Java sparrow song conforms to Mezerath's Law but not Zipf's Law of Abbreviation

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Abstract

Linguistic laws, which describe common statistical patterns in human language, are often studied in animal communication systems. Despite good evidence for the existence of these laws in non-human primates, data is still limited for other taxa. Birdsong is often used as a model for human language development due to similarities in vocal learning and production. Therefore, it is useful to explore features of human language in birdsong to determine the value and limitations of such comparisons. Here, we looked for patterns consistent with Menzerath's law, the tendency for longer sequences to be made up of smaller constituent parts, and Zipf's Law of Abbreviation, the tendency for more frequently used elements to be shorter in length, in the songs of Java sparrows (*Padda oryzivora*). We found that songs conformed to Menzerath's law at both the population and individual level; longer sequences were made up of shorter notes, and this pattern was achieved through note selection, rather than shortening existing notes. This adherence to Menzerath's law may reflect species-specific constraints on song durations. However, we found no evidence to support adherence to Zipf's Law of Abbreviation, either at population or individual level; more frequently used notes were not shorter in length. As they are used in courtship, songs may experience different selection pressure to other parts of the vocal repertoire, which could act against compression. Whilst there may be some

limitations in applying linguistic laws designed for human language to birdsong, especially Zipf's Law of Abbreviation, these laws may still provide insights into animal and human communication systems.

Keywords

Animal communication; Birdsong; Java Sparrow; Language; Linguistic Laws; Menzerath's Law; *Padda oryzivora*; Zipf's Law of Abbreviation

Introduction

Birdsong and spoken language share many similarities (Berwick et al., 2011; Bolhuis et al., 2010; Hyland Bruno et al., 2021). Both are made up of acoustic sequences, and there is overlap in the behavioural, neural, and genetic bases of vocal learning and production in songbirds and humans (Berwick et al., 2012, 2011; Bolhuis et al., 2010; Hyland Bruno et al., 2021). However, there are also differences. In particular the close relationship between structure and meaning in human language is thought not to exist in other animals (Bolhuis et al., 2010). Due to the similarities, birdsong is often used in comparative studies examining the evolution and development of human language (e.g., Berwick et al., 2011). Therefore, it is useful to explore features of human language in animal communication systems, especially birdsong, to help determine the value and limitations of these comparisons.

Linguistic laws describe common statistical patterns in human language, where they have been studied extensively (Semple et al., 2022). More recently, patterns consistent with linguistic laws have also been explored in animal communication systems (Semple et al., 2022). Two laws that often receive attention are Menzerath's law, the tendency for longer sequences to be made up of smaller constituent parts, and Zipf's Law of Abbreviation (ZLA), the tendency for more frequently used elements to be shorter in length. These laws are especially well studied in non-human primates (e.g., Bezerra et al., 2011; Clink et al., 2020; Clink & Lau, 2020; Gustison et al., 2016; Huang et al., 2020; Semple et al., 2010; Valente et al., 2021; Watson et al., 2020) and some other mammal taxa (e.g.,

Demartsev et al. 2019; Ferrer-i-Cancho et al. 2013). Studies examining the presence of linguistic laws in bird communications are still relatively limited (Favaro et al., 2020; Ferrer-i-Cancho et al., 2013; Hailman et al., 1985; James et al., 2021).

Adherence to Menzerath's law has been widely reported in non-human primates (Clink et al., 2020; Gustison et al., 2016; Heesen et al., 2019; Huang et al., 2020; Valente et al., 2021). Despite this, adherence to the law is not universal, and may depend on the subset of vocalizations examined; in mountain gorillas, Menzerath's law was apparent when single-unit sequences were included in analyses, but not when they were excluded (Watson et al., 2020). Patterns consistent with Menzerath's law have also been found in a range of songbird species, both at the repeat phrase and whole song level (James et al., 2021). However, the mechanisms by which these patterns arise have not been explored in detail in songbird species with complex vocalizations. In the African penguin (*Spheniscuc demersus*), patterns consistent with Menzerath's law are achieved through a combination of note choice and reducing the length of specific note types (Favaro et al., 2020). However, the vocal sequences of penguins are relatively simple compared to birdsong, so determining if the same mechanisms operate in more complex avian vocal sequences could be beneficial for comparative studies examining the evolution of language.

ZLA has been reported in a range of mammal taxa (e.g., Demartsev et al., 2019; Ferrer-i-Cancho & Hernández-Fernández, 2013; Semple et al., 2010; Valente et al., 2021), but is not universally found across studies (e.g., Bezerra et al., 2011; Clink et al., 2020). As with Menzerath's law, adherence to ZLA may depend on the subset of the repertoire studied; in common marmosets (*Callithrix jacchus*), long-distance calls did not adhere to ZLA, whereas short-range signals were consistent with the expected pattern (Ferrer-i-Cancho and Hernández-Fernández, 2013). Adherence to ZLA may also depend on the unit of analysis. Across gibbon species, ZLA has been reported at the note level, with shorter notes being used more frequently in loud morning calls for the cao vit (*Nomascus nasutus*) and western black-crested (*Nomascus concolor*) gibbons (Huang et al., 2020), but not at the phrase level in male solos of the Mueller's gibbon (*Hylobates muelleri*) (Clink et al., 2020). ZLA is not commonly studied in birds, although a small number of species have been examined to date (Favaro

et al., 2020; Ferrer-i-Cancho et al., 2013; Hailman et al., 1985). In the African penguin, shorter note types were used more frequently than longer ones, a pattern consistent with ZLA (Favaro et al., 2020). However, these calls are relatively simple and contain only a few note types. In the common raven (*Corvus corax*), patterns consistent with ZLA were not found for call usage; shorter call types were not more frequently used in the vocal repertoire (Ferrer-i-Cancho et al., 2013). To our knowledge, ZLA has not been examined in the songs of species with complex note repertoires.

Here, we looked for patterns consistent with Menzerath's law and ZLA in a published dataset of Java sparrow (*Padda oryzivora*) song (Lewis et al 2023). Each individual male Java sparrow produces a single song type that is repeatable but varies across renditions (Ota and Soma, 2014). This variability in note usage both among and within individuals makes the Java sparrow a good candidate for examining linguistic laws in birdsong. Our goals were i) to assess whether Java sparrow song adheres to Menzerath's law, and, if so, to determine whether birds achieve this by choosing shorter notes or by producing shorter versions of the same notes in longer songs; and ii) to determine whether Java sparrow song adheres to ZLA at the individual and population levels.

Methods

Study species

The Java sparrow (*Padda oryzivora*) is an oscine passerine and member of the family Estrildidae (Restall, 1996). Songs in this species are used in courtship but not for territory defense. Each male learns to produce a single song with 2-8 note types (Ota and Soma, 2014) from his social father (Lewis et al., 2023, 2021; Soma, 2011). Learning fidelity is high, with sons' songs resembling their fathers' songs in a range of measures (Lewis et al., 2023, 2021)). Each male sings one stereotyped song (Ota and Soma, 2014) with some variation between renditions.

Dataset

To investigate the presence of linguistic laws in Java sparrow song, we used the dataset from Lewis et al. (2023), which contains 676 undirected songs from 73 individuals. Birds in this dataset belonged to 10 social lineages. Each social lineage included a single founder, all of the males that learned their songs from that founder (i.e., his social sons), the social sons of those birds, and so on for up to five generations. Thus, songs within social lineages were not independent. Some birds (n=6) were reared in the presence of subtutors (an additional adult male that was not their social or genetic father). Spectrogram inspection suggests that subtutored birds generally produced songs that resembled their social fathers' song. Therefore, subtutored individuals were classed as belonging to their social fathers' lineage for this study. Songs were defined as series of notes with inter-note intervals <1 s (Kagawa and Soma, 2013; Lewis et al., 2021). Songs were manually segmented into individual notes using Koe (Fukuzawa et al., 2020) and classified into 16 note types, with high inter-observer repeatability (Lewis et al., 2021). As in Lewis et al. (2023), we cleaned 4 additional notes that were included in the dataset but separated by an interval >1 s. The dataset contained a total of 22,966 notes.

Java sparrow songs frequently contained a series of introductory notes, which are spectrally similar to other notes in the song but indicated by note repetition and variable, uncharacteristically long gap durations (>0.25s but <1s) (Lewis et al. 2023). As introductory notes contribute to sequence length, the presence of introductory notes may, therefore, affect our analysis of linguistic laws, in particular, Menzerath's law. To account for the presence of introductory notes, all analyses concerning Menzerath's law were conducted twice, with and without introductory notes included, to determine if patterns were similar in the two situations (Appendix 1). We identified introductory notes as in Lewis et al. 2023, reducing the inter-note interval for inclusion in the song to 0.25s until five consecutive notes with inter-note interval of <0.25s had been identified. The main song was considered to start at the first note in the series of 5. The full dataset included 20911 notes when song introductions were excluded. Results were qualitatively similar for analyses with and without introductory notes, and any differences are indicated in the 'Results' section.

Data Analysis

Menzerath's Law

We examined adherence to Menzerath's law by asking i) whether longer songs are made up of shorter notes in the population as a whole. This is how Menzerath's law has been studied in other animals (Gustison et al., 2016; Valente et al., 2021). Java sparrow songs are composed of different note types, and note duration depends on both the note type and the singer (Lewis et al., 2021). To examine how Menzerath's law might arise in Java sparrow song, we asked ii) whether notes of the same type are shorter when they appear in longer songs, and iii) whether longer songs are composed of shorter note types. Menzerath's law could arise at the population level even if it does not hold within individual birds due to individual differences in song production. For example, we would see this if some birds produce only long songs composed of short notes and other birds produce only short songs composed of long notes. Therefore, we conducted a second set of analyses to ask whether Menzerath's law holds within individuals. In particular, we asked, iv) whether individual Java sparrows sing shorter notes when they produce longer songs, v) whether individuals use shorter versions of the same note types in longer songs, and vi) whether individuals use shorter note types in longer songs.

To answer the above questions, we fit a series of linear mixed effect models using the lme4 (Bates et al., 2015) and lmerTest packages (Kuznetsovs et al., 2017) in R (ver 4.1.3) (R Core Team, 2022). To address question i) we regressed the logged duration of individual notes on the length of the song that contained them and on their logged position in the song. A significant negative relationship between the note duration and song length would be evidence for Menzerath's law, and a significant relationship between note duration and position in the song would indicate that note duration changed systematically over the course of each song (i.e., notes later in the song are shorter or longer than those at the beginning). To account for the non-independence of note durations within songs, individuals and social lineages, we included random effects of song, individual bird, and social lineage in the model. The random effects of song included a random intercept, to account for the possibility that some songs might have longer notes than others, and a random slope of position in

song, to account for the possibility that note length might change differently over the course of different songs. The random effects of bird and social lineage included intercepts, slopes of logged position in the song, and slopes of song length (number of notes in the song). The random intercept accounts for the possibility that different birds or social lineages might sing notes of different durations, the random slope of logged position accounts for the possibility that note duration may change differently over the course of songs in different individuals or lineages, and the random effect of song length accounts for the possibility that song length might affect note length differently in different individuals or lineages. There was no random slope of song length within songs because each song has only one length. The random slopes of song length within individuals and lineages allows that the strength of Menzerath's law may differ among individuals and lineages.

Adherence to Menzerath's law at the population level could be achieved in two ways; birds might sing shorter versions of the same note types in longer songs (question ii), or birds might use shorter note types in longer songs (question iii). To disentangle these two possibilities, we conducted two regressions identical to the one just described, but with different response variables. To address question ii) the response variable was the logged duration for each note in the dataset, mean centred within its note type. Thus, differences in note duration due to the note types are removed, and any patterns that remain must be due to differences in how notes of each type are produced. To address question iii) we replaced each logged note duration in the dataset with the mean logged duration for its note type in the whole dataset. Thus, variability within note types is removed, and any pattern that remains must be due to the note types that birds use in their songs.

Java sparrow songs might adhere to Menzerath's law across the whole population even if individual birds do not use shorter notes in longer songs. To investigate patterns associated with Menzerath's law within individual birds, we conducted a second set of regressions. In these analyses, we mean-centred the song length within each bird and used the individual mean-centred song length, rather than raw song length as a predictor. Any relationship between individual mean-centred song length and note duration in these analyses cannot be due to differences in song length among individuals,

because those have been removed from the predictor, and therefore must be because individual birds use shorter notes in longer songs. Analyses iv to vi are analogous to analyses i to iii, respectively.

Zipf's Law of Abbreviation (ZLA)

We used Kendall's rank correlation test to assess the significance of the relationship between the mean logged duration of each note type and its frequency of use in our study population. This approach has been used to study ZLA in human languages (Bentz and Ferrer-i-Cancho, 2016) and other animal communication systems (Ferrer-i-Cancho et al., 2013; Semple et al., 2010). Typically, a representative sample of the language (for humans) or vocalizations (for animals) is examined to determine whether length of the individual types is negatively correlated with their frequency of use.

Whilst this approach is analogous to that used in other studies, it may not be the most appropriate way to study ZLA in birdsong. Individual birds may use highly divergent or even non-overlapping sets of note types, making it difficult to create truly representative samples of note type use in the population. Even if representative samples can be obtained, differences in the use of note types among individuals could create patterns that look like ZLA at the population level even if no individual bird uses short note types more frequently than long ones. For example, this would arise if many birds sing only short note types and a few sing only long note types. While this pattern would be consistent with ZLA, the mechanism would not be. Zipf (1935) hypothesised that individuals shorten vocal units that they use more frequently to make communication more efficient, and, if this is true, we should see a negative relationship between the duration and frequency of use of vocal units within as well as among individuals. Another challenge to studying ZLA in birdsong is that birdsong can be highly stereotyped, and is often learned from other members of the population. This means that observations of note type use within and among individuals are not independent, and treating them as independent is likely to result in false positive inferences about adherence to ZLA in populations.

With these challenges in mind, we developed a test to assess whether birdsong in a given population adheres to ZLA. Consider a data set of annotated birdsongs in which notes have been classified to type. Let d_{ijk} be the logged duration of the kth instance of note type i produced by bird j, and let d_{ij} be the mean logged duration of note type i produced by bird j. We study logged durations because the unexplained variability in note duration increases with the mean, and logging standardises this variability. Let n_{ij} be the number of times bird j produces note type i. ZLA predicts a negative concordance between d_{ij} and n_{ij} within individual birds.

We assess concordance using Kendall's τ. For each bird j, we compute τ_j, the concordance between d_{ij} and n_{ij}, and we compute υ_j, the variance in our estimate of τ_j, where $\upsilon_j \approx \frac{2(2c_j+5)}{9c_j(c_j-1)}$ and c_j is the number of note types produced by bird j (Valz and McLeod, 1990). We then compute τ_{obs}, the observed population mean concordance with each τ_j weighted by its inverse variance: $\tau_{obs} = \sum \tau_j \upsilon_j^{-1} / \sum \upsilon_j^{-1}$. This τ_{obs} assigns more weight to birds that use more note types because their concordances are better estimates of the expected concordance for the population. This τ_{obs} is our test statistic. This is convenient because τ_{obs} has a clear biological interpretation: if we randomly choose one bird from the population and we randomly choose two different note types produced by that bird, $(1 + \tau_{obs})/2$ is the probability that the note type with the longer duration will also be performed more frequently.

We construct a null distribution for τ_{obs} while maintaining the observed similarities in song structure and note similarity among birds. This accounts conservatively for the social learning of birdsong. For each note type i we compute d_i, the mean logged duration of the note type with each bird weighted equally. Thus, $d_i = b^{-1} \sum_{j=1}^{b} d_{ij}$ where b is the number of birds in the data set. Then, we compute ε_{ij}, the deviance of the logged duration of each note type i when produced by bird j from the population mean logged duration for that note type. Thus, $\varepsilon_{ij} = d_{ij} - d_i$. If song structures are constrained but the duration of notes is independent of their frequency of use, then we can create a null distribution by permuting the population mean logged durations among the note types in the data set. Thus, for each note i we select a randomised duration r_i from the set of ds without replacement. Then, we

compute r_{ij}, a randomised mean logged duration for note *i* as it might have been produced by bird *j*, as either $r_{ij} = r_j + \varepsilon_{ij}$ for all *i* and *j* or $r_{ij} = r_j - \varepsilon_{ij}$ for all *i* and *j*, with equal probability. By either adding all deviances or subtracting all deviances from the randomised means, we account for variability in the durations of note types among birds while controlling for the fact that differences from the population mean duration may be learned with the song structure (Lewis et al., 2021). Finally, we compute the concordance between r_{ij} and n_{ij} for each bird in the randomised data, and we average across all birds with each concordance weighted by its inverse variance. This is analogous to our computation of τ_{obs} from the observed data, and results in one possible value of the test statistic that we might obtain under the null hypothesis. We repeat this process 10^4 times to produce a null distribution for τ_{obs}. The p-value for a negative concordance between d_{ij} and n_{ij} within individual birds is the proportion of observations in the null distribution that are less than or equal to τ_{obs}. This quantifies the strength of evidence for ZLA in the population.

Ethics statement

The dataset used in this study was initially collated for use in Lewis et al. (2021) and Lewis et al. (2023) The dataset contains information extracted from archival recordings from a laboratory population of Java sparrows (Padda oryzivora) housed at Hokkaido University. Archive data was collected between 2011 and 2019 under the following approvals: Hokkaido University (Permit numbers: 11-0028, 16-0020) and the University of Manchester AWERB (Permit number: D042).

Data Availability Statement

Data and code associated with this paper can be found at FigShare https://doi.org/10.48420/24763299. Data and code from the original Lewis et al. (2021) paper can be found at FigShare: https://doi. org/10.48420/14555247, and from the Lewis et al. (2023) paper at Figshare: http://doi.org/ 10.48420/22550149.

Results

Menzerath's law

We found evidence to support the presence of Menzerath's law in Java sparrow songs when considering all songs in the dataset (i.e., the population level models i - iii); across birds, as song length (number of notes) increased, notes within the song were shorter (β = -0.004, p=0.025; Table 1; Figure 1). Results were qualitatively similar when considering songs with introductory notes removed, with a trend towards shorter notes in longer songs (β = -0.003, p=0.084; Appendix 1). Although not significant, our results suggest that note length differed across the course of the song, with notes tending to be longer when appearing later in the song (with introductory notes β = 0.058, p=0.121 (Table 1); without introductory notes β = 0.042, p=0.263 (Appendix 1)). When examining the potential drivers of Menzerath's law in Java sparrow songs, we found that birds did not reduce the duration of notes within types in longer songs (with introductory notes p=0.988 (Table 1); without introductory notes p=0.850 (Appendix 1)) i.e., note type 'A' in a long song was not shorter than note type 'A' in a short song. There was also no change over the course of the song (with introductory notes p=0.973 (Table 1); without introductory notes p=0.949 (Appendix 1)); note type 'A' later in the song was not shorter than note type 'A' earlier in the song. However, we did find evidence that birds used note types with shorter average durations in longer songs (with introductory notes β = -0.004, p=0.002 (Table 1); without introductory notes β = -0.003, p=0.003 (Appendix 1)). In addition, birds used note types with longer average durations later in songs (β = 0.056, p=0.015; Table 1). Results were qualitatively similar when considering songs with introductory notes removed, with a trend towards the use of longer note classes later in the song (β = 0.038, p=0.051; Appendix 1). Overall, these results suggest that adherence to Menzerath's law is driven by preferential use of short note types, rather than by shortening note types in long songs.

Table 1: Results of GLMMs examining the effect of song length and note position in songs on note duration. All durations were logged.

Population level			
Question	*Measurement*	*Song length*	*Position in song (logged)*
Are longer songs made up of shorter notes?	Log note duration (log(s))	-0.004 p=0.025	0.058 p=0.121
Do longer songs contain shorter versions of the same note types?	Deviation from note type mean (log(s))	-6.24×10^{-6} p=0.988	-0.0007 p=0.973
Are longer songs made up of shorter note types?	Average logged duration of note type (log(s)	-0.004 p=0.002	0.056 p=0.015
Individual level			
Question	*Measurement*	*Song length*	*Position in song (logged)*
Are longer songs made up of shorter notes?	Log note duration (log(s)	-0.003 p=0.059	0.055 p=0.144
Do longer songs contain shorter versions of the same note types?	Deviation from note type mean (log(s))	-8.41×10^{-6} p=0.985	-0.0003 p=0.989
Are longer songs made up of shorter note types?	Average logged duration of note type (log(s))	-0.003 p=0.009	0.052 p=0.026

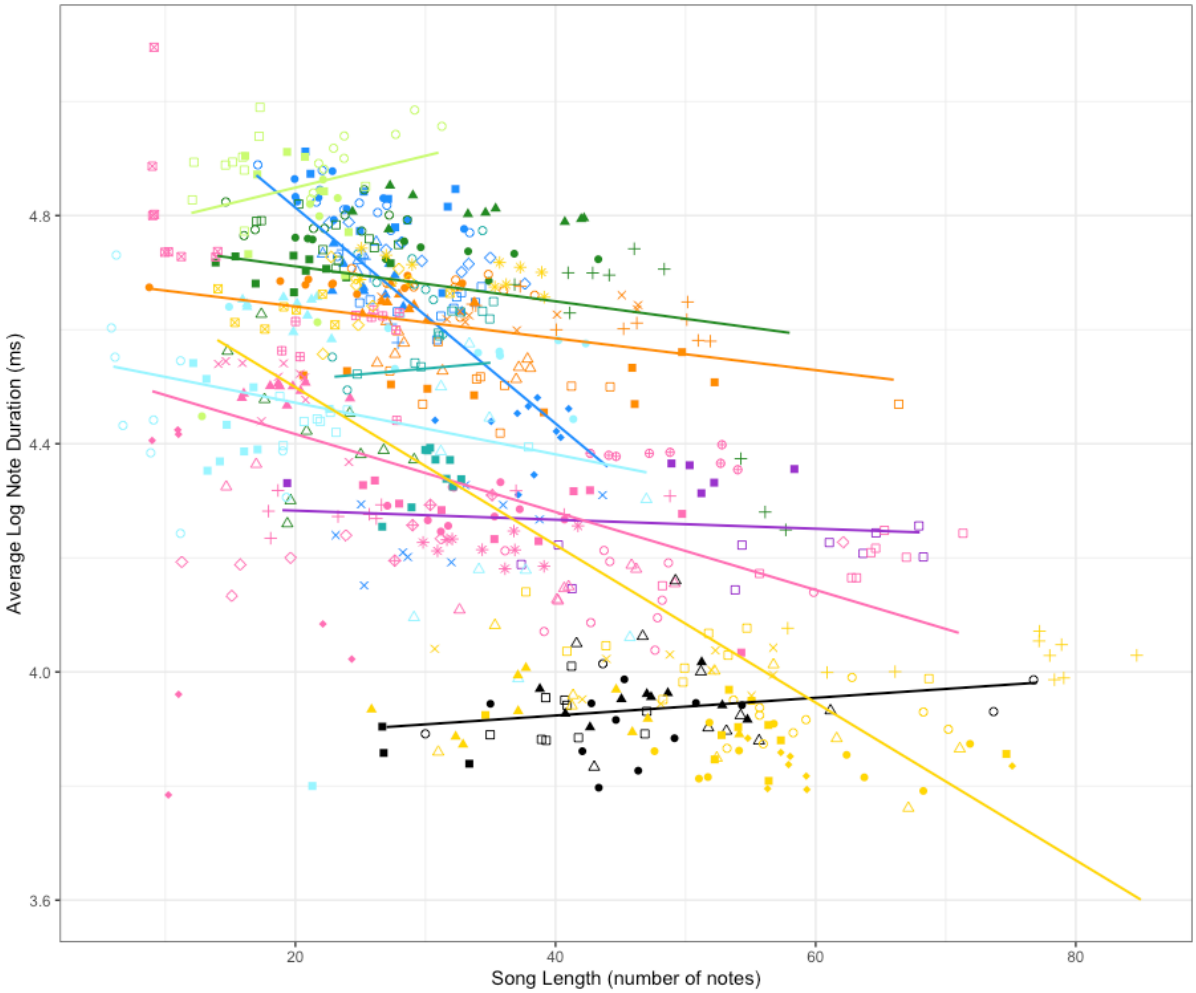

Figure 1: Average logged note duration within a song (ms) plotted against song length (number of notes). Each shape and colour combination represents a single individual. Individuals are coloured based on their social lineage, which relates to song phenotype. Regression lines are calculated for each social lineage and coloured accordingly.

We found weak evidence for Menzerath's law at the individual level (i.e., models iv-vi); individuals used shorter notes when they sang longer songs (with introductory notes β = -0.003, p=0.060 (Table 1); without introductory notes β = -0.002, p=0.084 (Appendix 1)). Again, there was no evidence that note duration became shorter towards the end of the song, and our results suggest a trend in the opposite direction (with introductory notes β = 0.055, p=0.144 (Table 1); without introductory notes β = 0.037, p=0.326 (Appendix 1)). The pattern in individuals was driven by the same factors as the population level findings; birds used shorter note types in longer songs (β = -0.003, p=0.009 (Table 1); without introductory notes β = -0.002, p=0.013 (Appendix 1)) and note types with longer

average duration later in songs (with introductory notes β = 0.052, p=0.026 (Table 1); without introductory notes β = 0.033, p=0.084 (Appendix 1)). There was no evidence that birds changed the length of individual note types based on song length (with introductory notes p=0.984 (Table 1); without introductory notes p=0.899 (Appendix 1)) or that notes of a given type were shorter later in songs (with introductory notes p=0.986 (Table 1); without introductory notes p=0.943 (Appendix 1)).

Zipf's law of abbreviation (ZLA)

We did not find evidence for ZLA at either the population or individual levels. Shorter note types were not used more frequently than longer note types across all songs in the population (Kendall's tau; τ=-0.150, p=0.209), and individual birds did not use shorter note types more frequently than longer note types (τ=-0.037, p=0.431). The results are qualitatively similar if we exclude note types used by only one bird (population level: τ=-0.282, p=0.090; individual level: τ=-0.030, p=0.441) or if we exclude note types used fewer than 5 times in total (population level: τ=-0.181, p=0.174; individual level: τ=-0.044, p=0.419).

Discussion

Java sparrow songs adhered to one of the two linguistic laws tested. We found evidence to support the presence of Menzerath's law in Java sparrow songs; longer sequences were made up of shorter notes across all songs in the population and across songs within individuals. This is due to birds using shorter note types more frequently in longer songs, rather than shortening individual note types in longer songs. We did not find strong evidence to suggest that note duration changed as the song progressed, although a trend towards longer notes later in the song was apparent. However, we found that birds included longer note types towards the end of their songs both across the population and within individuals. We did not find evidence for Zipf's Law of Abbreviation (ZLA) in Java sparrow songs; shorter note types were not used more frequently in the population as a whole or by individual birds.

Adherence to Menzerath's law at the level of repeat phrases has been reported previously in Java sparrows (James et al., 2021), and the same pattern is apparent in this study across full songs. In our study population, songs often contained notes that were not part of repeat phrases, meaning that whole song analysis was more appropriate. Adherence to Menzerath's law may be due in part to constraints on overall song duration, which may relate to energetic costs, female preferences, or species recognition. In Java sparrows, song length and song tempo are negatively correlated; birds that produce songs with more notes sing them at faster rates (Lewis et al, 2023). The current study advances this result by showing that this pattern holds not just for song tempo, but for also for the duration of the notes themselves. At the population level, the social learning of birdsong can create patterns consistent with Menzerath's law. Each male Java sparrow sings a single song type (Kagawa and Soma, 2013; Lewis et al., 2021; Soma, 2011), and the note types used and the order of note types in each male's song are learned from his social father (Lewis et al., 2021; Soma, 2011). Therefore, fathers and sons sing similar songs (Lewis et al., 2021; Soma, 2011). This means that correlations between song length and note duration may persist within lineages, with some singing fewer, longer notes and others singing more, faster notes. Our analyses controlled for non-independence of song characteristics within birds and social lineages, so learning alone cannot account for the patterns observed. This is further supported by the presence of Menzerath's law at the individual level; within an individual, longer songs were also made up of shorter notes.

Conformation to Menzerath's law has been reported in a range of other passerine species (James et al., 2021), indicating that this pattern may be widespread across the order. However, the methods by which Menzerath's law arises in birdsong have not been examined in detail. For this population, notes within songs were classified into discrete categories, meaning that we could investigate how patterns consistent with Menzerath's law were achieved in more detail. Longer songs consisted of note types with shorter average durations, and there was no evidence that individual note types were compressed in longer songs. Our results indicate that shortening of sequence components in Java sparrows is achieved through note selection alone, rather than through changes to note parameters. Note selection also contributes to adherence to Menzerath's law in the African penguin (Favaro et al., 2020), although changes to note parameters also plays a role. Mediation of Menzerath's law through

note selection was apparent at both the population and individual level in Java sparrows. As with overall adherence to Menzerath's law, this suggests that the pattern is not driven solely by a few social lineages with long songs made up of short notes, but that individuals also use this mechanism on a by-song basis.

It has been suggested that breathing and performance constraints may result in a negative relationship between sequence position and element duration, i.e., elements towards the end of the sequence are shorter (Gustison et al., 2016). However, we did not find this pattern in Java sparrows. At both the population and individual level, there was a trend towards longer notes later in sequences, and birds were significantly more likely to use longer note types later in their songs. A similar positive correlation between note position and duration has been found in a number of non-human primates, with note length positively associated with position in the vocal sequence (Clink and Lau, 2020; Huang et al., 2020; Valente et al., 2021). The presence of longer notes later in the song, where a decline in performance may be expected due to energetic constraints, could be an indicator of male quality. In Java sparrows, songs are used during courtship and mate selection. Therefore, indicators of quality, such as the positioning of long note types near the ends of songs may be preferred by females. However, it may be that short, fast sections, especially those close to theoretical performance limits (Kagawa and Soma, 2013; Podos, 1997), are more energetically costly, and the use of longer notes later in the sequence is indicative of performance constraints in this species. Faithful song learning in the Java sparrow, where birds closely imitate their tutor's song (Lewis et al., 2021; Soma, 2011), could contribute to the maintenance of songs with longer notes at the end of the sequence across generations regardless of performance constraints, especially in songs that are not near to performance limits.

We found no evidence that Java sparrow songs adhered to ZLA, either at the population or individual level. Shorter note types were not more commonly used across the population as a whole, or within individual birds' repertoires. The presence of ZLA has not been well studied in birdsong. Early studies in the black-capped chickadee found that call bouts with a smaller number of calls were more common than those with more calls (Hailman et al., 1985), but not that calls with fewer notes were

more common than those with more notes (Hailman et al., 1985). The frequency of specific note types was not examined. This raises an interesting question regarding the appropriate level of analysis for comparing the acoustic sequences of animals with human language, as it is difficult to equate the various levels of organization (Semple et al., 2022). In Java sparrows, note types are used in different combinations by different individuals, indicating that notes may be the recombinant unit in songs and are an appropriate unit for analysis. A similar approach was used to examine ZLA in the calls of African penguins, with the proportions of individual notes being examined (Favaro et al., 2020). Penguins' ecstatic display calls did adhere to ZLA, with shorter syllables making up greater proportions of the calls. However, the calls contained only three syllable types, one of which was inspiratory, making comparisons between these calls and Java sparrow songs difficult.

ZLA is generally more challenging to study than Menzerath's law due to the need for classification of notes or calls into discrete categories. It is not possible to know how birds perceive differences between specific notes. As such, classification by human observers or computational methods may not accurately represent the true categorization. Both human and computational classification methods may be more likely to divide longer note types into spurious subclasses simply because long note types have more features that can be observed. This means that statistical tests for patterns consistent with ZLA in birdsong may tend to produce false positives. We did not find evidence for ZLA in Java sparrows, so a tendency towards false positives was not a problem in our study.

A range of phenomena may select against compression of vocal signals (Ferrer-i-Cancho et al., 2013). Java sparrow songs are used in courtship and mate choice, and so may be under different selective pressures compared to other parts of the vocal repertoire. In this case, compression and signal efficiency might not be an advantage, as songs can be honest indicators used to advertise male quality (Gil and Gahr, 2002). This may act against compression in several ways. If longer notes (or the use of multiple long notes) are signals of quality, longer notes may be overrepresented in songs due to their effect on female preference. Similarly, certain note types with particularly attractive qualities, such as 'sexy syllables' in canaries (Leitner et al., 2001; Vallet and Kreutzer, 1995), may be over-represented. Faithful social learning of song features, as is apparent in Java sparrows (Lewis et

al., 2023, 2021), may also act against compression of vocal signals by preventing compression of note types and changes in the proportion of different note types within songs. Unlike human language, the individual 'meaning' of notes and songs, or how these are perceived by the receiver is not known. It is possible that signal compression affects perception by the receiver. In the closely related Bengalese finch, female-directed songs are more consistent in terms of acoustic structure of individual notes and sequence structure (Sakata et al., 2008). This suggests that even small changes to notes within songs may be salient to females. Java sparrows produce a range of call types in addition to songs (Restall, 1996). Calls often have specific meaning (Marler, 2004), and so this subset of the repertoire may exhibit different patterns relating to compression. In the common marmoset, long distance calls, which may be more affected by attenuation and signal degradation, did not conform to ZLA, whereas short range calls were consistent with the expected pattern (Ferrer-i-Cancho and Hernández-Fernández, 2013).

Overall, we find that Java sparrow songs adhere to Menzerath's law - longer sequences are made up of shorter constituent parts. However, they do not correspond with ZLA – more frequently used note types do not have shorter durations. It is likely that these laws reflect different components and constraints on birdsong. Adherence to Menzerath's law may relate to a constraint on song duration, where songs with more notes necessarily have a faster tempo. However, ZLA is more closely related to meaning and information transfer, which is difficult to attribute to birdsong. It has been suggested that some aspects of birdsong may be more suited to comparisons with human music, rather than language, due to their repetitive nature, aspects of performance, and lack of semantic meaning (Rothenberg et al., 2014). The case of meaning and information transfer may be a case where comparisons to music are more appropriate than comparisons to language. Our findings suggest that although there may be some limitations in applying linguistic laws designed for human language to birdsong, they may nonetheless provide insight into communication universals and warrant further investigation.

Author Contributions

RL was responsible for the initial idea and RL, AK, and TG conceptualised the study. The original dataset was collated by RL and MS. RL, MS, SdK, and TG contributed to data extraction. RL, AK and TG conducted the data analysis. The initial draft was written by RL, with all authors contributing to reviewing and editing the manuscript.

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Appendix 1: Results of GLMM examining the effect of song length and note position in songs (with introductory notes removed) on duration. All durations were logged.

Population level			
Question	*Measurement*	*Song length*	*Position in song (logged)*
Are longer songs made up of shorter notes?	Log note duration (log(s))	-0.003 p=0.092	0.042 p=0.263
Do longer songs contain shorter versions of the same note types?	Deviation from note type mean (log(s))	0.00007 p=0.850	0.0016 p=0.949
Are longer songs made up of shorter note types?	Average logged duration of note type (log(s)	-0.003 p=0.003	0.038 p=0.051
Individual level			
Question	*Measurement*	*Mean centred song length*	*Position in song (logged)*
Are longer songs made up of shorter notes?	Log note duration (log(s)	-0.002 p=0.084	0.037 p=0.326
Do longer songs contain shorter versions of the same note types?	Deviation from note type mean (log(s))	-5.59×10^{-5} p=0.899	-0.002 p=0.943
Are longer songs made up of shorter note types?	Average logged duration of note type (log(s))	-0.002 p=0.013	0.033 p=0.084