cultural evolution song hummingbirds phylogenetic reconstruction

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## Abstract

## Introduction

The idea that socially transmitted behaviours change and diversify over time in a manner analogous to organic evolution and phylogenetic diversification can be traced back to Darwin, who noted that “the formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel” ([Darwin 1871](#ref-Darwin1871)). The term culture can be used broadly to refer to socially transmitted information that influences behavioural patterns within animal groups ([Laland and Hoppitt 2003](#ref-laland2003animals)). While human language, beliefs, norms and material artefacts are well-known cultural domains, many forms of culture exist among diverse animals, such as vocal dialects ([Catchpole and Slater 2003](#ref-catchpole2003bird); [Aplin 2019](#ref-Aplin2019)), navigation routes ([Laland and Williams 1997](#ref-laland1997shoaling); [Jesmer et al. 2018](#ref-jesmer2018ungulate)), and tool use ([Whiten et al. 2005](#ref-whiten2005conformity); [Luncz and Boesch 2014](#ref-luncz2014tradition)). After the Modern Synthesis, the formal modelling of cultural change as evolution, whether in humans or non-human animals, became possible by drawing analogies between cultural and population genetic processes ([Cavalli-Sforza and Feldman 1981](#ref-cavalli1981cultural); [Boyd and Richerson 1985](#ref-boyd1985culture)). For instance, imperfect imitation could be compared to genetic mutation ([Kempe et al. 2012](#ref-kempe2012experimental)), biased transmission to natural selection ([Williams et al. 2013](#ref-williams2013three)) and random fluctuations in the frequency of traditions to genetic drift ([Bentley et al. 2004](#ref-bentley2004random)). However, unlike genetic evolution, in which the most fundamental units of transmission (nucleotides) are essentially universal, cultural evolution implies disparate units of transmission across taxa and in different social contexts (e.g. tools vs. songs). To properly address the long-standing question of whether cultural change over time is truly akin to evolution, we require means to systematically assess the power of evolutionary methods, across the great variety of cultural forms that have emerged in the history of animals ([Mesoudi 2017](#ref-mesoudi2017pursuing)).

Some behaviours can be described as sequences of ethological units. For example, visual displays can be encoded as a string of stereotyped motor patterns ([Ligon et al. 2018](#ref-Ligon2018); [Araya-Salas et al. 2019](#ref-Araya-Salas2019)) and bird and whale songs are typically structured as sequences of repeated and hierarchically nested sounds ([Payne and McVay 1971](#ref-payne1971songs); [Rivera-Cáceres et al. 2016](#ref-Rivera-Caceres2016); [Kershenbaum et al. 2016](#ref-Kershenbaum2014b); [Garland et al. 2017](#ref-garland2017song)). Encoding behaviour as a sequence can facilitate the adoption of phylogenetic approaches that take molecular data as their main input. Such approaches have been developed within a strong theoretical framework that continues to grow and increasingly accommodates biological realism ([Yang and Rannala 2012](#ref-yang2012molecular)). Substitution models applied to molecular sequence evolution are routinely combined with clock models and tree priors, such as the birth-death process, to understand the temporal dynamics of lineage diversification and turnover ([Morlon 2014](#ref-morlon2014phylogenetic); [Bromham et al. 2018](#ref-bromham2018bayesian)) Analogously, clock models, tree priors and substitution models may be used to elucidate the temporal dynamics of cultural diversification, when culture can be adequately modeled as behavioural sequences composed of discrete units. However, most phylogenetic models assume that once diverged, lineages evolve independently of one another, branching in a tree-like pattern. As in organisms with extensive hybridization and horizontal gene transfer ([Philippe and Douady 2003](#ref-philippe2003horizontal); [Bapteste et al. 2013](#ref-bapteste2013networks)), this assumption may be often violated in cultural evolution, because learning from same-cohort individuals should increase the potential for reticulate evolution ([Gray et al. 2007](#ref-gray2007pleasures)). Empirical knowledge on the robustness of classic phylogenetic models to horizontal transmission of culture (e.g. [Collard et al. 2006](#ref-collard2006branching)), and more generally the absolute fit of such models models to cultural data, is thus crucial in addressing the utility of phylogenetic approaches to study the cultural diversification of socially learnt behaviours.

Cultural evolution poses further challenges to the application of phylogenetic models. Most implementations of phylogenetic models on molecular data start with a sequence alignment. Alignments represent assumptions of homology between characters in matched positions along a sequence, but are typically treated as observations for phylogenetic inference ([Lutzoni et al. 2000](#ref-lutzoni2000integrating); [Redelings and Suchard 2005](#ref-redelings2005joint); [Lunter et al. 2005](#ref-lunter2005bayesian)). Numerous methods of sequence alignment have therefore been developed to capture the main features of molecular evolution, and in some cases to explicitly model mutation events ([Yang and Rannala 2012](#ref-yang2012molecular); [Chatzou et al. 2016](#ref-chatzou2016multiple)). Nonetheless, the accurate reconstruction of homology in sequence alignments is a pervasive challenge in molecular phylogenetics ([Warnow 2021](#ref-warnow2021revisiting)), that is only exacerbated when borrowing phylogenetic tools for the study of behavioural sequences ([Caetano and Beaulieu 2020](#ref-caetano2020comparative)). We clearly have a better understanding of the basic rules that govern the rates of different nucleotide substitutions than we do for changes in the dance moves of a courtship display or changes in the sequence of sounds of a mating call. A crucial question for the nascent field of cultural phylogenetics (sensu [Mesoudi 2017](#ref-mesoudi2017pursuing)) is therefore whether alignment algorithms developed for molecular data can be suitably modified to represent the processes behind cultural change and diversification.

Despite these challenges, culture also poses unmatched opportunities for the application of phylogenetic inference. Culture can change very rapidly in comparison to molecular evolution ([Perreault 2012](#ref-perreault2012pace)), allowing researchers to document multiple lineage diversification events as they occur and during the span of one or a few academic lifetimes. Cultural phylogenetics can therefore capitalize on a relatively rich historical record, that markedly contrasts the sparse fossil record of many organismal groups ([Kidwell and Holland 2002](#ref-kidwell2002quality)). Recently developed phylogenetic methods have shown that sampling ancestors of extant taxa and explicitly incorporating these data in the diversification process allow for more accurate estimation of divergence times ([Gavryushkina et al. 2014](#ref-gavryushkina2014bayesian), [2017](#ref-gavryushkina2017bayesian); [Zhang et al. 2016](#ref-zhang2016total)). This is accomplished by the fossilized birth-death process (FBDP) ([Heath et al. 2014](#ref-heath2014fossilized); [Gavryushkina et al. 2014](#ref-gavryushkina2014bayesian)), a model that jointly describes the probabilities of lineage splitting, extinction and fossilization that give rise to the sampled taxa, whether extant or fossil. Of course, the fossilization rate estimated in the FBDP may represent actual fossilization events, but can also be used to describe serially sampled viral strains ([Stadler and Yang 2013](#ref-stadler2013dating); [Gavryushkina et al. 2014](#ref-gavryushkina2014bayesian)), or, as in this case, historical records of behavioural patterns that are socially learnt and transmitted ([Rama 2018](#ref-rama2018three); [Ritchie and Ho 2019](#ref-ritchie2019influence); [Zhang et al. 2020](#ref-zhang2020dated)). Thus, when culture evolves rapidly and learnt behaviours are sampled serially, a vast record of ancestral lineages can bolster inferences of cultural diversification dynamics through the FBDP.

Cultural phylogenetics research that builds on Bayesian estimation of origination, extinction and preservation rates is recently growing, but remains restricted to specific domains of human culture ([Gjesfjeld et al. 2016](#ref-gjesfjeld2016competition), [2020](#ref-gjesfjeld2020quantitative); [Rama 2018](#ref-rama2018three); [Ritchie and Ho 2019](#ref-ritchie2019influence); [Sagart et al. 2019](#ref-sagart2019dated); [Zhang et al. 2020](#ref-zhang2020dated)). Studies applying the FBDP in particular have been focused on elucidating the history of diverse human language families ([Rama 2018](#ref-rama2018three); [Sagart et al. 2019](#ref-sagart2019dated); [Zhang et al. 2020](#ref-zhang2020dated)). Thus, a great untapped potential remains for investigating cultural diversification in non-human animals,and to address whether the analogy between organic evolution and cultural change holds for disparate cultural phenomena. Although ambitious, this goal is facilitated by the increasing use of quantitative methods in animal behaviour and bioacustics.

Long-billed hermit songs consist of variable pure tones and vibratory sounds.

Different males combine these elements differently.

Juveniles learn and sometimes modify pre-existing combinations. Then keep the same song throughout adult life.

Very little migration between leks, so leks can be considered independent evolutionary replicates,

This means we can use lbh leks to “replay the tape of evolution”

Here, we used the FBDP to model cultural diversification in five independent leks of long-billed hermits. We then investigated model reliability and absolute fit using posterior predictive simulation, comparing features of empirical song sequences to sequences generated by models under the FBDP. We further asked how biologically informed assumptions during sequence alignment impact model reliability and estimates of diversification dynamics. Finally, we explored how the use and completeness of historical records (analogous to fossil records) affect model reliability and the fit of alternative clock models to long-billed hermit song data.

## Methods

- Data collection (MAS)

Sound recordings of long-billed hermits were registered from 2008 to 2019 at four sites in the caribbean slope of Costa Rica: La Selva Biological Station (leks SUR and CCE), Finca las Brisas (BR1), Hitoy Cerere Biological Reserve (HC1) and La Tirimbina Lodge (TR1). We also included recordings from the 1960’-70’-80’s for the two leks at La Selva ([Stiles and Wolf 1979](#ref-Biologla1979)) and from 1990’s for HC1. Recordings were gathered with different equipment at different points in time (i.e. shotgun or parabolic microphones, analog or digital recorders). Nonetheless, the spectrographic structure of the signals (used for determining signal structure, see below) is not affected by the recording equipment in a detectable manner.

- Song structure coding (MAS)

### Sequence alignment (BW)

Alignment of behavioural sequences is complicated by the challenge of establishing homology between ethological segments or units ([Caetano and Beaulieu 2020](#ref-caetano2020comparative)). Here, we implemented and compared three alignment strategies based on two methods originally developed for multiple sequence alignment (MSA) of molecular data. In alignments of nucleotide and protein sequences gaps represent insertion or deletion mutations, so that characters at gapped sites lack homology across the dataset. Commonly used MSA methods differ in their treatment of insertion and deletion events in ways that can impact homology inferences in cultural as well as in molecular characters ([Löytynoja 2012](#ref-Loeytynoja2012)). MAFFT ([Katoh et al. 2002](#ref-katoh2002mafft); [Katoh and Standley 2013](#ref-katoh2013mafft)) uses a progressive alignment algorithm with a default gap-opening penalty (1.53) and no gap extension penalty by default, in versions > 6.626. The L-INS-i method follows the progressive alignment by iterative refinement, based on consistency and weighted sum-of-pairs scores. In MAFFT versions > 7.371 user-defined alphabets and scoring matrices can be implemented in addition of nucleotide and amino acid alternatives. MAFFT is therefore a flexible program to align behavioural sequences in which changes analogous to multi-site insertions and deletions have occurred, and which are composed by a variable number of character states and character-state categories. In our first alignment strategy, which we hereafter refer to as ‘MAFFT-agnostic,’ we used the MAFFT L-INS-i method with default gap penalties and a customized scoring matrix in which all transitions between alternative character states were equally likely.

Our second alignment strategy also used the MAFFT L-INS-i method and default gap penalties, but we made the assumption that when hummingbirds modify pre-existing songs they are more likely to replace a trill by a different type of trill and a tone by a different type of tone than to change from vibratory to pure sounds or vice versa. We implemented this assumption by enforcing a higher cost of mismatches between sound categories than within either trills or pure tones. To determine an appropriate difference in mismatch scores, we made two further assumptions, namely that cultural evolution is independent between leks and also between individuals within leks . Because insertions and deletions of song segments occur independently among individuals, alignment length should increase as sequences are more distantly related ([Löytynoja 2012](#ref-Loeytynoja2012)). We would thus expect longer alignments in data sets composed of sequences from different leks than in data sets composed of sequences from the same lek, as these sequences have a more recent common ancestor. Following this logic, we selected mismatch scores for substitutions within and between sound categories (trill vs. pure tone) that maximize the alignment length for pools of sequences from different leks relative to the alignment length for the same number of sequences originating from the same lek. We hereafter refer to this alignment strategy as ‘MAFFT-optimal.’

For our third alignment strategy, we used the phylogenetically informed alignment program PRANK ([**loytynoja2005algorithm?**](#ref-loytynoja2005algorithm); [**loytynoja2008phylogeny?**](#ref-loytynoja2008phylogeny)). PRANK also uses a progressive algorithm but handles the placement of insertions and deletions differently, by using outgroup information in the subsequent alignment step. PRANK thus uses the sequence phylogeny to differentiate insertions from deletions, and thereby avoids site overmatching by penalizing insertions in a single stage of the alignment ([**loytynoja2005algorithm?**](#ref-loytynoja2005algorithm)). Unlike MAFFT, PRANK is an evolutionary aware program in that insertions, deletions and substitutions are modelled explicitly on a phylogenetic tree. However, PRANK does not currently support customized alphabets and substitution-rate matrices. To use PRANK we assumed that pure tones can be treated as ambiguous between upward and downward tones, and medium-speed trills can similarly be treated and ambiguous between fast and slow trills. We therefore used IUPAC ambiguity code for DNA nucleotides to rename song segments, with tones as purines and trills as pyrimidines. As per PRANK’s defaults we used a TN93 nucleotide substitution model with empirical base frequencies and transition/transversion rate ratio (κ) = 2. Therefore, as in the ‘MAFFT-optimal’ alignment, in the ‘PRANK-TN93’ alignment we explicitly assumed a higher transition rate within vibratory and pure sound categories than between them. For this alignment we used the default gap-opening rate and extension probabilities (0.025 and 0.75 respectively) and we omitted the -F option that fixes inferred insertions but increases sensitivity to guide-tree accuracy.

### Phylogenetic analysis (BW)

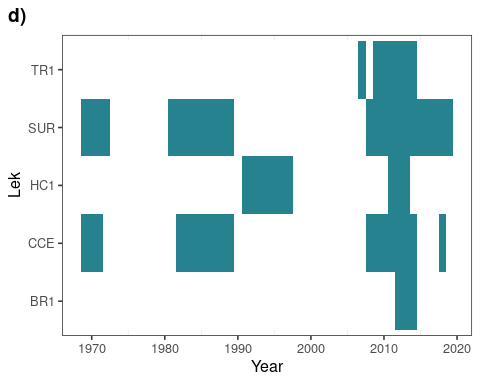
All phylogenetic analyses were conducted in RevBayes v. 1.0.12 and v. 1.1.0 , a computation environment that uses probabilistic graphical models for Bayesian inferences in phylogenetics and evolution ([**hohna2016revbayes?**](#ref-hohna2016revbayes)). Our phylogenetic model was a fossilized birth-death process (FBDP) which describes the joint prior distribution of the tree topology, divergence times and lineage sampling times before the present ([Heath et al. 2014](#ref-heath2014fossilized)). In the FBDP, extant taxa and lineages sampled before the present are part of the same macroevolutionary process. For many applications of the FBDP, extinct or ancestral taxa can only be sampled through fossils. However, in the case of fast-evolving songs that are culturally transmitted among individuals, historical records of songs are equivalent to fossil data. Historical records contain the character sequences of songs that existed in the past and may be ancestral to extant songs or may have gone extinct. As in the FBDP with fossil data, the probability that a historical song is an ancestor of extant songs depends on the rates of lineage turnover and the rate of recovery of historical records (hereafter recovery rate). The recovery rate is the rate at which ancestral songs are sampled from the lineage diversification process and it is a random variable drawn from a prior distribution, such as the birth and death rates of a traditional birth-death model. Sampling ancestors as part of the same evolutionary process as we have done here improves estimation of diversification and clock rates ([Gavryushkina et al. 2014](#ref-gavryushkina2014bayesian)) and sampling character data from ancestors further improves estimates of divergence times in simulated data ([**luo2020simulation?**](#ref-luo2020simulation)).

Our dataset on historical records of songs in hummingbird leks has three advantages in comparison to most fossil datasets used in phylogenetic analyses. First, there is no stratigraphic uncertainty. We can be certain that historical songs occurred in the year when they were recorded. Second, there are no partial fossils. Songs recorded in the past are just as complete as the most recent ones, creating no additional ambiguity in character states of historical songs. Third, the historical record is relatively rich. In all leks, there are multiple years sampled consecutively and in two leks (SUR and CCE) historical records go back to 1969 (Fig. 1d). Because leks are small and hummingbirds are actively displaying their calls, we can assume detection is nearly perfect and thus there is no missing taxa in any of the sampled years.

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**Figure S1.** Historical sampling of socially transmitted songs in the long-billed hermit. **a)** a nice picture of the birdie. **b or c)** a spectrogram pointing to tones and trills **c or b)** a map with the locations of leks. **d)** Distribution of historical records in five leks. Years when songs were recorded are marked in colour.

A possible complication in our analysis is that long gaps without sampling are interspaced in the three leks with deeper historical records (HC1, CCE and SUR). However, the temporal distribution of these ancestral samples is not unlike that of fossils, which are typically aggregated in discrete strata of exposed rocks ([**holland2016non?**](#ref-holland2016non)). The FBDP is robust to some forms of bias in fossil sampling, including non-continuous recovery ([Heath et al. 2014](#ref-heath2014fossilized)). Nonetheless to better understand the effects of deep, yet discontinuous historical sampling we conducted all analyses for these leks both with the complete dataset, including long gaps without lineage sampling, and with the more recent and continuously sampled dataset. We present both sets of results for comparison. Finally, to investigate the general impact of sampling historical records on phylogenetic inference of song evolution, we the conducted an additional set of analyses, including only songs observed in the last year of sampling. For these analyses without historical records, we used the three leks (BR1, SUR and TR1) that had 3 or more distinct songs in their last year of sampling.

Another potential issue arises from the years with highly frequent sampling, in which identical songs could be sampled at multiple time points. This is uncommon for fossil data, as it would entail the discovery of fossils with the same character state combination in multiple horizons. Here, we focus on the results of analyses in which all historical occurrences are considered in the evolutionary process, including identical songs sampled in consecutive years. However, we also conducted all analyses accounting only once for each unique song, at its earliest occurrence. The results of these analyses with only the earliest occurrence of songs are presented in the Supporting Material.

Phylogenetic analyses were conducted with all three alignment strategies (MAFT-agnostic, MAFT-optimal and PRANK-TN93) for each lek. We used a exponential prior with rate parameter = 10 for the speciation, extinction and historical sampling rates, and a broad uniform prior,bounded between 1000 and 0 years, on the root age of all leks. Song sequences were assumed to evolve under a generalised time-reversible (GTR) model with exchangeability rates and stationary frequencies drawn from a flat Dirichlet prior. Site-rate heterogeneity was modelled with a discretised gamma distribution with four rate categories and with equal shape and scale parameters, in turn drawn from an exponential prior with rate = 10. We tested both global and relaxed clocks for song evolution. Branch rates under the global clock were drawn from an exponential prior with rate = 10. Branch rates under the relaxed clock were uncorrelated and drawn from an exponential prior, with mean in turn from an exponential hyperprior with rate = 10. We compared clock models using marginal likelihood approximation via the stepping stone algorithm ([**xie2010improving?**](#ref-xie2010improving)). Clock-model comparisons were conducted for each lek (BR1, CCE, HC1, SUR, TR1), alignment (MAFFT-agnostic, MAFFT-optimal, PRANK-TN93), historical dataset (oldest records included, recent records only, no fossils) and use of historical records per song (using all, using earliest). For diversification dynamics, tree comparisons and tests of model reliability (see below), we present results under the preferred clock model here and for the alternative model in the Supporting Material.

We conducted two independent MCMC runs for each analyses, with 150 000 generations and an additional 15 000 of burn-in and parameter tuning every 200. To improve mixing we used the Metropolis-Coupled MCMC sampler with three heated chains and default swapping parameters. To avoid autocorrelation in the posterior we saved samples every 100th generation. We assessed MCMC performance using the package ‘coda’ ([**Plummer2006?**](#ref-Plummer2006)) in R v. 4.0.4 ([**RCT2021?**](#ref-RCT2021)). We checked for convergence between independent runs visually and using the Gelma-Rubin potential scale-reduction factor (psrf). We assumed convergence if psrf < 1.05 for all variables, as well as the multivariate estimate. We also inspected autocorrelations between draws (targeted below 0.1) and effective sample sizes (targeted above 200) for all model variables. We summarise MCMC diagnostics in the Supporting Material.

### Model reliability (BW)

We used predictive data simulations to test for absolute model fit, also implemented in RevBayes ([**hohna2018p3?**](#ref-hohna2018p3)). During parameter inference, a Stochastic-Variable-Monitor stored the stochastic variable values for each posterior sample. Then, these values were used to simulate new datasets based on the inference model. We specified a thinning of 2 for the stochastic variable trace, thus simulating 3 000 datasets for the ‘large’ models (CCE, SUR) and 1 500 datasets for the ‘small’ models (BR1, HC1, TR1).

We present data-based test statistics comparing simulated to empirical datasets, as tests of absolute model fit. We calculated 10 such statistics: 1) the number of invariant sites in the alignment, 2) the number of segregating sites in the alignment, 3) the maximum length of invariant blocks, 4) the maximum length of variable blocks, 5) the number of invariant blocks, 6) the maximum pairwise difference between two sequences in an alignment, 7) the minimum pairwise difference between two sequences in an alignment, and three measurements of genetic diversity: 8) Watterson’s θ, an estimate of ““population mutation rate” ([**watterson1975number?**](#ref-watterson1975number)), 9) Tajima’s D, a measurement of whether a population evolves neutrally ([**tajima1989statistical?**](#ref-tajima1989statistical)), 10) , the average number of pairwise differences in the alignment, used to calculate Tajima’s D. For more details about these statics and how they are calculated see Höhna et al.([**hohna2018p3?**](#ref-hohna2018p3)).

For each test, we report a posterior predictive effect size (PPES) and a two-tailed posterior predictive p-value ([**hohna2018p3?**](#ref-hohna2018p3)). The PPES of each statistic corresponds to the difference between the median of the posterior distribution of simulated data sets and the empirical value, normalized by the SD of the posterior distribution ([**hohna2018p3?**](#ref-hohna2018p3)). The two-tailed posterior predictive p-value is calculated by first obtaining a lower and upper tail p-value and multiplying the smaller of the one-tailed p-values by two. The lower one-tailed p-value is the proportion of simulated data sets in which the value for the test statistic is less than or equal to the observed value. The upper one-tailed test is the proportion of simulated data sets in which the value for the test statistic is greater than or equal to the observed value. Especially with small data sets, it is possible that test statistics in mutliple simulated data sets are equal to test statistics in the empirical data. In these cases the smaller of the two one-tailed p-values could be greater than 0.5. The posterior predictive p-value could be greater than 1 and has a maximum value of 2, when the test statistic in all simulated data sets is identical to the test statistic from the observed data.

### Treespace and parameter sensitivity (MAS, BW)

We explored how tree topology congruence by… .

We also asked if inferences of diversification dynamics and song evolution were influenced by the use of different alignment strategies. To do this we compared the posterior distributions of parameter estimates between the MAFFT-agnostic, MAFFT-optimal and PRANK-TN93 alignment strategies. For diversification dynamics we compared speciation, extinction and net diversification rates, and for song evolution we focussed on substitutions rates between broad sound categories (vibratory trill to pure tone and vice versa) and substitution rates within sound categories (e.g. between fast and slow trills). We considered parameter estimates sensitive to alignment strategies if their 95% highest posterior density (HPD) intervals did not overlap. We similarly explored sensitivity to fossil use and clock models in the Supporting Material.

## Results

### Model reliabilty

### Clock model selection

### Treespace congruence, song evolution and diversification dynamics

## Discusion

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