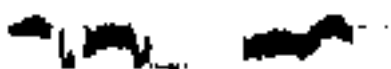
Syllable 214 

Syllable 115 

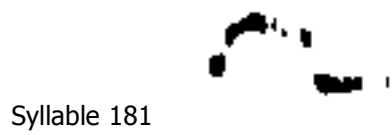
Curves:



(different individual)



(3rd individual)



Syllable 181



Syllable 208



Syllable 215



Syllable 13



Syllable 82



Syllable 150



Syllable 42

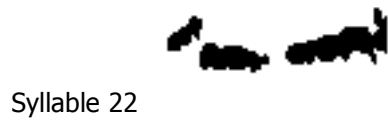


Syllable 73



Syllable 29

Round-headed:



Pointed Lines:

Syllable 127 A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 14

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 1

Syllable 103 A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning. (different individual)

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 10

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 163

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 60

A black ink trace of a syllable, showing a series of peaks and valleys, with a prominent peak near the beginning.

Syllable 113

U-shaped headed lines

Syllable 47



Syllable 56



Syllable 57



Syllable 21



Syllable 147



Syllable 55



Syllable 69



(different individual)



Syllable 19



Line with Tail

Syllable 183

Syllable 161

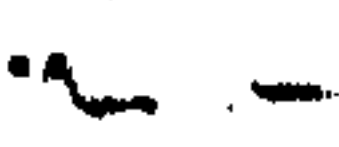
Multi-part Line:

Syllable 202 too light

Syllable 91  (different individual)

Syllable 111 

Syllable 132 

Syllable 172 

Syllable 135 

Syllable 206 

Vertical Lines:

Syllable 195

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 41

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 157

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

(different individual)

Syllable 152

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 165

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 7

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 81

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

(different individual)

Syllable 16
Syllable 77 too light

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 68

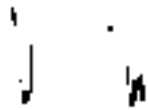
A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 131

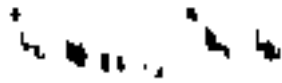
A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.

Syllable 145

A vertical line plot showing a series of black vertical lines of varying heights, forming a dense, somewhat irregular shape.



Syllable 118
Syllable 93 too light



Syllable 31



Syllable 20



Syllable 169



Syllable 125



Syllable 107
Syllable 159 too light
Syllable 97 too light



Syllable 170



Syllable 162



Syllable 5



Syllable 23

Curve-headed Line:



Syllable 34

(different individual)



Syllable 36

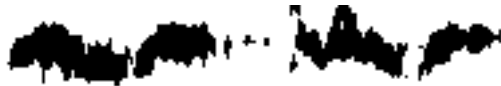
(different individual)



Syllable 85



Syllable 182



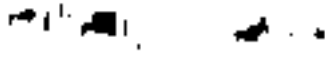
Syllable 63



(different individual)



Syllable 6



Syllable 12

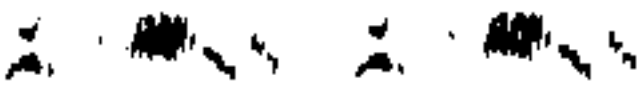


Syllable 76



Syllable 15

Multiple parts:

Syllable 141  (different individual)

Syllable 54 

Syllable 187 

Syllable 179 

Syllable 140 

Syllable 204 

Syllable 189 

Syllable 79 

Syllable 212 

Syllable 110 

Syllable 51 

Syllable 17 

Syllable 213 

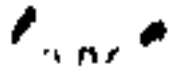
Syllable 200



Syllable 194



Syllable 70



Syllable 83



Syllable 90



Syllable 2



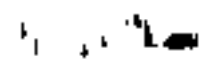
Syllable 137



Syllable 190



Syllable 158 too light



Syllable 121

Syllable 61 too light



Syllable 130



Syllable 62 too light



Syllable 207



Syllable 28

Syllable 114 too light

Syllable 178

Syllable 94

Syllable 119

Syllable 143

Syllable 84

Syllable 201 too light

Syllable 198

Syllable 186

Syllable 25

Syllable 99

Syllable 112

Syllable 180

Syllable 4



Syllable 211
Syllable 96 too light



Syllable 59
Syllable 108 too light



Syllable 185



Syllable 89



Syllable 217



Syllable 53



Syllable 18



Syllable 86



Syllable 9



Syllable 148
Syllable 120 too light

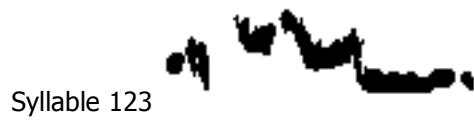


Syllable 197



Syllable 50

Zigzags:



(different individual)

Roller coasters:



Syllable 154



Syllable 139



Syllable 33



Syllable 191

Syllable 100 too light



Syllable 156



Syllable 151



Syllable 129

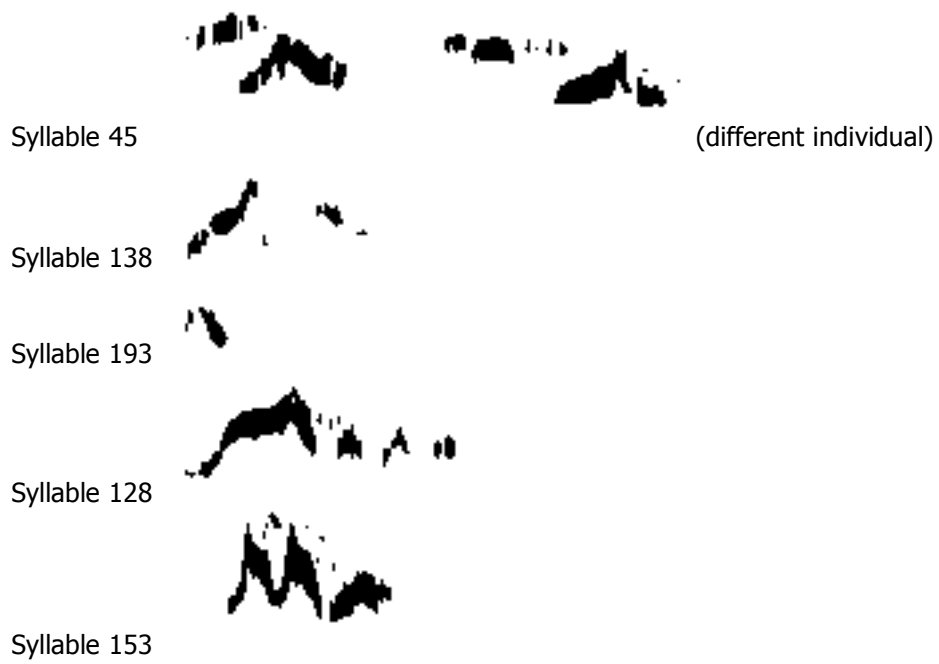


Syllable 74



Syllable 172

Points:



Hooked -headed:

Syllable 144



Syllable 134



(different individual)

Syllable 155

