Content bias in the cultural evolution of house finch song (ABM ODD)

1 Purpose & Patterns

The purpose of this agent-based model is to understand how transmission biases influence the cultural evolution of birdsong during periods of rapid demographic change. The details of the model were developed with house finches in mind, but the basic structure is theoretically generalizable to other songbirds. The conceptual background and design principles of the model can be seen in 4.

We used this model to generate simulated data to compare with real data using approximate Bayesian computation, in order to make inferences about the presence and relative strength of transmission biases among house finches in the New York area. The pattern of interest in both the simulated and real data is the frequency distribution of syllables in the population over time, characterized by summary statistics described in 4.11.

2 Entities, State Variables, & Scales

The two entities in the model are birds and syllables. Each bird has the following state variables:

1. A repertoire of syllables with size r_s, drawn from a normal distribution based on the observed data.

2. A demonstrator attractiveness index, t_m, drawn from Euler's number raised to a random exponent from a normal distribution with standard deviation v (so that the indices are non-negative and centered around 1).

3. A geographic index, g, from a uniform distribution between 1 and 100, which is used to simulate geographic location.

Each syllable has a single state variable: an attractiveness index (M, of 1 (attractive) or 0.05 (unattractive), where p_{att} is the proportion of all syllables that are attractive).

There are two scales in the model: temporal and spatial. Each timestep in the model is a single year, in which birth, learning, and mortality all occur. Our knowledge of range sizes and dispersal distances in the eastern house finch

population is quite poor. As such, we modeled space using a simple geographic index (g) described above, where birds are more likely to act as demonstrators to new birds with closer indices to them (details in 3). The maximum bound of g, which we arbitrarily set to 100, simply changes the geographic resolution of the model.

3   Process Overview & Scheduling

First, the model is run for an initial burn-in phase of 100 years with a constant population size to reach an equilibrium-level of syllable diversity. Then, the model is run from 1970 to 2019 with a dynamic population size based on the real data. Below is the order of events during each year of the ABM:

1. If the year is 1975, 2012, or 2019 then summary statistics are calculated and stored (lines 104-115 in R/ABM.R).

2. A new set of N_{new} birds are produced, where N_{new} is the difference between the current population size (after overwinter mortality) and the projected population size in that year (line 118 in R/ABM.R).

3. Each new bird is assigned a geographic index (g) and a repertoire size (r_s) (lines 121-122 in R/ABM.R).

4. Each new bird learns a repertoire of syllables from a set of demonstrators (line 123 in R/ABM.R, with full source code for the *learn* function in src/learn.cpp). The process of learning is described below:

   (a) D demonstrators are assigned pseudorandomly based on their geographic indices (lines 26-27 in src/learn.cpp). The probability of a bird a acting as a demonstrator to a bird b is $1/(|g_a - g_b| + 1)$.

   (b) Repertoires and attractiveness indices of demonstrators are stored in a separate object (lines 30-36 in src/learn.cpp).

   (c) A list of all of the unique syllables in the demonstrator repertoires is created (lines 39-48 in src/learn.cpp).

   (d) T_x, the average attractiveness of the demonstrators singing each syllable, is calculated (lines 51-64 in src/learn.cpp).

   (e) F_x, the frequency of each syllable, is calculated and raised to the exponent α (lines 67-70 in src/learn.cpp).

   (f) M_x, the attractiveness of each syllable, is retrieved (line 73 in src/learn.cpp).

   (g) $P(x)$, the probability of adopting each syllable, is calculated as $P(x) = F_x^{\alpha} \cdot M_x \cdot T_x$ (lines 76-79 in src/learn.cpp).

   (h) These probabilities are used to pseudorandomly sample a new repertoire of syllables for the new bird that is learning (line 82 in src/learn.cpp).

   (i) Syllables in the new repertoire are replaced with probability μ to simulate innovation (lines 85-89 in src/learn.cpp).

5. Each new bird is assigned a demonstrator attractiveness index and added to the global population data table (line 126 in R/ABM.R).

6. Half of the birds in the global population data table are randomly removed to simulate overwinter mortality (line 129 in R/ABM.R). In the event that the extrapolated population size in the next year is less than half of the current population size, then enough birds are randomly removed to bring the population size down to half of what it is in the next year (lines 63-64 in R/ABM.R).

4 Design Concepts

4.1 Basic Principles

The model was adapted from Lachlan et al. (2018), and is based on standard conceptions of content bias, frequency bias, and demonstrator bias in the field of cultural evolution, as described by Boyd and Richerson (1985). Content bias occurs when some cultural variants are more likely to be learned because of the content of those variants (e.g. frequency bandwidth and complexity) (Rendell et al., 2011). Frequency biases (e.g. conformity bias and novelty bias) occur when the commonness or rarity of cultural variants affects their adoption (Rendell et al., 2011). Demonstrator bias occurs when cultural variants produced by particular demonstrators are preferred (Rendell et al., 2011). By encoding all three of these biases as parameters in the model, alongside other processes like innovation and population turnover, we can simulate cultural evolutionary outcomes under a wide variety of conditions (see 5, 2, and 3).

Simulations indicate that content, frequency, and demonstrator biases change the shape of cultural frequency distributions at the population-level (Lachlan et al., 2018). Content bias, for example, tends to reduce the number of rare variants in the population by increasing the turnover of unattractive new variants. Demonstrator bias, on the other hand, tends to cause a decrease in cultural diversity by reducing the number of potential demonstrators (Lachlan et al., 2018). This is why the frequency distribution (summarized according to 4.11) is the pattern of interest in the model (see 1).

4.2 Emergence

The output of the model is the frequency distribution of syllables in the population in each timestep, which emerges from levels of innovation, the number of demonstrators, changes in population size, and the strength and direction of the parameters related to transmission biases (see 5).

4.3 Adaptation

Adaptation appears in the model when new birds learn syllables (see 3). First, birds are either more or less likely to adopt common syllables depending on the

value of α. Second, birds are more likely to learn syllables produced by more attractive demonstrators, variation in which depends on the value of v. Third, birds are more likely to learn syllables that are themselves more attractive, variation in which depends on the value of p_{att}.

4.4   Objectives

The adaptive behavior of the agents is not objective-seeking in this model.

4.5   Learning

There is no learning in the model, as birds do not adjust their state variables after the "learning" stage (see 3) in their first year of life.

4.6   Prediction

There is no prediction in the model, as birds do not change their behavior based on predictions about the environment or the behavior of other birds.

4.7   Sensing

Birds are assumed to have access to the attractiveness and the full syllable repertoires of their assigned demonstrators, as well as the frequencies of the syllables within those repertoires.

4.8   Interaction

Interaction occurs when new birds learn from a set of demonstrators, as described in 2 and 3.

4.9   Stochasticity

Stochasticity is embedded in the model in several ways. First, each iteration of the model is initialized with different parameter values drawn from prior distributions (see 5). Second, random and pseudo-random sampling occur throughout: overwinter mortality (random sampling of individuals), demonstrator assignment (pseudo-random sampling weighted by geographic indices), learning (pseudo-random sampling weighted by the probability of adopting each syllable) (see 3), and innovation (random sampling of syllables in the repertoire and of syllables from the number of possible syllables).

4.10   Collectives

Collectives do not appear in the model.

4.11 Observation

In 1975, 2012, and 2019, the following summary statistics were calculated from a random sample of the same size as the corresponding observed sample (Kandler & Crema, 2019; Lachlan et al., 2018):

- The proportion of syllables that only appear once

- The proportion of the most common syllable type

- The number of syllable types

- Simpson's diversity index

- Shannon's diversity index

- Pielou's evenness index

- The exponent of the fitted power-law function to the progeny distribution

We chose these summary statistics because they capture diversity with an emphasis on both common and rare variants, as well as the general shape of the frequency distribution.

5 Initialization

The model is initialized with the following parameter values drawn from prior distributions (lines 36-42 in R/ABM.R):

- Initial population size (N_B)

- Number of possible syllables (N_S)

- Innovation rate (μ)

- Number of demonstrators (D)

- Proportion of syllables that are attractive (p_{att})

   - Smaller values of p_{att} are indicative of stronger content bias, as fewer syllables are attractive to learners.

- Level of conformity bias (α)

   - Values of $\alpha > 1$ are indicative of conformity bias, while values of $\alpha < 1$ are indicative of novelty bias.

- Variation in demonstrator attractiveness (v)

   - Higher values of v are indicative of of stronger demonstrator bias, as there is more variation in demonstrator attractiveness.

Then, we estimated the population size in each year by extrapolating from N_B using data from the Christmas Bird Count (CBC)[1] (lines 45-50 in R/ABM.R). Annual trends were estimated by calculating the percent change in the average number of house finches encountered per party hour in Brooklyn, Queens, and Nassau County for each year. For example, if the simulated population size in year x was 100 and the CBC indicated a 25% increase between x and $x+1$, then the population size in year $x + 1$ would be 125. Only only males are included in the model then extrapolated population sizes are cut in half.

Next, we generate a vector of the attractiveness values for the N_S possible syllables in the population (lines 56-57 in R/ABM.R), where p_{att} is the proportion of them that are attractive ($M = 1$) as opposed to unattractive ($M = 0.05$).

Finally, we create our starting population of birds stored in a data table, each of whom has a demonstrator attractiveness index (t_m), a geographic index (g), and a repertoire of syllables of size r_s (line 67 in R/ABM.R). Before the burn-in phase we go ahead and simulate the first round of overwinter mortality (line 70 in R/ABM.R).

6 Input Data

The only input data for the model are the population trends from the CBC (described in 5), stored in example/cbc_trend.RData.

7 Submodels

The model has no submodels.

References

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[1] https://www.audubon.org/conservation/science/christmas-bird-count