



## Precise and nonscalar timing of intervals in a bird vocalization

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Animals can time their behaviours at predictable intervals. Their precision for doing so, however, may depend on the duration of the intervals. Laboratory experiments with animals show that timing precision decreases in proportion to the duration of the interval, a phenomenon known as scalar timing. In these experiments, animals are trained to wait for arbitrary intervals of time to get rewarded. In nature, animals time intervals as part of many stereotyped behaviours, regardless of whether the intervals are learned. It is unknown whether timing in this context is also scalar. Here, we tested for scalar timing in the song of the scaly-breasted wren, *Microcerculus marginatus*, which consists of whistles separated by intervals that increase in duration from less than 1 s to more than 10 s. We found that in nearly half of the songs, the timing of whistles was better explained by a model of constant precision rather than one of scalar timing. Moreover, in songs showing support for constant precision, the precision at the longest intervals was higher than that of nonhuman mammals and birds trained in the laboratory for timing presses at an operant device. The precision of the wren is also higher than that of humans, except when the latter count to increase their performance at timing. This study highlights the value of studying natural behaviours to uncover diverse strategies in interval timing among animals.

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Animals time their actions to anticipate external events or to regularly space elements of their behaviour. For example, in the former scenario, the individual awaits the arrival of food after a cue that predicts it, while in the latter, the animal may perform a display, such as singing a song, that involves stopping at regular intervals (Buhusi & Meck, 2005; Meck & MacDonald, 2003; Ng et al., 2020). Both cases require a mechanism to keep track of time, which may consist of neural pacemakers or monitoring of periodic body movements (Merchant & de Lafuente, 2014; Safaie et al., 2020). When anticipating external events, the working memory of the animal accesses a readout of this mechanism to determine how much longer the animal needs to wait (Buhusi & Meck, 2005; Gibbon, 1977; Merchant & de Lafuente, 2014). This ability has been exploited in numerous laboratory experiments of behavioural conditioning, showing that animals as diverse as insects, birds and mammals are capable of learning intervals ranging from a few seconds to several minutes in duration (Bizo et al., 2006; Buhusi & Meck, 2005; Gibbon et al., 1997). Performing stereotyped displays, on the other hand, may not require learning intervals or

loading elapsed times into the working memory of the animal. Nevertheless, the mechanisms for keeping track of time, in principle, do not need to be different from those used in behavioural conditioning. To address the possibility of a common mechanism, we can start by searching for behavioural indicators of such mechanisms in both stereotyped and conditioned behaviours.

In conditioned behaviours, the precision with which animals estimate time intervals has overwhelmingly been shown to decrease as intervals become longer. This phenomenon is known as scalar timing, because the variance of timing estimates scales in proportion to the duration of the timed interval (Bizo et al., 2006; Buhusi & Meck, 2005; Gibbon, 1977; Gibbon et al., 1997; Merchant & de Lafuente, 2014; Toda et al., 2017; Wearden et al., 1997). Scalar timing has been found even in humans, except when they count to keep track of time (Grondin & Killeen, 2009; Hinton & Rao, 2004). Scalar timing occurs in a wide range of interval durations. Examples include durations as short as 450 ms in macaques (Zarco et al., 2009) and as large as 50 min in pigeons (Dews, 1970; Gibbon et al., 1997). Whether the range of scalar timing differs across species is unknown. Several mechanistic models have been proposed to explain scalar timing (Buhusi & Meck, 2005; Buhusi & Oprisan, 2013; Gibbon, 1977; Gibbon et al., 1997). A recent one, based on neural networks, proposed that it emerges spontaneously due to expected levels of electrophysiological noise in the nervous

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system (Buhusi & Oprisan, 2013). Given that the scalar property may arise at such a fundamental level of interval timing, scalar timing may be widespread across behavioural contexts.

On the other hand, specializations for precise timing may be advantageous in some contexts. Animal displays, for instance, often include regular temporal patterns, coordination and synchrony (Bradbury & Vehrencamp, 2011; Hebets et al., 2016). Precision in these behaviours may increase the quality of the displays, allowing signallers to defend resources during agonistic displays or attract a mate during sexual displays. Display signals tend to be stereotyped, meaning that they follow a pattern that is widespread in a population or species, even despite some level of individual variation and regardless of whether the behaviour is innate or learned (Konishi, 2010). Stereotyped behaviours with a temporal component contain only a limited set of interval durations. Repeated practice with timing such intervals may allow animals to increase their precision. Additionally, the persistence of stereotyped behaviours throughout generations may give evolution enough time to come up with specializations that cope with noise in the nervous system and increase timing precision for those behaviours. Despite these possibilities, few measurements of interval timing and associated measurements of precision have been documented in stereotyped behaviours in the wild (Henderson et al., 2006; Ng et al., 2020).

Birdsong, which contains regular silent intervals separating notes, syllables, and even phrases, has been proposed as a model system for studying interval timing in a natural, stereotyped behaviour (Meck & MacDonald, 2003). Birds are capable of fine temporal discrimination of sounds and control of vocal production. For instance, budgerigars, *Melopsittacus undulatus*, and songbirds have a temporal resolution close to 1 ms for discriminating sounds, which is about three times higher than that of humans (Dooling & Prior, 2017). Duetting wrens can precisely coordinate exchanges occurring in half a second or less (Fortune et al., 2011; Logue & Krupp, 2016; Mann et al., 2006; Rivera-Cáceres, 2015). Timing precision and underlying neural mechanisms over longer interval durations in birdsong, however, have not been studied.

One remarkable example of timing intervals of various durations is provided by the song of the scaly-breasted wren, *Microcerculus marginatus*. This small bird, native to tropical forests of Central and South America, produces a song with introductory notes sung at a fast pace, followed by whistles characteristically separated by quiet intervals of increasing duration (Hardy, 1987) (Appendix, Figs A1, A2, A3, Supplementary Video S1). The first interval typically lasts less than 1 s, while the last one may last more than 10 s (Appendix, Fig. A4). Here, we tested for scalar timing in songs of *M. marginatus*. We fitted two mathematical models of increase in interval duration to each song. One model assumed constant precision in timing throughout the song, and the other assumed scalar timing. We then used these models to estimate timing variability and compared the estimates to those reported in the literature for other species of birds and mammals. To our knowledge, this work represents the first test of scalar timing in a stereotyped, natural behaviour.

## METHODS

### Recordings of *M. marginatus* Vocalizations

We downloaded 26 recordings of *M. marginatus* from XenoCanto.org (Xeno-canto Foundation, 2020), from 22 localities, ranging from Panama to Brazil (Appendix, Figs A2, A3, Table A2). We downloaded only those recordings rated as having the highest audio quality ('A' recordings). In addition, we placed a Wildlife Acoustics SM2 recorder (Wildlife Acoustics, Maynard, MA, U.S.A.)

at Mashpi Rainforest Reserve, in northwestern Ecuador, to automatically record the soundscape for 12 h each day, during 1 month in the summer of 2018. For recordings from the same locality, we do not know whether more than one individual was recorded. In the most conservative scenario, assuming that only one individual was recorded per locality ( $N = 23$ ), the number of individuals in our study is in the range of that used in other studies of interval timing (mean  $\pm$  SD =  $13 \pm 11$  individuals, from 5 studies) (Agostino et al., 2020; Bizo et al., 2006; Hinton & Rao, 2004; Toda et al., 2017).

### Measuring Silent Intervals

Recordings were inspected in Audacity v.2.0.53 (<https://audacityteam.org/>). Spectrograms were created using Hanning windows of 512 samples, with 50% overlap between windows. The recordings downloaded from XenoCanto.org had different sampling rates (mean  $\pm$  SD =  $62.0 \pm 25.1$  kHz), and thus the time resolution of the spectrograms varied ( $4.93 \pm 2.32$  ms). Such variation, which was in the order of a few milliseconds, is not expected to have a strong effect on our measurements of interval duration, especially for intervals that are several seconds long in duration. *Microcerculus marginatus* whistles were easy to recognize in the recordings because they are tonal sounds ranging in frequencies between 1 and 9 kHz, with decreasing frequency as the song progresses. Harmonics are sometimes observed, but they are faint. Before producing the whistles, the wrens produce a rapid succession of introductory notes, distinguished from the whistles by having more than one harmonic. Intervals between these notes are short (around 0.5 ms long) and do not seem to change significantly in duration, as seen in a spectrogram (Appendix, Fig. A1). Thus, we did not analyse intervals between the introductory notes. Whistles were manually labelled, zooming as much as possible into the spectrogram to see the onset and offset of sound. Labels were exported from Audacity as text files and analysed in R (R Core Team, 2020). Using a custom script (code available at <https://osf.io/au9jd/>), we extracted the time stamps of the whistles and calculated the duration of silent intervals between them.

### Modelling Precision in Interval Timing of the Song

We fitted models of interval increase to each song. Our models allowed us to test for scalar timing (ST), a condition in which precision progressively decreases as intervals increase in duration, or constant precision (CP) in timing on each song. The models consisted of a series of latent intervals that represented the upward trend in interval duration throughout the song. Increase in latent intervals was modelled using the first-order autoregressive equation

$$t_i = \alpha + \beta t_{i-1} \quad (1)$$

where  $t_i$  is the current interval duration,  $\alpha$  and  $\beta$  are constants, and  $t_{i-1}$  is the previous latent interval duration. Observed intervals were modelled as a draw from a gamma distribution centred around each corresponding latent interval. Gamma distributions were used because time intervals are positive numbers. The spread of the distribution represented the timing variability of *M. marginatus*. Under the CP model, the spread is constant throughout the song. Thus,

$$y_i \sim \text{gamma}(\mu = t_i, \sigma) \quad (2)$$

where  $y_i$  is the observed interval,  $\mu$  and  $\sigma$  are the mean and standard deviation, respectively, of the gamma distribution and  $t_i$  is the current latent interval.

Under the ST model, the coefficient of variation was constant, and thus  $\sigma$  differed for each latent interval and was calculated using the equation

$$\sigma_i = t_i CV \quad (3)$$

where CV is the coefficient of variation.

Models were fitted in 'rstan' (Stan Development Team, 2020). Prior probabilities for all parameters were flat. Constraints were set as follows:  $\sigma$  (CP model) was set to be positive, CV (ST model) was set to be positive and lower than 2 (in a review of the literature, the largest CV reported for interval timing in the range of 1–10 s was less than half that value; Gibbon et al., 1997), and  $t_i$ , the first latent interval, was set to be positive and lower than the average  $y_i$ . The sampling algorithm was the no-U-turn sampler of Hamiltonian Monte Carlo (NUTS) (Betancourt, 2018; Hoffman & Gelman, 2011), which is the default option in 'rstan'. Moreover, this method is recommended when parameters are correlated, such as  $\alpha$  and  $\beta$  in our study ( $R^2 = 0.75$ ,  $P < 0.001$ ). Four parallel NUTS chains were run for 10 000 generations. Convergence was assessed using the Rhat statistic (Gelman & Rubin, 1992; Stan Development Team, 2020) and assumed to be reached if  $Rhat < 1.05$ , which is a widely recommended threshold (Stan Development Team, 2020). Models that did not reach convergence were discarded.

To assess the goodness-of-fit of the autoregressive part of the model to the data, we calculated a pseudocoefficient of determination ( $R^2$ ). The coefficient was calculated from the sample of the posterior distribution with the highest likelihood.  $R^2$  was calculated from the CP model only because more songs reached convergence under that model than under the ST one, and parameter estimates were correlated between both models (Pearson correlation:  $\alpha$ :  $r = 0.95$ ;  $\beta$ :  $r = 0.97$ ).  $R^2$  was calculated by using the equation

$$R^2 = \frac{\sum_{i=1}^n (y_i - t_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (4)$$

where  $n$  is the total number of intervals and  $\bar{y}$  is the average observed interval. To compare support of each song for the CP and the ST models, we compared the likelihoods of the models using Bayes factors (BF). Values of BF larger than 3 for a given song indicated support for CP, while those lower than 0.3 indicated support for ST (Jeffreys, 1998).

#### Comparing Interval Timing of *M. marginatus* to That of Other Species

Our estimates of timing variability were compared to measurements of variability reported in the literature for other species of birds and mammals (Agostino et al., 2020; Bizo et al., 2006; Grondin & Killeen, 2009; Hinton & Rao, 2004; Toda et al., 2017). The literature review was not meant to be exhaustive; rather, it aimed to capture work that is often cited in reviews of interval timing (Buhusi & Meck, 2005; Grondin, 2014; Merchant & de Lafuente, 2014). We searched for measurements of timing variability at durations above 1 s, because most intervals in the song of *M. marginatus* are longer than that (Appendix, Figs A3, A4). Moreover, many studies suggest that at around 1 s, animals use different mechanisms to time intervals (Buhusi & Meck, 2005; Gibbon et al., 1997). Timing above 1 s is known as interval timing and is involved in decision making. Timing below 1 s is known as subsecond timing, which is generally involved in motor coordination (Buhusi & Meck, 2005). Timing variability differs between these two contexts (Buhusi & Meck, 2005; Gibbon et al., 1997). Given that few intervals of *M. marginatus* occur below 1 s, we kept our comparisons in the interval timing range above 1 s to ease comparisons

with the literature. Moreover, timing below 1 s can be influenced by motor constraints, including respiratory rhythms in vocalizations (Lejeune & Wearden, 2006; Love et al., 2019). By keeping comparisons of interval timing above 1 s, we increased the likelihood that the observed differences in timing precision were not related to differences in motor constraints across species.

Studies in primates suggest that rhythmic timing is based on different mechanisms than timing single or nonrhythmic intervals (Gibbon et al., 1997; Merchant et al., 2015; Zarco et al., 2009). Because intervals in the song of the wrens follow a pattern, wrens engage in rhythmic timing. However, we do not know whether the differences in rhythmic timing and nonrhythmic timing in primates translate to birds or to stereotyped, natural behaviours. Because of this uncertainty, we searched for studies of both rhythmic and nonrhythmic timing, thus providing a broad level of comparison regardless of underlying mechanisms. Rhythmic timing is explicitly studied by entraining animals to a rhythm, often containing sub-second intervals, and then testing whether the animal can reproduce the rhythm (Merchant et al., 2015; Zarco et al., 2009). None of the studies that we included in our comparison followed this paradigm. However, all of them were done under circumstances that may promote entrainment, such as testing for timing of the same interval during a session and using constant intertrial intervals. Thus, we considered these studies to have potentially led to rhythmic timing.

When training animals to reproduce an interval, the mean of the produced intervals may deviate from the actual interval used for training, which we will refer to as the 'target interval'. This deviation is known as the bias property of timing and it is independent of scalar timing, which is the variation around the mean produced interval and not the target interval (Pérez & Merchant, 2018). Thus, we compared species across mean produced intervals, and not target intervals (Appendix, Table A3).

In the literature, timing variability is usually reported as coefficients of variation around mean produced intervals. In our study, rather than calculating those coefficients directly from data, we estimated them from our CP and ST models. Direct calculations required the birds to time the same interval several times in a song, rather than progressing through different interval durations as *M. marginatus* does. For songs with strong support for the ST model, the coefficient of variation was directly obtained from the 'maximum a posteriori model' of ST (MAP-ST) fitted to those songs (equation (3)). For songs with strong support for the CP model, the coefficient of variation was derived from the estimate of the standard deviation obtained from the MAP-CP model, using the equation

$$CV_i = \sigma/t_i \quad (5)$$

where  $CV_i$  is the coefficient for a given latent interval  $t_i$ . For songs that did not show support for CP over ST or vice versa, we calculated the coefficient of variation as a function of latent interval under both the MAP-ST and MAP-CP models, as explained above. Then, we averaged the estimates from both models.

## RESULTS

#### Precision in Timing across Intervals in the Song of the Scaly-breasted Wren

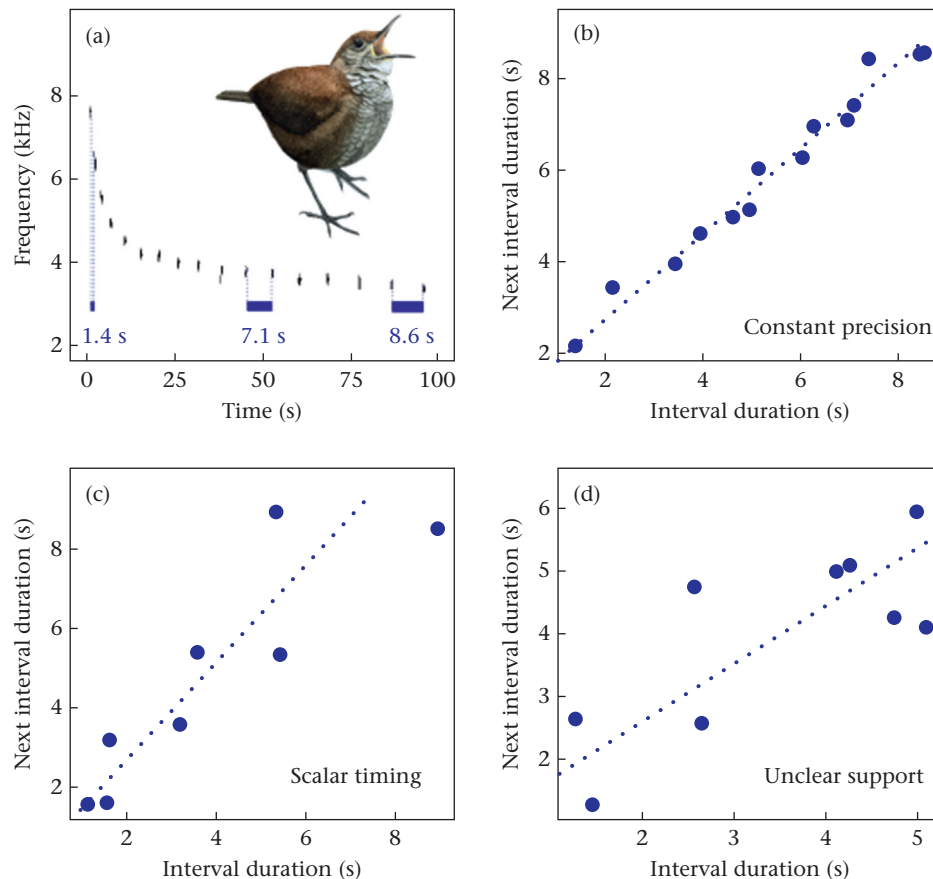
We analysed the sequence of intervals of increasing duration in the song of the scaly-breasted wren. We obtained 34 songs in which duration increased linearly between consecutive intervals (Appendix, Fig. A3). Models of interval increase reached convergence for 28 songs, from 16 localities and thus at least 16 different

individuals (Appendix, Additional methods, Figs A2, A3, Table A1). Models for four songs did not converge under the ST model and for one under the CP model. The sequence of latent intervals was modelled via an autoregressive process (equation (1)). Our model of interval increase assumed that the birds aimed to generate a sequence of latent intervals and that the observed intervals deviated from their latent intervals due to timing variability. According to our model the duration of any latent interval was, on average, equal to the duration of the preceding latent interval times  $1.01 \pm 0.07$  (median  $\pm$  MAD;  $N = 27$  songs) and plus  $0.52 \pm 0.25$  s (median  $\pm$  MAD). As seen, multiplication plays a small, if any, role in increasing the duration of the intervals in the song of *M. marginatus*. However, four songs were outliers and were best modelled by multipliers less than 1. According to our model, latent intervals closely approximated observed intervals (median  $\pm$  MAD across songs:  $R^2 = 0.94 \pm 0.03$ ), suggesting that timing variability was low.

Furthermore, we tested whether intervals followed a pattern of scalar timing (ST), according to which timing variability increased linearly with interval duration. In 10 songs (43.48%), from six different localities, interval timing was better explained by a model assuming constant precision (CP) across intervals rather than one assuming ST (Fig. 1b, Appendix, Fig. A3). ST was preferred over CP in only one song (Fig. 1c). For 12 songs, neither model was preferred (Fig. 1d).

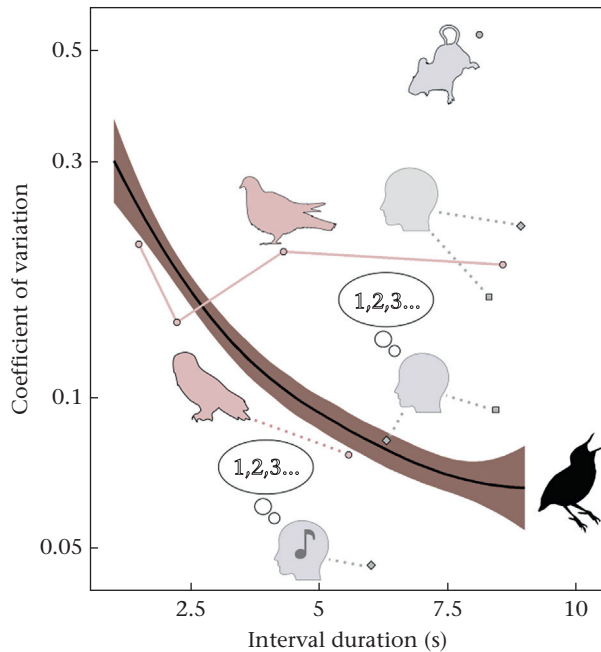
### Analysis of Timing across Multiple Species

To compare the magnitude of timing variability in *M. marginatus* against that of other animals, we collected estimates of timing variability in the literature for intervals between 1 and 10 s long, in mice (Toda et al., 2017), pigeons (Bizo et al., 2006), humans (Grondin & Killeen, 2009; Hinton & Rao, 2004) and an owl (Agostino et al., 2020) (Fig. 2, Appendix, Table A3). We found that at shorter intervals, variability in *M. marginatus* is comparable to that of key-pressing pigeons and humans (Fig. 2). At 8 s, a time point for which we have data also for food anticipation in mice (Fig. 2), *M. marginatus* showed the lowest timing variability among the four species. In contrast to the other behaviours documented in the literature, the natural vocal behaviour in the tawny owl, *Strix aluco*, showed intercall intervals of 6 s with a precision that was slightly higher than that of the wren. The tawny owl produced intervals of only one duration within the range from 1 to 10 s; therefore, we do not know whether relative variability for the owl changes in that range. Humans that count to estimate time intervals tend to have coefficients of variation that are slightly higher or similar to those of the wrens (Fig. 2). Professional musicians with 10 years of experience who count to keep track of time have higher precision at 6 s than the average precision of the wrens (Fig. 2). However, at least two songs of *M. marginatus* showed higher precision than the average precision of the musicians (Appendix, Fig. A5).



**Figure 1.** Timing precision in the song of *M. marginatus*. (a) Spectrogram of a song shows an increase in the duration of intervals between notes. Sample durations are shown in blue for the beginning, middle and end of the song. Inset: illustration of *M. marginatus* by Gonzalo Nazati. (b) Lag plot of the song in (a), an example in which the timing of notes is better explained by constant precision (CP) than by scalar timing (ST) (Bayes factors for CP over ST ( $BF_{CP/ST}$ )  $> 3$  in 10 out of 23 songs; Appendix, Fig. A4). Such precision is reflected in the uniform deviation of the intervals from the trend line (dashed). (c) Lag plot of the only song in our study for which the models supported ST [ $BF_{CP/ST} < 1/3$ ]. In this case, the deviation from the trend line scales in proportion with interval duration. (d) Lag plot of an exemplar song for which neither scalar timing nor constant precision was supported over the other [ $1/3 \leq BF_{CP/ST} \leq 3$ ]. Examples for (a–b), (c) and (d) are songs 18, 30 and 15, respectively (credits in the Appendix, Tables A1, A2). Songs 18 and 30 were downloaded from Xeno-Canto and used under a CC BY-NC-SA 3.0 license.





**Figure 2.** Comparison of precision in interval timing in the range of 1–10 s, between songs consistent with constant precision ( $BF_{CP/ST} > 3$ ) in *M. marginatus* and timing behaviours in other species of birds and mammals. Precision is measured using coefficients of variation (CV); smaller CVs indicate higher precision. At intervals longer than 3 s, estimates of precision in the songs of *M. marginatus* (black line, LOESS average; shade, 95% confidence interval of average) are higher than published values for pigeons (Bizo et al., 2006), mice (Toda et al., 2017) and humans (Hinton & Rao, 2004). Depending on the study, humans that count to operationally increase precision of timing have lower (Hinton & Rao, 2004) or similar precision to that of the wren (Grondin & Killeen, 2009). In the plot, the only humans who have higher precision than the wrens are musicians with more than 10 years of training (human silhouette with musical note (Grondin & Killeen, 2009). Outliers among the songs of *M. marginatus*, however, show higher precision than that of the musicians (Appendix, Fig. A5). At intervals near 6 s, tawny owls have slightly higher precision than the wren (Agostino et al., 2020). Intervals produced by the owl and the wren were measured in natural vocalizations. All other data come from laboratory studies of behavioural conditioning. For *M. marginatus*, interval durations correspond to estimates of latent intervals of the maximum a posteriori model of constant precision (MAP-CP) of each song (equations (1), (2)). For the other species, the intervals are mean produced intervals. CVs are displayed on a logarithmic scale. Estimates of CV for *M. marginatus* were derived from MAP-CP models (equation (5)). Black silhouette, *M. marginatus*; pink, other birds; grey, mammals. Solid lines connect data points from the same study and, in the case of humans, the same condition of testing (counting versus no counting). For humans, symbols distinguish the studies from which the data were sourced: diamonds: Grondin and Killeen (2009); squares: Hinton and Rao (2004) (see Appendix, Table A3).

## DISCUSSION

We tested whether interval timing in the song of *M. marginatus* is scalar, such that variability in timing intervals scales with interval duration. A model of scalar timing versus one of constant precision was preferred for only one song in our study (Fig. 1c, Appendix, Fig. A4). In contrast, the model of constant precision was preferred for nearly half of the songs of *M. marginatus* (Fig. 1b, Appendix, Fig. A4). Thus, our results contrast with widespread support in the literature for scalar timing in animals (Gibbon, 1977; Gibbon et al., 1997; Grondin, 2014; Hinton & Rao, 2004; Ng et al., 2020; Toda et al., 2017), suggesting that the wrens have specialized mechanisms for timing their songs. Humans have also been reported to have variability that is lower than expected by scalar timing, but only when humans count to estimate time (Hinton & Rao, 2004; Wearden et al., 1997). Songs supporting constant precision over scalar timing came from six localities (Appendix, Fig. A3), and thus were not limited to a single individual or

locality. The extent to which constant precision occurs in the species, however, requires more detailed quantification. Further research on the mechanisms by which *M. marginatus* achieves such precision is also necessary.

Violations to scalar timing have been reported in other nonhuman animals, such as pigeons (Bizo et al., 2006; Grondin, 2014). In those cases, precision increases for timing intervals in a restricted range of 1–3 s (Fig. 2). Beyond this range, however, it decreases and reaches values that are even lower than those expected by scalar timing (Bizo et al., 2006). In contrast, *M. marginatus* is capable of precision that is higher than expected by scalar timing for intervals ranging from 1 to 10 s (Appendix, Fig. A4). Moreover, *M. marginatus* is capable of higher precision than that reported for interval timing in conditioned behaviours (Fig. 2) (Bizo et al., 2006; Grondin & Killeen, 2009; Hinton & Rao, 2004; Toda et al., 2017). At 8 s, songs that supported constant precision showed lower variability than that of four species of animals for which there are available data on timing intervals of 1–10 s in duration (Fig. 2). The precision of the wren was even higher than that of humans, unless humans count to aid themselves in timing (Grondin & Killeen, 2009; Hinton & Rao, 2004). Professional musicians who count to time had higher precision than other humans and animals, including *M. marginatus* (Fig. 2). Practice with producing intervals in music may explain the high precision of musicians (Grondin & Killeen, 2009). However, two songs of *M. marginatus* showed even higher precision than the average of the musicians (Appendix, Fig. A5). These songs could be outliers resulting from natural individual variation in the species. Alternatively, just as practice increases precision in musicians, the high precision in the two songs of the wren may also result from practice.

To achieve high levels of precision, wrens may use mechanisms that are different from those used for timing conditioned behaviours (see Appendix, Additional Discussion). Interval timing during conditioning, despite being scalar, can accommodate intervals of arbitrary duration (Bizo et al., 2006; Buhusi & Meck, 2005; Gámez et al., 2018; Gibbon, 1977; Gibbon et al., 1997; Grondin, 2014; Hinton & Rao, 2004; Merchant & de Lafuente, 2014; Wearden et al., 1997; Zarco et al., 2009). In the song of the wren, the pattern of interval timing is stereotyped, because throughout most of the range of the species, the increase in interval can be explained by an autoregressive process with little variation across individuals (Fig. 1, Appendix, Fig. A3). We propose two hypotheses that link stereotypy to timing precision. One hypothesis assumes that timing in the song of the wren is learned and the other that it is innate. *Microcerculus marginatus* belongs to a clade of birds known as oscines, which contains several species in which timing of song has both learned and innate components (Love et al., 2019; Matheson & Sakata, 2015; Mets & Brainard, 2018). Thus, these hypotheses are not mutually exclusive.

Oscines learn to sing by memorizing a song produced by other birds and then practising the song to correct errors in production (Sober & Brainard, 2009). Most studies on error-correction in birdsong are based on correction of deviations in pitch. We propose that practice may also improve the precision of timing of the songs. This possibility could explain the variance that we found in timing precision across songs (Fig. 1, Appendix, Fig. A5). Birds that show scalar timing or have low precision may be at earlier stages of practice. In humans, practice has been proposed to explain the low coefficient of variation among professional musicians with more than 10 years of experience (Grondin & Killeen, 2009) (Fig. 2). It is possible that practice has a similar effect in *M. marginatus*.

On the other hand, precise timing in the song of *M. marginatus* may be genetically encoded. Specialized circuits in the brain of *M. marginatus* may produce the pattern of intervals in absence of

learning. These circuits may cope with physiological noise in neurons, which has been proposed to lead to scalar timing (Buhusi & Oprisan, 2013). Neural specializations that accomplish this effect may need a long time to evolve, and thus, the behavioural output may evolve slowly, leading to stereotypy. Under this scenario, variation in timing precision, which we found in *M. marginatus* (Fig. 1, Appendix, Fig. A5), may be explained by maturational effects or biological differences across individuals, such as sex differences. The latter is a possibility if precision is sexually selected and such selection is stronger for one sex.

Across animals, conspecific vocalizations tend to be stereotyped, and thus precise timing may not be uncommon among vocalizations. Indeed, precise timing in vocalizations may help convey information about the reproductive or territorial status of the sender, which is encoded in the temporal structure of the signal (Grafe, 1996; Hultsch & Todt, 1982; Ng et al., 2020). In this study, we compared the vocalization of the wren to the sequence of calls of the distantly related tawny owl (Agostino et al., 2020), in which intervals of 6 s were timed with a precision that were even higher than that of the scaly-breasted wren (Fig. 2). Owls are not part of a clade of birds considered to have vocal production learning (Wirthlin et al., 2019), and thus, their timing may be innate. It is possible that precise timing in bird vocalizations may have already been present at least in the last common ancestor of telluraves, which is a clade that not only contains wrens and owls, but also falcons, parrots, kingfishers and eagles (Yuri et al., 2013). The last common ancestor of these animals may have had neural circuits for precise timing of their vocalizations. In lineages that descended from that ancestor, the circuits may have evolved independently, leading to species-specific innate temporal patterns. To address the possibility of widespread precise timing in telluraves, and birds in general, we need large comparative studies of interval timing in bird vocalizations.

Scalar timing has been proposed to emerge from natural noise in neural circuits, and thus, it may be the default mode of interval timing in animals (Buhusi & Oprisan, 2013). That *M. marginatus* is capable of a nonscalar, precise mode of timing strongly suggests the presence of a mechanism that allows the wren to escape inaccuracies emerging from neural noise and which may be different from the mechanism used by animals in behavioural conditioning (Buhusi & Meck, 2005; Buhusi & Oprisan, 2013; Gibbon, 1977; Gibbon et al., 1997). Moreover, the discovery of precise timing in a birdsong highlights the importance of studying diverse natural behaviours to account for the range of timing strategies used by animals.

## Data Availability

Data and code are available at <https://osf.io/au9jd>.

## Author Contributions

Conceptualization: C.A.R.S., F.G.D., J.A.C.; Methodology: C.A.R.S., F.G.D., J.A.C.; Investigation: C.A.R.S., F.G.D.; Visualization: C.A.R.S.; Funding acquisition: C.A.R.S., F.G.D., J.A.C.; Project administration: C.A.R.S.; Supervision: J.A.C.; Writing – original draft: C.A.R.S.; Writing – review & editing: C.A.R.S., F.G.D., J.A.C.

## Declaration of Competing Interest

We declare that we have no competing interests.

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## Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.06.004>.

## References

- Agostino, P. V., Lusk, N. A., Meck, W. H., Golombek, D. A., & Peryer, G. (2020). Daily and seasonal fluctuation in tawny owl vocalization timing. *PLoS One*, *15*(4), Article e0231591. <https://doi.org/10.1371/journal.pone.0231591>
- Betancourt, M. (2018). *A conceptual introduction to Hamiltonian Monte Carlo*. arXiv: 1701.02434v2 [stat.ME].
- Bizo, L. A., Chu, J. Y. M., Sanabria, F., & Killeen, P. R. (2006). The failure of Weber's law in time perception and production. *Behavioural Processes*, *71*(2–3), 201–210. <https://doi.org/10.1016/j.beproc.2005.11.006>
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, *6*(10), 755–765. <https://doi.org/10.1038/nrn1764>
- Buhusi, C. V., & Oprisan, S. A. (2013). Time-scale invariance as an emergent property in a perceptron with realistic, noisy neurons. *Behavioural Processes*, *95*, 60–70. <https://doi.org/10.1016/j.beproc.2013.02.015>
- Chi, Z., & Margoliash, D. (2001). Temporal precision and temporal drift in brain and behavior of zebra finch song. *Neuron*, *32*(5), 899–910. [https://doi.org/10.1016/S0896-6273\(01\)00524-4](https://doi.org/10.1016/S0896-6273(01)00524-4)
- Dews, P. B. (1970). The theory of fixed-interval responding. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules. The century psychology series* (pp. 43–61). New York: Appleton-Century-Crofts.
- Dooling, R. J., & Prior, N. H. (2017). Do we hear what birds hear in birdsong? *Animal Behaviour*, *124*, 283–289. <https://doi.org/10.1016/j.anbehav.2016.10.012>
- Fortune, E. S., Rodríguez, C., Li, D., Ball, G. F., & Coleman, M. J. (2011). Neural mechanisms for the coordination of duet singing in wrens. *Science*, *334*(6056), 666–670. <https://doi.org/10.1126/science.1209867>
- Gámez, J., Mendoza, G., Prado, L., Betancourt, A., & Merchant, H. (2019). The amplitude in periodic neural state trajectories underlies the tempo of rhythmic tapping. *PLoS Biology*, *17*(4), Article e3000054. <https://doi.org/10.1371/journal.pbio.3000054>
- Gámez, J., Yc, K., Ayala, Y. A., Dotov, D., Prado, L., & Merchant, H. (2018). Predictive rhythmic tapping to isochronous and tempo changing metronomes in the nonhuman primate. *Annals of the New York Academy of Sciences*, *1423*(1), 396–414. <https://doi.org/10.1111/nyas.13671>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472. <https://doi.org/10.1214/ss/1177011136>
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*(3), 279–325. <https://doi.org/10.1037/0033-295X.84.3.279>
- Gibbon, J., Malapani, C., Dale, C. L., & Gallistel, C. (1997). Toward a neurobiology of temporal cognition: Advances and challenges. *Current Opinion in Neurobiology*, *7*(2), 170–184. [https://doi.org/10.1016/S0959-4388\(97\)80005-0](https://doi.org/10.1016/S0959-4388(97)80005-0)

- Grafe, T. U. (1996). The function of call alternation in the African reed frog (*Hyperolius marmoratus*): Precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology*, 38(3), 149–158. <https://doi.org/10.1007/s002650050227>
- Grondin, S. (2014). About the (non)scalar property for time perception. *Advances in Experimental Medicine and Biology*, 829, 17–32. [https://doi.org/10.1007/978-1-4939-1782-2\\_2](https://doi.org/10.1007/978-1-4939-1782-2_2)
- Grondin, S., & Killeen, P. R. (2009). Tracking time with song and count: Different Weber functions for musicians and nonmusicians. *Attention, Perception, & Psychophysics*, 71(7), 1649–1654. <https://doi.org/10.3758/APP.71.7.1649>
- Hardy, J. W. (1987). The vocalizations of the slender-billed wren (*Hylorchilus sumichrasti*): Who are its close relatives? *Auk*, 104(3), 528–530. <https://doi.org/10.2307/4087557>
- Hebets, E. A., Barron, A. B., Balakrishnan, C. N., Hauber, M. E., Mason, P. H., & Hoke, K. L. (2016). A systems approach to animal communication. *Proceedings of the Royal Society B: Biological Sciences*, 283(1826), Article 20152889. <https://doi.org/10.1098/rspb.2015.2889>
- Henderson, J., Hurly, T. A., Bateson, M., & Healy, S. D. (2006). Timing in free-living rufous hummingbirds, *Selasphorus rufus*. *Current Biology*, 16(5), 512–515. <https://doi.org/10.1016/j.cub.2006.01.054>
- Hinton, S. C., & Rao, S. M. (2004). One-thousand one... one-thousand two...: Chronometric counting violates the scalar property in interval timing. *Psychonomic Bulletin & Review*, 11(1), 24–30. <https://doi.org/10.3758/bf03206456>
- Hoffman, M. D., & Gelman, A. (2011). *The no-U-turn sampler: Adaptively setting path lengths in Hamiltonian Monte Carlo*. arXiv:1111.4246 [stat.CO].
- Hultsch, H., & Todt, D. (1982). Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). *Behavioral Ecology and Sociobiology*, 11(4), 253–260. <https://doi.org/10.1007/BF00299302>
- Jarvis, E. D. (2019). Evolution of vocal learning and spoken language. *Science*, 366(6461), 50–54. <https://doi.org/10.1126/science.aax0287>
- Jeffreys, H. (1998). *The theory of probability*. Oxford: Clarendon Press.
- Konishi, M. (2010). From central pattern generator to sensory template in the evolution of birdsong. *Brain and Language*, 115(1), 18–20. <https://doi.org/10.1016/j.bandl.2010.05.001>
- Lejeune, H., & Wearden, J. H. (2006). Scalar properties in animal timing: Conformity and violations. *Quarterly Journal of Experimental Psychology*, 59(11), 1875–1908. <https://doi.org/10.1080/17470210600784649>
- Logue, D. M., & Krupp, D. B. (2016). Duetting as a collective behavior. *Frontiers in Ecology and Evolution*, 4, 7. <https://doi.org/10.3389/fevo.2016.00007>
- Long, M. A., & Fee, M. S. (2008). Using temperature to analyse temporal dynamics in the songbird motor pathway. *Nature*, 456(7219), 189–194. <https://doi.org/10.1038/nature07448>
- Love, J., Hoepfner, A., & Goller, F. (2019). Song feature specific analysis of isolate song reveals interspecific variation in learned components. *Developmental Neurobiology*, 79(4), 350–369. <https://doi.org/10.1002/dneu.22682>
- Lynch, G. F., Okubo, T. S., Hanuschkin, A., Hahnloser, R. H. R., & Fee, M. S. (2016). Rhythmic continuous-time coding in the songbird analog of vocal motor cortex. *Neuron*, 90(4), 877–892. <https://doi.org/10.1016/j.neuron.2016.04.021>
- Mann, N. I., Dingess, K. A., & Slater, P. J. B. (2006). Antiphonal four-part synchronized chorusing in a Neotropical wren. *Biology Letters*, 2(1), 1–4. <https://doi.org/10.1098/rsbl.2005.0373>
- Manning, F., & Schutz, M. (2013). Moving to the beat improves timing perception. *Psychonomic Bulletin & Review*, 20(6), 1133–1139. <https://doi.org/10.3758/s13423-013-0439-7>
- Matheson, A. M. M., & Sakata, J. T. (2015). Relationship between the sequencing and timing of vocal motor elements in birdsong. *PLoS One*, 10(12), Article e0143203. <https://doi.org/10.1371/journal.pone.0143203>
- Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W., & Bethge, M. (2018). DeepLabCut: Markerless pose estimation of user-defined body parts with deep learning. *Nature Neuroscience*, 21(9), 1281–1289. <https://doi.org/10.1038/s41593-018-0209-y>
- Meck, W., & MacDonald, C. (2003). Time flies and may also sing: Cortico-striatal mechanisms of interval timing and birdsong. In W. Meck (Ed.), *Functional and neural mechanisms of interval timing* (Vol. 19). Boca Raton, FL: CRC Press.
- Merchant, H., & de Lafuente, V. (2014). Introduction to the neurobiology of interval timing. *Advances in Experimental Medicine and Biology*, 829, 1–13. [https://doi.org/10.1007/978-1-4939-1782-2\\_1](https://doi.org/10.1007/978-1-4939-1782-2_1)
- Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M., & Fitch, W. T. (2015). Finding the beat: A neural perspective across humans and non-human primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), Article 20140093. <https://doi.org/10.1098/rstb.2014.0093>
- Mets, D. C., & Brainard, M. S. (2018). Genetic variation interacts with experience to determine interindividual differences in learned song. *Proceedings of the National Academy of Sciences of the United States of America*, 115(2), 421–426. <https://doi.org/10.1073/pnas.1713031115>
- Ng, L., Garcia, J. E., Dyer, A. G., & Stuart-Fox, D. (2020). The ecological significance of time sense in animals. *Biological Reviews of the Cambridge Philosophical Society*, 96(2), 526–540. <https://doi.org/10.1111/brv.12665>
- Patel, A. D. (2006). Musical rhythm, linguistic rhythm, and human evolution. *Music Perception*, 24(1), 99–104. <https://doi.org/10.1525/mp.2006.24.1.99>
- Pérez, O., & Merchant, H. (2018). The synaptic properties of cells define the hallmarks of interval timing in a recurrent neural network. *Journal of Neuroscience*, 38(17), 4186–4199. <https://doi.org/10.1523/JNEUROSCI.2651-17.2018>
- Picardo, M. A., Merel, J., Katlowitz, K. A., Vallentin, D., Okobi, D. E., Benezra, S. E., Clary, R. C., Pnevmatikakis, E. A., Paninski, L., & Long, M. A. (2016). Population-level representation of a temporal sequence underlying song production in the zebra finch. *Neuron*, 90(4), 866–876. <https://doi.org/10.1016/j.neuron.2016.02.016>
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ravignani, A., Dalla Bella, S., Falk, S., Kello, C. T., Noriega, F., & Kotz, S. A. (2019). Rhythm in speech and animal vocalizations: A cross-species perspective. *Annals of the New York Academy of Sciences*, 1453(1), 79–98. <https://doi.org/10.1111/nyas.14166>
- Ravignani, A., Fitch, W. T., Hanke, F. D., Heinrich, T., Hurgitsch, B., Kotz, S. A., Scharff, C., Stoeger, A. S., & de Boer, B. (2016). What pinnipeds have to say about human speech, music, and the evolution of rhythm. *Frontiers in Neuroscience*, 10, 274. <https://doi.org/10.3389/fnins.2016.00274>
- Rivera-Cáceres, K. D. (2015). Plain wrens *Cantorchilus modestus zeledoni* adjust their singing tempo based on self and partner's cues to perform precisely coordinated duets. *Journal of Avian Biology*, 46(4), 361–368. <https://doi.org/10.1111/jav.00575>
- Safaie, M., Jurado-Parras, M.-T., Sarno, S., Louis, J., Karoutchi, C., Petit, L. F., Pasquet, M. O., Eloy, C., & Robbe, D. (2020). Turning the body into a clock: Accurate timing is facilitated by simple stereotyped interactions with the environment. *Proceedings of the National Academy of Sciences of the United States of America*, 117(23), 13084–13093. <https://doi.org/10.1073/pnas.1921226117>
- Sober, S. J., & Brainard, M. S. (2009). Adult birdsong is actively maintained by error correction. *Nature Neuroscience*, 12(7), 927–931. <https://doi.org/10.1038/nn.2336>
- Stan Development Team. (2020). *RStan: The R interface to Stan* (Version 2.19) <https://mc-stan.org/>.
- Toda, K., Lusk, N. A., Watson, G. D. R., Kim, N., Lu, D., Li, H. E., Meck, W. H., & Yin, H. H. (2017). Nigroreticular stimulation stops interval timing in mice. *Current Biology*, 27(24), 3763–3770. <https://doi.org/10.1016/j.cub.2017.11.003>. e3.
- Wearden, J. H., Denovan, L., Fakhri, M., & Haworth, R. (1997). Scalar timing in temporal generalization in humans with longer stimulus durations. *Journal of Experimental Psychology: Animal Behavior Processes*, 23(4), 502–511.
- Wirthlin, M., Chang, E. F., Knörnschild, M., Krubitzer, L. A., Mello, C. V., Miller, C. T., Penning, A. R., Vernes, S. C., Tchernichovski, O., & Yartsev, M. M. (2019). A modular approach to vocal learning: Disentangling the diversity of a complex behavioral trait. *Neuron*, 104(1), 87–99. <https://doi.org/10.1016/j.neuron.2019.09.036>
- Xeno-canto Foundation. (2020). *xeno-canto: Sharing bird sounds from around the world*. Retrieved from <https://www.xeno-canto.org/>. (Accessed 16 July 2020).
- Yuri, T., Kimball, R. T., Harshman, J., Bowie, R. C. K., Braun, M. J., Chojnowski, J. L., Han, K.-L., Hackett, S. J., Huddleston, C. J., Moore, W. S., Reddy, S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Braun, E. L. (2013). Parsimony and model-based analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology*, 2(1), 419–444. <https://doi.org/10.3390/biology2010419>
- Zarco, W., Merchant, H., Prado, L., & Mendez, J. C. (2009). Subsecond timing in primates: Comparison of interval production between human subjects and rhesus monkeys. *Journal of Neurophysiology*, 102(6), 3191–3202. <https://doi.org/10.1152/jn.00066.2009>

## Appendix

### Additional Methods

#### Filtering out other interval sequences produced by *M. marginatus*

In many cases, the intervals tended to increase in duration throughout the entire song. In others, the last part of the song was not characterized by this increase, but followed other, complex patterns. These patterns are seen in scatterplots of interval duration against position in the song (Appendix, Fig. A2). We selected only the portion of the song in which intervals tended to increase in duration. In some songs from Costa Rica and Panama, the increase followed a sigmoidal trajectory. Given its restricted geographical range, this type of interval progression may have evolved, either culturally or biologically, in isolation from the more widespread type of increase. Modelling sigmoidal trajectories is difficult using a simple, constant rule applied to each interval, such as the one we used to model the interval progression in all other songs. Although studying the sigmoidal patterns may reveal important insights on interval timing in *M. marginatus*, we excluded them from this study ( $N = 6$ ) because they may constitute a different type of progression, with its unique evolutionary trajectory.

### Additional Discussion

#### Potential mechanisms for precise timing

How can wrens time intervals so precisely? Monitoring periodic body movements is known to improve precision in interval timing



in pigeons (Manning & Schutz, 2013; Safaie et al., 2020). The wren may similarly monitor periodic breath cycles or tail movements. Unfortunately, available videos of *M. marginatus* singing (Table A4) were of poor resolution or too short, showing the bird during only two or three internote intervals. These conditions did not allow us to identify whether periodic body movements could match the offset of intervals, but computer vision in a large sample of high-quality videos (Mathis et al., 2018) may allow identification of such movements. Alternatively, neural innovations specific to vocal behaviour may be linked to the observed precision. In other species of songbirds, specialized circuits in the forebrain control timing in song; specifically, in HVC (proper name) and the robust nucleus of the arcopallium (Chi & Margoliash, 2001; Long & Fee, 2008; Lynch et al., 2016; Picardo et al., 2016). Firing rates in these circuits are correlated with timing of individual elements in song, and experimental manipulations of neural activity change the pace of song (Chi & Margoliash, 2001; Long & Fee, 2008; Lynch et al., 2016; Picardo et al., 2016). If neural specializations subserve precise timing in the wren, they are likely found in these circuits.

The comparisons to other species showed that at 6 s intervals, the precision of the tawny owl is very close to that of the wren, and even slightly higher (Fig. 2). Although the tawny owl precisely times one interval, *M. marginatus* can do so for several intervals of increasing duration, suggesting a more advanced form of interval timing. In contrast to owls, wrens are species of oscines, a clade of birds in which vocal production learning (VPL) is widespread (Jarvis, 2019; Wirthlin et al., 2019). This trait has been proposed to coevolve with precise rhythm perception, production and entrainment (Patel, 2006; Ravignani et al., 2016), all of which may be related to interval timing (Ravignani et al., 2019). As it has already been seen in other species of oscines, the same neural circuits that are specialized for VPL control the timing of elements in song (Chi & Margoliash, 2001; Long & Fee, 2008; Lynch et al., 2016; Picardo et al., 2016). Thus, those circuits may confer wrens or oscines the ability for an advanced form of interval timing for song. The song system has been proposed to have evolved from motor circuits in the forebrain (Jarvis, 2019). In primates, motor circuits show neural dynamics that correlate with interval timing and with the scalar property (Gámez et al., 2019). Thus, interval timing in birdsong may be subserved by circuits that evolved from those that were already specialized for interval timing, although showing scalar timing. Specializations for precise timing may have evolved after the song system split from other motor circuits.

**Table A1**  
Songs of *M. marginatus* analysed in this study

Song	Recording	Features
01	ML317472601	Linear increase
02	ML317473381	Undetermined
03	ML317473391	Linear increase
04	ML317473881	Linear increase
05	ML317473961	Linear increase
06	ML317474541	Linear increase
07	ML317474911	Linear increase
08	ML317475451	Undetermined
09	ML317475481	Undetermined
10	ML317475921	Undetermined
11	ML317476031	Linear increase
12	ML317476121	Linear increase
13	ML317476851	Linear increase
14	ML317534211	Linear increase
15	ML317534711	Linear increase
16	XC112248	Linear increase, oscillation
17	XC135661	Linear increase
18	XC140764	Linear increase
19	XC140764	Linear increase
20	XC140764	Linear increase
21	XC143069	Linear increase
22	XC15766	Linear increase, oscillation
23	XC16058	Linear increase
24	XC17512	Linear increase
25	XC217258	Linear increase
26	XC225748	Linear increase
27	XC251125	Linear increase
28	XC253667	Sigmoidal trajectory
29	XC262461	Linear increase
30	XC262462	Linear increase, oscillation
31	XC262993	Linear increase
32	XC271375	Sigmoidal trajectory
33	XC271376	Sigmoidal trajectory
34	XC29629	Linear increase, oscillation
35	XC30935	Linear increase, oscillation
36	XC30936	Linear increase
37	XC372318	Sigmoidal trajectory
38	XC37428	Linear increase
39	XC387985	Linear increase, oscillation
40	XC391560	Linear increase
41	XC391560	Linear increase
42	XC70709	Sigmoidal trajectory
43	XC71409	Sigmoidal trajectory, oscillation
44	XC96647	Linear increase, oscillation



**Table A2**Recordings of *M. marginatus* analysed in this study and deposited at [Xeno-Canto.org](https://xeno-canto.org)

Recording	Recordist	Locality	Latitude	Longitude
ML317472601	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317473381	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317473391	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317473881	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317473961	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317474541	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317474911	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317475451	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317475481	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317475921	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317476031	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317476121	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317476851	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317534211	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
ML317534711	Fernanda Duque	Sendero Aulladores, Mashpi Lodge, Pichincha, Ecuador	0.164444	-78.88639
XC112248	Taylor Brooks	Playa de Oro, Esmeraldas Province, Ecuador, Ecuador	0.972300	-78.55530
XC135661	Scott Olmstead	Reserva Mangaloma, Pichincha, Ecuador	0.122800	-78.99420
XC140764	Nick Athanas	Ecolodge El Almejal, Colombia	6.113300	-77.43360
XC143069	Fernand Deroussen	Henri Pittier National Park, Mario Briceno Iragorry, Aragua, Venezuela	10.349500	-67.68430
XC15766	Bradley Davis	Pousada Rio Azul, PA, Brazil	-9.245600	-55.98700
XC16058	Ken Allaire	Yuturi Lodge, Orellana, Ecuador	-0.548900	-76.04140
XC17512	Andrew Spencer	Yasuní Research Station, Parque Nacional Yasuní, Orellana, Ecuador	-0.674200	-76.39780
XC217258	Cedric Mroczko	Milpe, Pichincha, Ecuador	0.028700	-78.86280
XC225748	Peter Boesman	Presa Las Cuevas road, Tachira, Venezuela	7.933333	-71.78333
XC251125	Niels Krabbe	Pichincha: Río Guaycuyacu, Ecuador	0.217000	-78.89000
XC253667	William Adsett	Altos del Torreón, Altos de Cerro Azul, Panama	9.166000	-79.40400
XC262461	Olaf Jahn	Esmeraldas: Playa de Oro, village and vicinity, Río Santiago, Ecuador	0.883000	-78.80000
XC262462	Olaf Jahn	Esmeraldas: Playa de Oro, village and vicinity, Río Santiago, Ecuador	0.883000	-78.80000
XC262993	Jonas Nilsson	Los Ríos: 'Río Palenque Science Center', Ecuador	-0.593000	-79.36300
XC271375	Peter Boesman	Cerro Azul area, Panama	9.221621	-79.40068
XC271376	Peter Boesman	Altos del Maria area, Panama	8.646428	-80.03100
XC29629	Rick Bowers	Estación Biológica Las Cruces, San Vito de Coto Brus, Puntarenas, Costa Rica	8.783400	-82.95010
XC30935	Andrew Spencer	Rio Silanche, Pedro Vicente Maldonado, Pichincha, Ecuador	0.143100	-79.13340
XC30936	Andrew Spencer	Rio Silanche, Pedro Vicente Maldonado, Pichincha, Ecuador	0.143100	-79.13340
XC372318	Kent Livezey	Metetí, Darién, Panama	8.505400	-77.97590
XC37428	Fernando Fávoro	Serra do Pardo National Park, near Pardo River, Altamira, Pará., Brazil	-5.501400	-53.27950
XC387985	Rolf A. de By	Buenaventura, Valle del Cauca, Colombia	3.620000	-76.89920
XC391560	George Paul	Orellana: Right (s) bank of Río Napo at Pompeya, Ecuador	-0.450000	-76.58300
XC70709	William Adsett	Altos del Torreón, Altos de Cerro Azul, Eastern Panama, Panama	9.166700	-79.40010
XC71409	Andrew Spencer	Las Esquinas Rainforest Lodge, Puntarenas, Costa Rica	8.675900	-83.20510
XC96647	Andrew Spencer	Playa de Oro, Esmeraldas, Ecuador	0.850100	-78.76670

**Table A3**

Coefficients of variation obtained from other studies

Target interval (s)	Mean produced interval (s)	Coefficient of variation	Species	Source
1.00	1.50	0.20	<i>Columba livia</i>	Bizo et al. (2006)
2.00	2.00	0.14	<i>Columba livia</i>	Bizo et al. (2006)
4.00	4.31	0.20	<i>Columba livia</i>	Bizo et al. (2006)
–	5.57	0.34	<i>Strix aluco</i>	Agostino et al. (2020)
6.00	6.00	0.05 <sup>a</sup>	<i>Homo sapiens</i>	Grondin and Killeen (2009)
6.00	6.30	0.08 <sup>b</sup>	<i>Homo sapiens</i>	Grondin and Killeen (2009)
6.00	8.90	0.22	<i>Homo sapiens</i>	Grondin and Killeen (2009)
7.50	8.10	0.54	<i>Mus musculus</i>	Toda et al. (2017)
8.00	8.56	0.19	<i>Columba livia</i>	Bizo et al. (2006)
8.00	8.42	0.10 <sup>b</sup>	<i>Homo sapiens</i>	Hinton and Rao (2004)
8.00	8.29	0.16	<i>Homo sapiens</i>	Hinton and Rao (2004)

These data points are plotted in Fig. 2. Here, we show the studies corresponding to each data point. Target intervals are the intervals used to train subjects to time in operant conditioning studies. The mean produced interval is the mean of the intervals produced by the subjects. Coefficients of variation are calculated around the mean produced intervals. In the study of Agostino et al. (2020), variability was studied in natural vocalizations, and thus no target intervals were presented to the subjects.

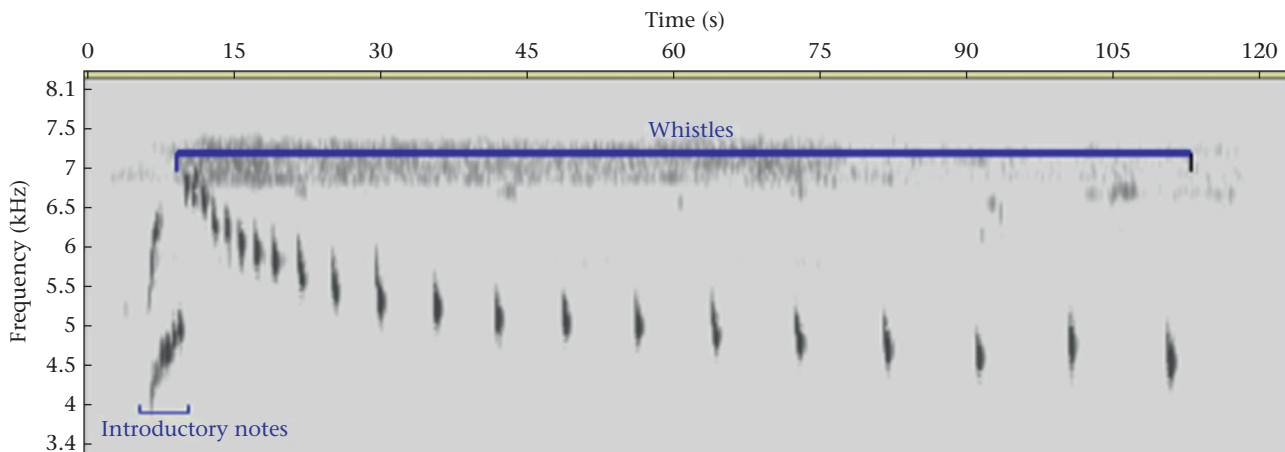
<sup>a</sup> Variability of professional musicians with at least 10 years of experience who counted to estimate the interval.

<sup>b</sup> Variability of humans who counted to estimate the interval.

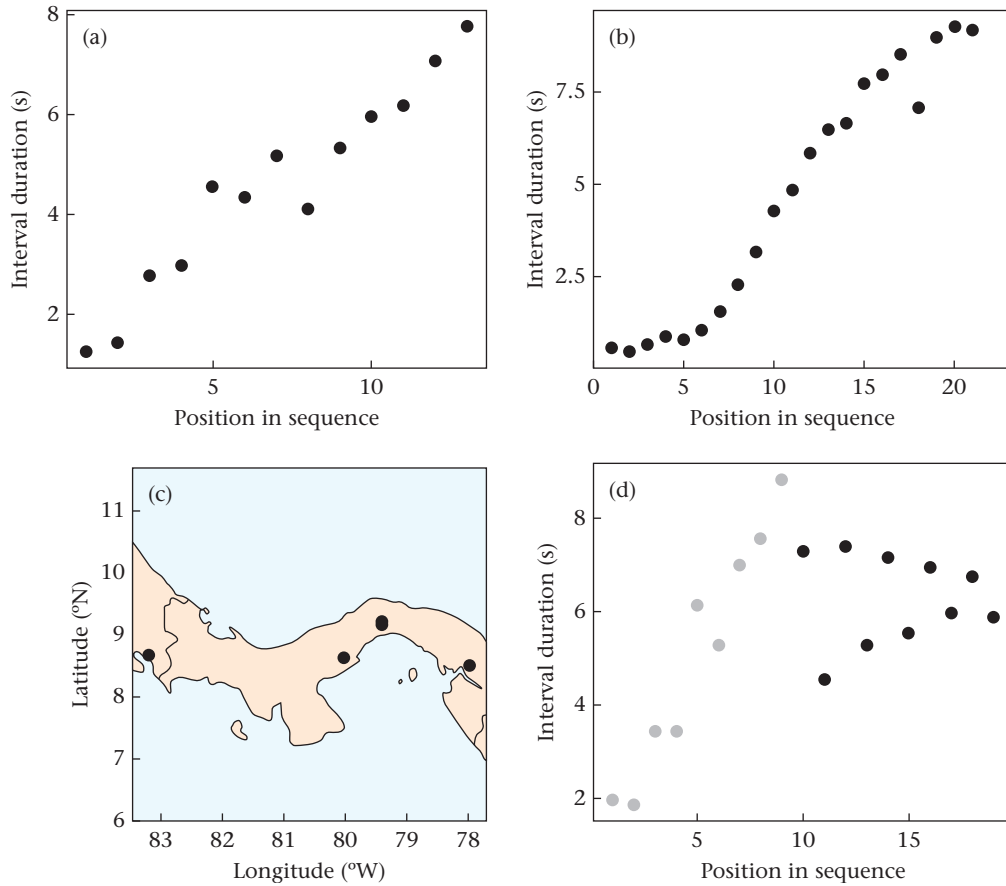
**Table A4**Videos from the Macaulay Library (ML) showing singing individuals of *M. marginatus*

ML catalogue number	Recordist	Date	Country	Locality	Duration (s)
309653781	Hervé Jacob	25 Jan 2021	Ecuador	Reserva Biologica del Rio Bigal	35
309653491	Hervé Jacob	25 Jan 2021	Ecuador	Reserva Biologica del Rio Bigal	25
300826711	Marianne Walsh	11 Aug 2013	Peru	Amazon Conservatory of Tropical Studies Field Station	40
242829861	Jonathan Slifkin	2 May 2019	Costa Rica	Cloudbridge Nature Reserve	18
224223831	Guillermo Saborío Vega	16 Apr 2020	Costa Rica	Turubari Park	23
201967621	David Ascanio	15 Mar 2009	Venezuela	RF de Palmichal	58
201522101	Josep del Hoyo	29 Dec 2016	Panama	Chorro El Macho	53
201216111	Richard Garrigues	19 Apr 2016	Costa Rica	Rancho Naturalista	23
201146541	Juan Sanabria	1 Nov 2014	Peru	RN Tambopata	58
201141461	Juan Sanabria	1 Nov 2014	Peru	RN Tambopata	54
201030581	Keith Blomerley	28 Nov 2010	Ecuador	Shiripuno Lodge	63

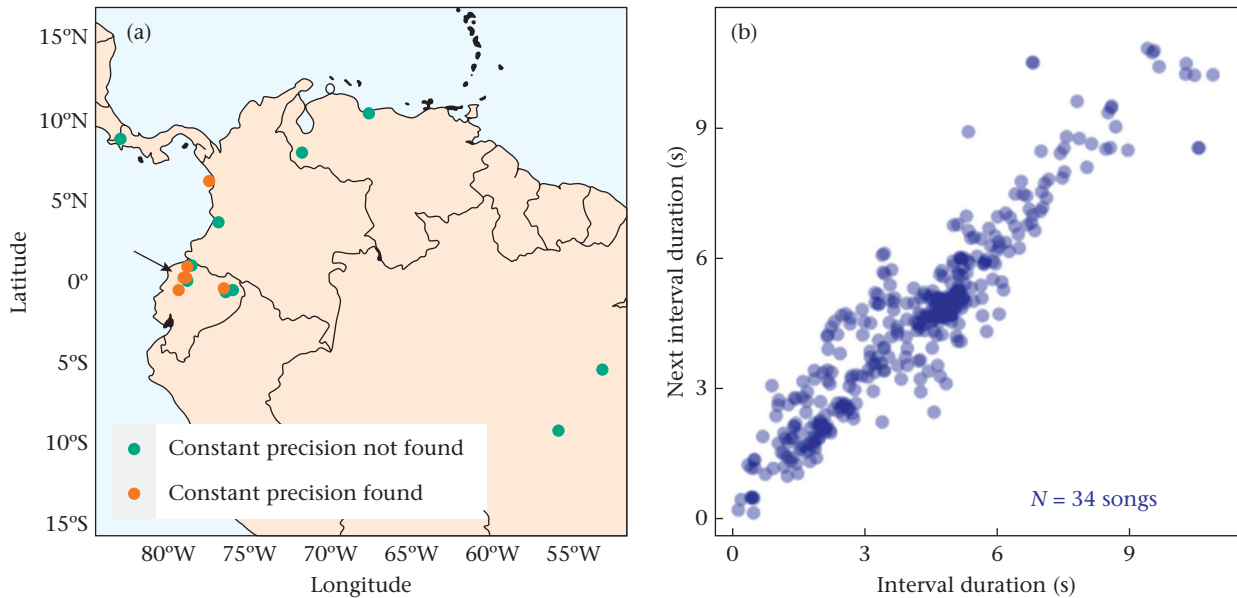
None of the body movements seen in the videos helped us predict the onset of a whistle. The videos, however, were short in duration or had poor lighting conditions. Any video can be accessed by appending the catalogue number to the URL <https://www.macaulaylibrary.org/asset/>. For example, <https://www.macaulaylibrary.org/asset/201522101>.



**Figure A1.** Types of notes in the song of *M. marginatus*. The song of *M. marginatus* consists of two types of notes, as seen in the spectrogram, which are distinguished by their shape, harmonic content and position in the song. We named the types 'introductory notes' and 'whistles'. Introductory notes, when produced, are always located at the beginning of the song and have very short silent intervals, sometimes not discernible in the spectrogram. The frequency of these notes progressively increases, and the notes are often accompanied by bold harmonics. Sometimes introductory notes are not recorded because they may be sung at low amplitude. In contrast, whistles are separated from each other by clearly visible silent intervals. Their harmonics are often faint and, sometimes, hardly recorded at all. While the frequency in introductory notes increases, the opposite occurs with whistles until they reach approximately 4 kHz. The duration of intervals between introductory notes, as opposed to those between whistles, does not seem to vary, and thus, the former were excluded from the analysis. The song identity number is 32 (Appendix, Table A1). Spectrogram parameters: Hanning windows; window length = 512 samples; overlap between windows = 50%; time resolution (at 44 100 Hz of recording sampling rate) = 5.88 ms.

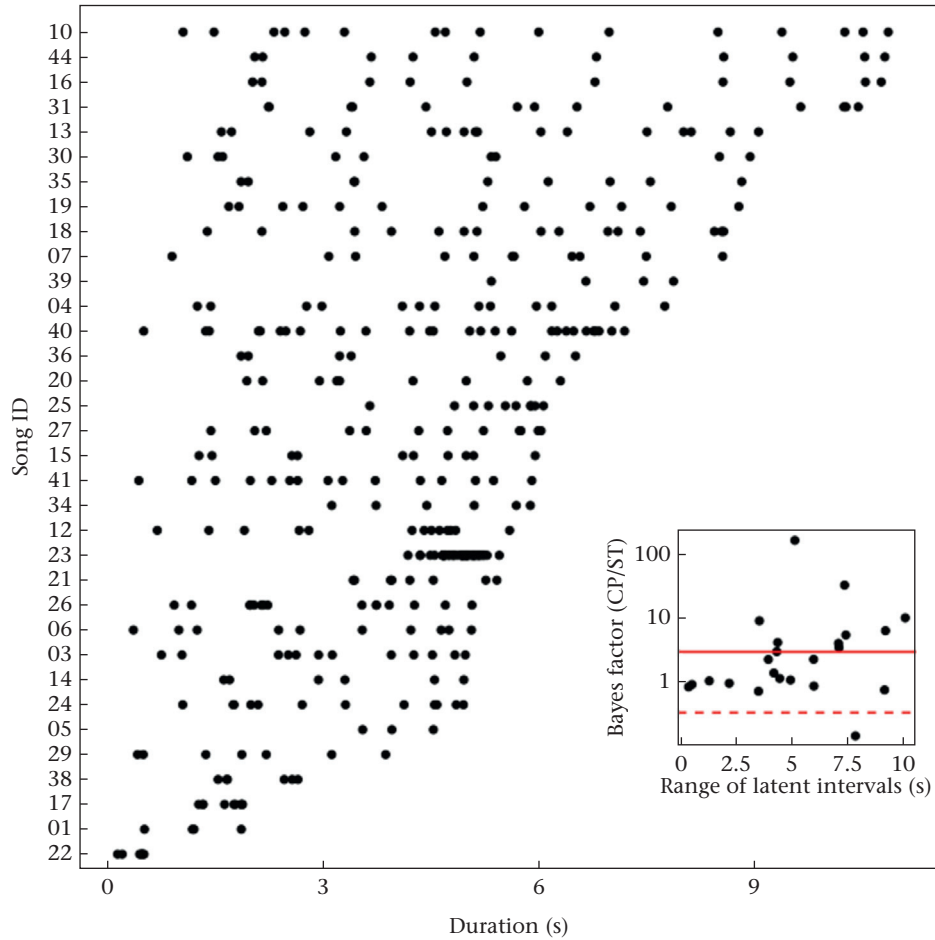


**Figure A2.** Patterns in the duration of intervals between whistles in the song of *M. marginatus*. Intervals between whistles in songs of *M. marginatus* show three regular patterns of within-song variation. (a) Linear increase: when the intervals are seen in a plot of duration against position in the sequence, they appear to follow a straight line (exemplar is song 04). (b) Sigmoidal increase: intervals follow a sigmoidal shape (exemplar is song 37). (c) This pattern seems to be a dialect, because it is shown only in birds living in Panama and eastern Costa Rica; black dots in the map show the geographical distribution of recordings analysed showing sigmoidal increase. (d) Oscillation: this pattern (black) is always produced after a linear or sigmoidal increase (exemplar is song 35). Sequences showing sigmoidal increase and oscillation seem to follow these patterns precisely. However, timing error for these sequences cannot be modelled using autoregressive equations; they require more complex models than those developed for this paper.

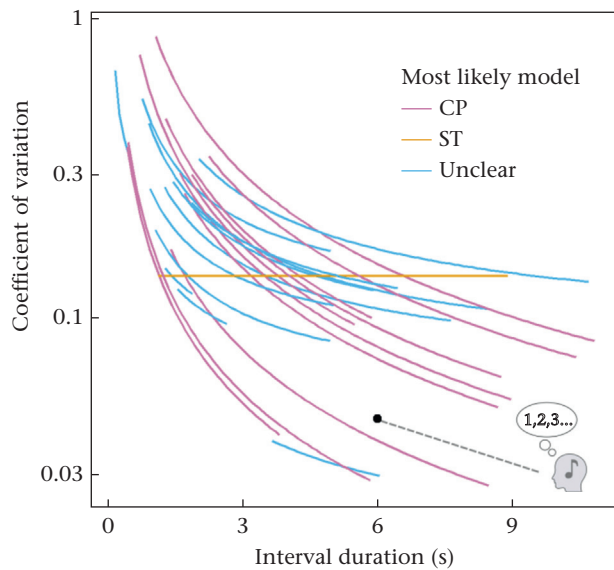


**Figure A3.** Songs with linear increase in interval duration. (a) Map showing the localities where the songs with linear increase ( $N = 34$ ) were recorded (Tables A1, A2) and those in which we found songs that supported constant precision over scalar timing. The small arrow points to Mashpi, which is the locality where we made our recordings. (b) Lag plot of interval durations for songs with linear increase, showing a common pattern of interval increase. Further information about each song exemplar is presented in Table A1.





**Figure A4.** Durations of intervals in linear increases of interval duration. The songs are ordered according to maximum reached duration. Ranges of interval duration vary widely across songs. Inset: several songs at the upper extreme of the interval range tend to show evidence of constant precision in timing (Bayes factor [CP/ST] > 3). The solid red line indicates the lower threshold for accepting the constant precision (CP) model over scalar timing (ST) model, while the red dashed line indicates the upper threshold for accepting the ST model over the CP model. Bayes factors are shown in logarithmic scale.



**Figure A5.** Coefficient of variation as a function of latent interval duration in songs of *M. marginatus*. Each trace corresponds to a song for which models of scalar timing (ST) and constant precision (CP) were fitted. The colour of the trace shows the model that most likely explains interval increase in each song. Lower coefficients of variation indicate lower precision in timing. To highlight the level of precision that wrens can achieve when timing their songs, we included the average coefficient of variation of professional musicians counting to time intervals of 6 s in duration (black dot and dashed line, labelled with musical note; see Fig. 2; Grondin & Killeen, 2009). This value was the lowest average that we found in the literature for birds and mammals estimating intervals between 1 and 10 s (Fig. 2). As seen in the plot, although most songs of *M. marginatus* had coefficients of variation that were higher than the average of the musicians, two songs showed lower coefficients of variation and thus more precise timing. The coefficients of variation for *M. marginatus* were estimated from the maximum a posteriori model of CP (MAP-CP) or ST (MAP-ST), depending on the case. For the song that showed stronger support for the ST model, the coefficient of variation was equal to the estimate provided by the MAP-ST model (equation (3)). Because under the ST model the coefficient of variation is constant, that song is represented by a horizontal line in the plot. For songs that showed stronger support for the CP model, the coefficient of variation was equal to the estimate of the standard deviation of the MAP-CP model (equation (2)) divided by the duration of the latent interval; thus, the coefficient of variation decreases as a function of latent interval. For songs with unclear support for either the ST or CP model, we estimated coefficients of variation from both the MAP-ST and MAP-CP models and then averaged the result. Consequently, these songs are not represented by horizontal lines, as expected by the ST model, nor are their slopes as pronounced as expected by their corresponding MAP-CP models.