Content bias in the cultural evolution of house finch song

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We used three years of house finch, *Haemorhous mexicanus*, song recordings spanning four decades in the introduced eastern range to assess how individual level cultural transmission mechanisms drive population level changes in birdsong. First, we developed an agent-based model (available as a new R package called 'TransmissionBias') that simulates the cultural transmission of house finch song given different parameters related to transmission biases, or biases in social learning that modify the probability of adoption of particular cultural variants. Next, we used approximate Bayesian computation and machine learning to estimate what parameter values likely generated the temporal changes in diversity in our observed data. We found evidence that strong content bias, likely targeted towards syllable complexity, plays a central role in the cultural evolution of house finch song in the New York metropolitan area. Frequency and demonstrator biases appear to be neutral or absent. Additionally, we estimated that house finch song is transmitted with extremely high fidelity. Future studies can use our simulation framework to better understand how cultural transmission and population declines influence song diversity in wild populations.

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Learned birdsong, which is socially transmitted and accumulates changes across generations, is a powerful model system for the study of cultural evolution (Aplin, 2019; Freeberg, 2000; Lipkind & Tchernichovski, 2011; Mundinger & Lahti, 2014). Over the course of transmission, changes can accumulate through a variety of means, resulting in spatial and temporal diversity in song structure (Parker et al., 2012; Slater, 1989). Transmission biases, or biases in social learning that predispose individuals to favour particular cultural variants, are important selective forces (Cavalli-Sforza & Feldman, 1981) that can result in significant changes at the population level (Boyd & Richerson, 1992; Durham, 1990; Leonard & Jones, 1987; Ormrod, 1992). Conformity bias (a bias for more common variants), for example, appears to play a key role in the cultural transmission of foraging techniques in great tits, *Parus major*, and birdsong in swamp sparrows, *Melospiza georgiana* (Aplin et al., 2014; Lachlan et al., 2018).

In the last several decades, researchers have begun to explore how these transmission processes can be extracted from large-scale cultural data sets. This top—down approach, in which mechanisms of cultural transmission are inferred by looking at population level changes in the variants themselves, was originally pioneered by archaeologists (Bentley & Shennan, 2003; Neiman, 1995) and has since been applied to various cultural domains including dog breeds (Bentley et al., 2007), music (Youngblood, 2019) and birdsong (Byers et al., 2010; Lachlan et al., 2018). For example, chestnut-sided warblers, *Setophaga pensylvanica*, have songs with accented and unaccented endings that exhibit slightly different patterns of geographical variation (Byers et al., 2010). By comparing their rates of turnover and mutation, researchers were able to conclude that only one of the two song traditions is subject to stabilizing selection, likely caused by some form of transmission bias (Byers et al., 2010). In the current study we utilize a more recent version of this approach called generative inference, which allows researchers to test hypotheses related to specific forms of transmission bias (Kandler & Powell, 2018).

Generative inference is a powerful simulation-based method that uses agent-based modelling and approximate Bayesian computation to infer underlying processes from observed data (Kandler & Powell, 2018). Agent-based modelling allows researchers to simulate generations of interacting individuals that culturally transmit information according to certain parameters, some of which are variable and some of which are constant, based on what is known about the system. By running many iterations of these simulations with

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different parameter values and comparing the output to the observed data, it is possible to infer the parameter values that likely generated the observed data (Crema et al., 2014, 2016; Kandler & Crema, 2019; Kandler & Shennan, 2015). Lachlan et al. (2018) recently investigated the cultural transmission of swamp sparrow song using an agent-based model that incorporated three forms of transmission bias. They found that conformity bias best explained the cultural composition of their population (Lachlan et al., 2018). For the current study, we modified Lachlan et al.'s (2018) model to simulate dynamic population size and geographical location. We used this model with a new version of approximate Bayesian computation that incorporates random forest machine learning (Raynal et al., 2019) to infer whether transmission bias has played a role in the cultural evolution of house finch song.

The house finch is a socially monogamous, nonterritorial passerine (Thompson, 1960) with learned song (Mann et al., 2020) that culturally evolves (Mundinger, 1980) and is likely subject to sexual selection (Nolan & Hill, 2004). It is native to the western United States and Mexico, but was introduced from California to Long Island around 1940 (Aldrich & Weske, 1978; Elliott & Arbib, 1953) and has since expanded throughout the eastern and central United States (Belthoff & Gauthreaux, 1991). The house finch is an excellent model for such a study because we have a collection of songs from over a thousand individuals from an extensive geographical area in the introduced eastern range recorded during 1971—1975 (Mundinger, 1975), 2010—2016 (Ju et al., 2019) and 2018—2019. Our recent comparative study of house finch songs recorded in 1975 and 2012 in Long Island showed that local dialects have become less distinct and both song and syllable diversity have increased at the population level (Ju et al., 2019). Additionally, although none of the songs from 1975 have persisted, around half of the syllable types recurred in 2012 (Ju et al., 2019). We proposed three possible drivers for the increase in diversity: (1) higher innovation rates; (2) more demonstrators (as a result of increased density); and (3) more dispersal. Although the average dispersal distance and number of demonstrators probably increased during the population expansion of the 1980s, these variables would also have been affected by the significant bottleneck that occurred in the 1990s as a result of mycoplasmal conjunctivitis (Hawley et al., 2006). In addition, it is unclear, with the methods used, whether the increase in diversity is the result of neutral or biased cultural transmission.

The aim of the this study was to infer whether transmission bias played a role in the cultural evolution of house finch song during a rapid demographic expansion and crash in the introduced eastern range. We investigated the three forms of cultural transmission bias, first described by Boyd and Richerson (1985), that likely play a role in birdsong (Lachlan et al., 2018): content bias, frequency bias and demonstrator bias. 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). The most widespread form of content bias in birds is a preference for species-typical song (Aplin, 2019; Nelson et al., 2004). In white-crowned sparrows, *Zonotrichia leucophrys*, for example, birds are more likely to learn phrases from songs that contain a species-specific introductory whistle (Soha & Marler, 2000). Content biases can be adaptive, given that females choose mates based on particular acoustic features (Hernandez et al., 2008; Mennill et al., 2006). Since female house finches prefer elaborate song (Mennill et al., 2006; Nolan & Hill, 2004), and complex syllables are overrepresented in our more recent recordings (Ju et al., 2019), content bias, specifically for syllable complexity, may be present in male house finches.

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). In birds, conformity is the most well-

documented form of frequency bias (Aplin, 2019; Jenkins, 1977; Lachlan et al., 2018; Slater & Ince, 1979). White-crowned sparrows, for example, selectively retain the songs of their neighbours after establishing territories, resulting in stable local dialects (Nelson & Poesel, 2009). Under certain conditions, conformity bias is thought to be broadly adaptive because it allows individuals to quickly adopt common variants (Boyd & Richerson, 1985; Henrich & Boyd, 1998), and it is particularly important in birds because females of some species prefer males who sing local songs (O'Loghlen & Rothstein, 1995; Searcy et al., 1997). That being said, the adaptive nature of conformity bias depends on several assumptions that may not hold for all systems (Eriksson et al., 2008). For example, strong conformity can prevent potentially advantageous innovations from spreading (Kandler & Laland, 2009) and maybe even lead to population collapse (Whitehead & Richerson, 2009). To our knowledge, the only clear evidence of novelty bias in birdsong is in medium ground finches, *Geospiza fortis* (Gibbs, 1990). In this species, males appear to preferentially learn rarer songs, and those that sing rarer songs survive longer and produce more offspring. Gibbs (1990) attributes this novelty bias to the high population density of territorial males, a situation in which birds with more distinct songs may spend less time displaying and more time foraging and avoiding predation. Other possible examples of novelty bias, such as song 'revolutions' in corn buntings, *Emberiza calandra*, and continent level shifts in white-throated sparrow, *Zonotrichia albicollis*, songs, (Garland & McGregor, 2020; Otter et al., 2020), could also result from content bias and need to be investigated further. In house finches, a nonterritorial species in which females prefer local songs (Hernandez & MacDougall-Shackleton, 2004), conformity bias may be more likely to be adaptive than novelty bias.

Demonstrator bias occurs when cultural variants produced by particular demonstrators are preferred (Rendell et al., 2011). In indigo buntings, *Passerina cyanea*, for example, young birds preferentially learn songs produced by males with which they socially interact (Payne, 1981). In other species, birds are more likely to learn from males that are older (Jenkins, 1977) or more aggressive (Clayton, 1987). In the house finch, a species in which both song and redness are used in mate choice (Hill, 1991; Mennill et al., 2006), it is possible that young birds pay more attention to redder demonstrators. Given that social context influences song production (Ciaburri & Williams, 2019), demonstrator bias in house finches could also be the result of observational learning (Hoppitt & Laland, 2008), in which young birds pay attention to which males spend the most time with females and choose demonstrators accordingly.

One of the biggest challenges in extracting transmission biases from population level data is dealing with equifinality, or the fact that different transmission mechanisms can yield similar results (Barrett, 2018). This is particularly relevant for this study, as content, frequency and demonstrator biases can yield similar population level patterns (Acerbi et al., 2016). For example, a content bias for songs containing particular syllables, such as the introductory whistle in white-crowned sparrows (Soha & Marler, 2000), could generate stable dialects that are consistent with conformity bias. Alternatively, a content bias for complex syllables that only the highest-quality males can produce could manifest as novelty bias. However, despite potential similarities in emergent patterns, simulations indicate that content, frequency and demonstrator biases have discriminable effects 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). By simulating all three processes simultaneously, we aim to infer which is dominant in the cultural evolution of house finch song.

METHODS

Recording

We used recordings from 1975 (Mundinger, 1975), 2012 (Ju et al., 2019) and 2019 that were collected in the New York metropolitan area (Brooklyn, Bronx, Queens and Nassau County) (Fig. 1). The 1975 and 2012 recordings were identical to those recently analysed by Ju et al. (2019), whereas the 2019 recordings were specifically collected for this study. Recordings from 1975 were collected with a Nagra III reel-to-reel tape recorder and a Sennheiser 804 shotgun microphone and converted to digital files (32 bit, 96 kHz) by the Cornell Lab of Ornithology in 2013 (Ju et al., 2019). Recordings from 2012 (16 bit, 44.1 kHz) and 2019 (32 bit, 48 kHz) were collected with a Marantz PD661 solid-state recorder and a Sennheiser ME66 shotgun microphone. The recordings from 1975 were down-sampled to 48 kHz prior to analysis (Luscinia processes both 44.1 kHz and 48 kHz files). In all three years special precautions were taken to avoid recording the same bird twice (Ju et al., 2019; Mundinger, 1975). Each site was visited only once. Within a site, only one individual was recorded within a 160 m radius until they stopped singing or flew away.

Song Analysis and Clustering

Song analysis was conducted in Luscinia (http://rflachlan. github.io/Luscinia/), a database and analysis program developed specifically for birdsong. Songs were analysed with a high-pass threshold of 2000 Hz, a maximum frequency of 9000 Hz and 5 dB of noise removal. We excluded 965 songs (26.2%) from the analysis due to high levels of noise or overlap with other bird species. Continuous traces with more than 20 ms between them were classified as syllables (Mundinger, 1975). Some syllables were further separable into elements, or traces with less than 20 ms between them. See Fig. 2 for an example of an analysed song. Cluster analysis could not be performed in Luscinia due to computational limitations, so we exported the raw mean frequency measurements and analysed them in R. Mean frequency here refers to the mean frequency in each 1 ms bin, so it is a continuous trace across the length of syllables. Mean frequency was log-transformed prior to clustering (Lachlan et al., 2018). First, the normalized
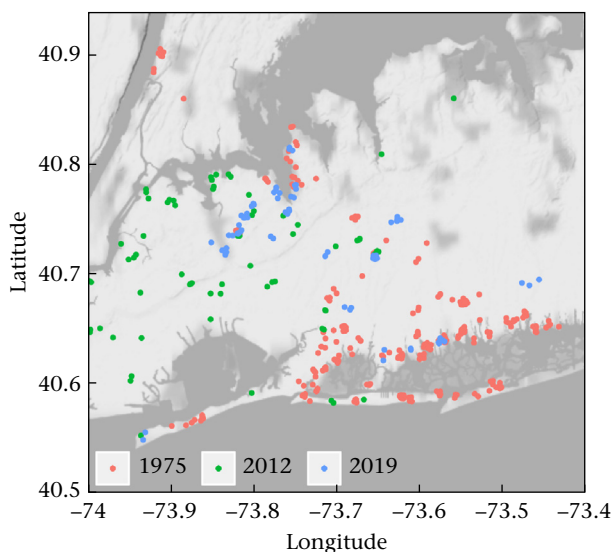

Figure 1. Locations of recordings from 1975, 2012 and 2019 in the New York metropolitan area (Brooklyn, Bronx, Queens and Nassau County).

distances between all of the syllables were calculated via dynamic time warping (DTW) with a window size of 10 (10% of the average signal length) using the 'dtwclust' package (Sardá-Espinosa, 2019). A window size of 10% of the signal length is commonly used in speech processing research and seems to be a practical upper limit for many applications (Ratanamahatana & Keogh, 2005). Infinite distances (0.19% of cases) caused by comparisons of syllables with extreme signal length differences were assigned the maximum observed distance value. Next, hierarchical clustering and dynamic tree cut were used to cluster the syllables into types (Ju et al., 2019; Roginek et al., in press). Hierarchical clustering was conducted with the UPGMA method implemented in the 'fastcluster' package (Müllner, 2013; see Appendix, Fig. A1), and dynamic tree cut was conducted with the 'dynamicTreeCut' package (Langfelder et al., 2016). For dynamic tree cut, we ran the hybrid algorithm with a minimum cluster size of 1 to maximize the representation of rare syllable types. We chose a deep split value of 3 because it resulted in relatively good cluster validity indices (see Appendix, Table A1) and a similar number of syllable types compared with previous studies of house finch song (Ju et al., 2019; Roginek et al., in press).

To control for variation in repertoire coverage, we only included birds from whom we recorded enough songs to cover at least 75% of their syllable repertoire (Ju et al., 2019). To do this, we plotted the cumulative proportion of syllables types captured with each additional song for the 106 individuals with at least 10 recorded songs as per Ju et al. (2019) (see Appendix, Fig. A2). On average, 78.0% of an individual's repertoire was captured in the first eight songs, so we only calculated repertoire sizes and observed summary statistics from birds with at least eight recorded songs.

Simulation and Generative Inference

The agent-based model was adapted from Lachlan et al. (2018) and written in R and C++. For computational efficiency, we only included males in our model. Female house finches uncommonly sing in the wild (Bitterbaum & Baptista, 1979; Kornreich et al., 2021), and thus are unlikely to act as demonstrators to juvenile birds. The model of cultural transmission is initialized with N_B birds and N_S possible syllables. A diagram of the first time step for a newborn bird in the agent-based model can be seen in Fig. 3. Repertoire sizes (r_s) are drawn randomly from a normal distribution based on the observed data and rounded to the nearest integer. Each bird is assigned a demonstrator attractiveness index (t_m), calculated by raising Euler's number to a random exponent drawn from a normal distribution with a mean of 0 and a standard deviation of v (so that the indices are non-negative and centred around 1). Each bird is also assigned a random geographical index (g) between 1 and 100, which is used to simulate geographical location. Each syllable is assigned an attractiveness index (M) of 1 (attractive) or 0.05 (unattractive), where p_{att} is the proportion of all syllables that are attractive. At the start of each year a new generation learns syllables from a pseudorandom set of D demonstrators, where the probability of bird A acting as a demonstrator to bird B is $1/(|g_A - g_B| + 1)$ (i.e. more geographically distant adults are less likely to act as demonstrators). Dispersal rates in western Long Island can be as high as 91.3% (Youngblood, 2020), and males appear to learn most of their repertoire after dispersal (Bitterbaum & Baptista, 1979), indicating that choosing demonstrators pseudorandomly by geographical location after dispersal is appropriate.

The probability of a bird learning a syllable, $P(x)$, depends upon the frequency of that syllable among the demonstrators (F_x), the attractiveness of the syllable (M_x) and the mean attractiveness of the demonstrators singing the syllable (T_x). To simulate frequency-based bias, F_x is raised to the exponent α, where $\alpha > 1$ corresponds to conformity bias and $\alpha < 1$ corresponds to novelty bias (lower
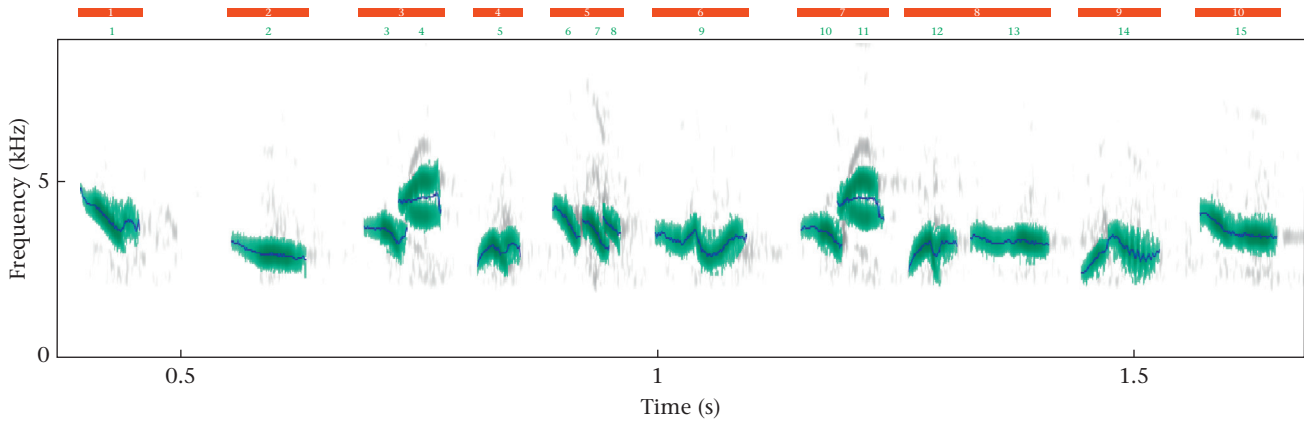
Figure 2. The first 10 syllables from a song recorded in 1975 and analysed in Luscinia. Each red bar corresponds to a syllable, and each green number corresponds to an element within that syllable. The blue traces represent mean frequency. In this song, syllable 3 and syllable 7 were classified as the same syllable type during dynamic time warping, and all other syllables are unique types. Note that the mean frequency traces of syllables were log-transformed prior to clustering.
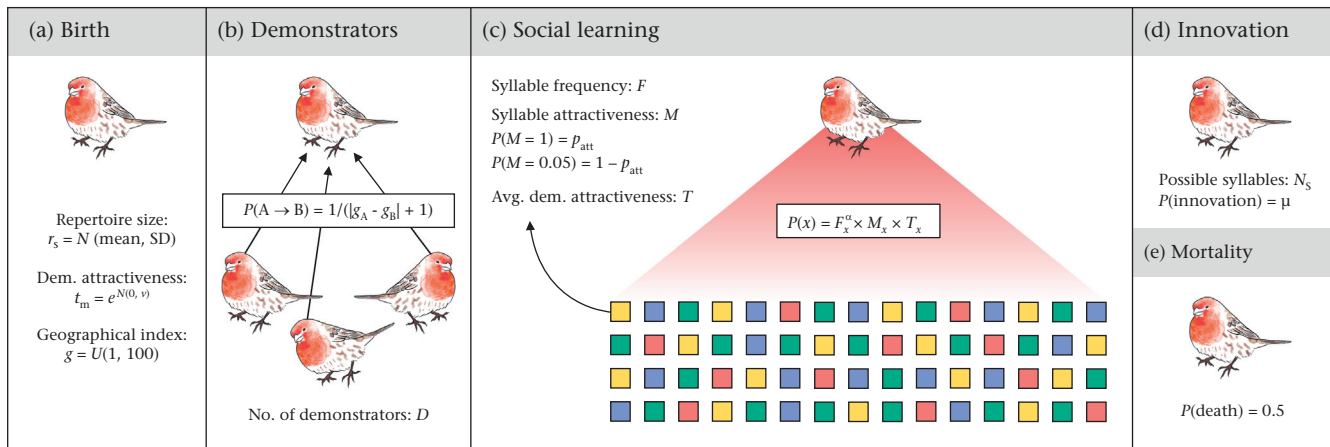

Figure 3. Diagram of the first time step for a newborn bird in the agent-based model. (a) Each bird is assigned a repertoire size (r_s, from a normal distribution based on the observed data), a demonstrator attractiveness index (t_m, from Euler's number raised to a random exponent from a normal distribution with standard deviation v) and a geographical index (g, from a uniform distribution between 1 and 100); v corresponds to demonstrator bias. (b) Birds are pseudorandomly assigned a set of D demonstrators, where the probability of individual A learning from B is the inverse of the absolute difference between their geographical indices. (c) Birds socially learn from this set of demonstrators. The syllables sung by all demonstrators are compiled into a single pool, where the probability of learning a syllable type x is a function of its frequency (F), its attractiveness (M) and the average attractiveness of the demonstrators who sing it (T). Syllable frequencies are raised to the exponent α, which corresponds to frequency bias; p_{att}, or the proportion of syllable types in the population that are attractive, corresponds to content bias. (d) Birds innovate by replacing syllables in their repertoire with new syllable types from the maximum number of possible syllable types (N_S). (e) Birds have a 50% chance of overwinter mortality. Those that survive act as demonstrators to future generations. House finch drawing by Emily Cote.

bound of 0). As such, $P(x) = F_x^\alpha \times M_x \times T_x$. During the learning process, new syllable types are innovated with probability μ. We use the term innovation to describe the generation of new variants, as is common in both animal and human cultural evolution research (Aplin, 2019; Caldwell et al., 2016), but our model is agnostic about the exact processes involved (copy error, guided variation, etc.). Innovated syllables are drawn from the initial pool of possible syllables (N_S), to reflect the production limitations imposed by species-specific physiological and cognitive constraints (Burnell, 1998; Mann et al., 2020). Mortality is simulated at the end of each year by randomly selecting 50% of the agents to remove (overwinter survival varies from 39% to 63% in different populations; Badyaev & Martin, 2000; Badyaev et al., 2000; Badyaev et al., 2008), and at the beginning of each year, new individuals are added to bring the population up to size.

In summary, p_{att}, α and v correspond to content, frequency and demonstrator bias, respectively. Smaller values of p_{att} are indicative of stronger content bias, as fewer syllables are attractive to learners. Values of $\alpha > 1$ are indicative of conformity bias, while values of $\alpha < 1$ are indicative of novelty bias. And lastly, higher values of v are

indicative of stronger demonstrator bias, as there is more variation in demonstrator attractiveness.

To model changes in population size, we extrapolated from N_B using data from the Christmas Bird Count (CBC) (https://www.audubon.org/conservation/science/christmas-bird-count). Annual trends were estimated by calculating the percentage of 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. These annual trends from the CBC are given in the Appendix, Fig. A3. The resulting population estimates were halved in the model, since only males were included.

Following an initial burn-in phase, each iteration of the model was run from 1970 to 2019. A 100-year burn-in phase appears to be sufficient to reach an equilibrium level of diversity (Appendix, Fig. A4). In 1975, 2012 and 2019, the following summary statistics were calculated from a random sample of the same size as the corresponding observed sample: (1) the proportion of syllables that only appear once; (2) the proportion of the most common syllable

type; (3) the number of syllable types; (4) Simpson's diversity index; (5) Shannon's diversity index; (6) Pielou's evenness index; (7) the exponent of the fitted power-law function to the progeny distribution (Kandler & Crema, 2019; Lachlan et al., 2018). 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. The three sets of seven summary statistics from each simulation were compared with the same summary statistics from the same years in the observed data set during parameter estimation.

Parameter estimation was conducted with the random forest algorithm of approximate Bayesian computation, using the 'abcrf' package in R (Raynal et al., 2019). Random forest is a form of machine learning in which a set of decision trees are trained on bootstrap samples of variables and used to predict an outcome given certain predictors (Cutler et al., 2012). Traditional approximate Bayesian computation methods function optimally with fewer summary statistics, requiring researchers to reduce the dimensionality of their data (Blum et al., 2013). We chose to use random forest for parameter estimation because it appears to be robust to the number of summary statistics and does not require the exclusion of potentially informative variables (Pudlo et al., 2015). In addition, it requires fewer iterations of the model compared to other methods, making it much less computationally intensive (Pudlo et al., 2015). Random forest approximate Bayesian computation was conducted with the following steps.

(1) We ran 200 000 iterations of the model to generate simulated summary statistics for different values of the parameters: N_B, N_S, μ, D, p_{att}, α and v.

(2) We combined the output of these simulations into a reference table with the simulated summary statistics as predictor variables and the parameter values as outcome variables.

(3) We constructed a random forest of 1000 regression trees for each of the seven parameters using bootstrap samples from the reference table. A maximum tree depth of five was used to avoid overfitting.

(4) Each trained forest was provided with the observed summary statistics, and each regression tree was used to predict the parameter values that likely generated the data.

The following parameters were assigned log-uniform prior distributions, so that more sampling occurred near the lower bounds: N_S = {596−800}, μ = {0.001−0.3}, v = {0.01−6} and D = {2−10} (modified from Lachlan et al., 2018). Increased sampling near the lower bounds improves the resolution of posterior distributions for parameters that are more likely to have low or moderate values (Lachlan et al., 2018). The lower bound of N_S was set to 596, which is the number of syllables identified in our data set. The following parameters were assigned uniform prior distributions, so that sampling was unbiased across the entire range: N_B = {2000−10 000} p_{att} = {0.01−1} and α = {0.25−3} (modified from Lachlan et al., 2018). Assuming an average population density

of 3.8 birds/km² (Lewis, 1997; Veit & Lewis, 1996), our estimate for the average population size of the New York metropolitan area (1203.4 km²) was 4573. We chose a wide uniform prior distribution for initial population size that included this estimate but allowed for significant variation over time (Table 1).

Logistic Regression

To assess whether syllables with particular characteristics had higher persistence, we conducted Bayesian logistic regression with all of the syllable types detected in 1975 using the 'rstanarm' package (Goodrich et al., 2020). We started out with the following predictor variables used by Ju et al. (2019): average frequency (Hz), minimum frequency (Hz), maximum frequency (Hz), bandwidth (Hz), duration (ms), concavity (changes in the sign of the slope of the mean frequency trace/ms) and excursion (cumulative absolute change in Hz/ms). Concavity and excursion are both indicators of syllable complexity (Ju et al., 2019; Podos et al., 2016). Concavity was calculated after smoothing the mean frequency trace using a polynomial spline with a smoothing parameter of 5 (chosen by visual inspection). The predictor variables were averaged across all of the observations of each syllable type. Maximum frequency, average frequency and bandwidth were left out of the modelling due to multicollinearity issues (variance inflation factor, VIF > 4). Whether or not the syllable type persisted to 2019 (logical: true/ false) was used as the outcome variable. We used Student's t distributions with a scale of 2.5 as priors to allow for a relatively wide range of parameter estimates.

RESULTS

The dynamic tree cut identified 596 syllables types across the 2724 songs from 331 individuals that we analysed. After applying the eight-song threshold to ensure that we had at least 75% of individuals' syllable repertoires, we calculated the observed summary statistics from the remaining 36, 75 and 29 individuals from 1975, 2012 and 2019, respectively (Appendix, Table A2). The observed mean (± SD) repertoire size of 61.16 ± 17.55 was used for all of our simulations.

The posterior distributions for p_{att}, α and v can be seen in Fig. 4 and Table 2. The median estimate for p_{att} was 0.21, with a 95% CI that fell far short of 1. This indicates that the cultural changes in our data set are consistent with strong content bias. The median estimate for α was 0.80, which is consistent with moderate novelty bias, but as the posterior distribution peaked at 1 and the 95% CI overlapped 1, we cannot rule out unbiased transmission relative to frequency. The 95% CI for v encompassed almost all of the prior distribution, and the out-of-bag error for the random forest was orders of magnitude higher than the other parameters. This indicates that demonstrator bias is either not present or does not influence cultural changes at the population level. The 10 most important summary statistics used by the random forests to estimate each parameter, identified using the Gini impurity method, can be seen in the Appendix, Table A3.

The posterior distributions for the other parameters are given in the Appendix (Fig. A5) and Table 2. The 95% CIs for N_B and D were nearly equivalent to the prior distributions, indicating that neither had a significant effect on the cultural changes in our data set. N_S had a median estimate of 635 and a broad 95% CI that excluded values above 777. This means that, at the current resolution of the hierarchical clustering, we captured at least 76.71% of the possible syllable types in the population. Lastly, the median estimate for μ was 0.0067 with a 95% CI that excluded values above 0.17, suggesting that house finches culturally transmit song with high fidelity like swamp sparrows (Lachlan et al., 2018). This result should

Table 1
The description and prior distribution for each dynamic parameter in the agent-based model.

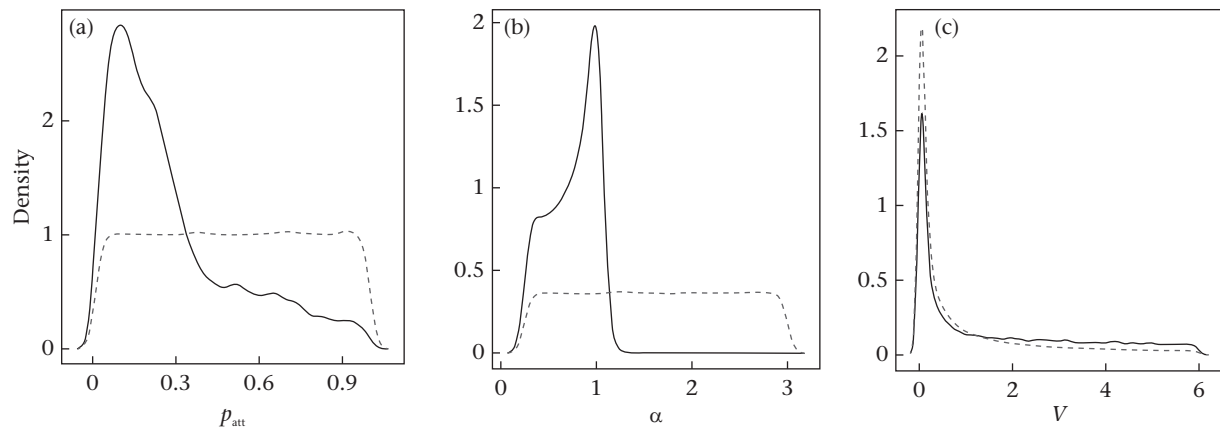|	Description	Prior	Type
N_B	Initial population size	{2000−10 000}	Uniform
N_S	Total number of syllables	{596−800}	Log-uniform
μ	Innovation rate	{0.001−0.3}	Log-uniform
D	Number of demonstrators	{2−10}	Log-uniform
p_{att}	Proportion of attractive syllables	{0.01−1}	Uniform
α	Level of conformity bias	{0.25−3}	Uniform
v	Variation in demonstrator attractiveness	{0.01−6}	Log-uniform

Figure 4. The prior (dotted lines) and posterior (solid lines) distributions for the three dynamic parameters in the agent-based model related to transmission biases. p_{att}, α and v correspond to content, frequency and demonstrator bias, respectively.

Table 2
The median, 95% credible interval and out-of-bag normalized mean absolute error of the posterior distribution for each dynamic parameter in the agent-based model.

	Median	95% CI	NMAE
N_B	5830	[2174, 9789]	0.46
N_S	635	[598, 777]	0.045
μ	0.0067	[0.0011, 0.17]	1.55
D	4	[2, 10]	0.51
p_{att}	0.21	[0.023, 0.89]	0.64
α	0.80	[0.28, 1.06]	0.35
v	0.73	[0.012, 5.64]	16.55

Table 3
The median, 95% credible interval and standard deviation for each parameter included in the Bayesian logistic regression.

	Median	95% CI	SD
Min frequency (Hz)	0.54	[0.20, 0.93]	0.18
Duration (ms)	−1.34	[−1.75, −0.97]	0.21
Concavity	0.56	[0.27, 0.89]	0.16
Excursion	−0.26	[−0.53, 0.02]	0.14

Concavity is the number of changes in the sign of the slope of the mean frequency trace/ms, and excursion is the cumulative absolute change in Hz/ms; 95% credible intervals that do not overlap with 0 indicate a statistically significant effect.

be interpreted with caution, as μ may be underestimated by the log-uniform prior distribution, and the out-of-bag error was relatively high compared to other parameters.

When both α and v were near neutrality ($0.99 < \alpha < 1.01$, $v < 0.02$), there were significant positive correlations between p_{att} and the proportion of syllables that only appeared once ($R = 0.17$, $p < 0.05$), the number of syllable types ($R = 0.84$, $p < 0.0001$), Simpson's diversity index ($R = 0.69$, $p < 0.0001$), Shannon's diversity index ($R = 0.86$, $p < 0.0001$), Pielou's evenness index ($R = 0.52$, $p < 0.0001$) and the exponent of the fitted power-law function ($R = 0.22$, $p < 0.05$); and there was a significant negative correlation between p_{att} and the proportion of the most common syllable type ($R = −0.69$, $p < 0.001$). This indicates that stronger content bias (lower value of p_{att}) reduces cultural diversity in favour of attractive syllable types independently of other factors, which may explain why we were unable to get strong estimates for parameters like population size and the number of demonstrators.

The results of the Bayesian logistic regression are shown in Table 3. The persistence of syllable types from 1975 to 2019 was positively predicted by both minimum frequency and concavity, and was negatively predicted by duration. Excursion did not significantly predict syllable persistence.

DISCUSSION

By applying simulations and machine learning to three years of birdsongs spanning four decades, we have provided evidence that content bias plays a central role in the cultural evolution of house finch song in the New York metropolitan area. Syllables with higher concavity, or syllables with more transitions in slope, were more likely to persist between 1975 and 2019. As such, we hypothesize that the strong content bias observed in this study is targeted towards syllable complexity. This is roughly consistent with previous research that found that syllables with higher excursion (another

indicator of complexity) were more prevalent in individuals' repertoires in 2012 (Ju et al., 2019), although this variable was not significant in our model. In house finches, courtship songs are longer and contain longer syllables than solo songs (Ciaburri & Williams, 2019), and males that sing longer songs at a faster rate are more attractive (Nolan & Hill, 2004) and have higher reproductive performance (Mennill et al., 2006). If female preferences for elaborate and energetically costly songs extend to the syllable level, then males with a content bias for syllable complexity will have higher reproductive success.

Additionally, we estimated that house finch song is transmitted with a median fidelity of 99.99% and a lower bound (5% quantile) of 83%. This is consistent with the high fidelity of swamp sparrow song learning estimated by Lachlan et al. (2018). Future studies should investigate whether departures from perfect fidelity in house finches are directional and maximize vocal performance (e.g. increased complexity). For example, swamp sparrows accurately copy attractive tutors and speed up the trill rates of slower tutors (Lahti et al., 2011). House finches shorten and increase the frequency of canary, *Serinus canaria*, trills learned in captivity (Mann et al., 2020) and may also modify conspecific syllables in nonrandom ways.

Interestingly, we did not find evidence for conformity bias, which appears to be relatively common in birds (Aplin, 2019; Jenkins, 1977; Slater & Ince, 1979) and was recently identified in swamp sparrows using similar methods (Lachlan et al., 2018). A previous study that found that female house finches prefer local over foreign songs, which is often associated with selection for conformity bias in males (O'Loghlen & Rothstein, 1995), tested birds from the introduced range (Ontario, Canada) with songs from the native range (Arizona, U.S.A.) (Hernandez & MacDougall-Shackleton, 2004). Preference differences between such distant and ecologically distinctive locations may be more reflective of morphological divergence (e.g. traits like bill depth; Badyaev et al., 2008; Giraudeau et al., 2014) than

regional song variation relevant for mate choice. Additionally, female preferences for local song in the same study appeared to be genetically inherited rather than learned (Hernandez & MacDougall-Shackleton, 2004). If song preferences in both females and males are independent of early experience, then frequency and demonstrator biases are less plausible in house finches. We also found that syllables with a higher minimum frequency and a lower duration were more likely to persist between 1975 and 2019. A similar effect of minimum frequency on syllable persistence was observed by Ju et al. (2019), who attributed it to the effect that low-frequency urban noise has on birdsong. If syllables with lower minimum frequencies are more likely to be masked by urban noise or less likely to be sung by males in noisy conditions, then they will be less likely to persist into the next generation (Luther & Baptista, 2010). Urban noise has been associated with increased minimum frequency in other house finch populations (Fernández-Juricic et al., 2005) and appears to be a plastic behavioural change on the part of males (Bermúdez-Cuamatzin et al., 2009, 2011). The negative effect of duration on syllable persistence is more puzzling, as male house finches in noisy environments shorten some song types and extend some syllable types (Bermúdez-Cuamatzin et al., 2011). It is also unlikely to be due to content bias, as males appear to sing longer syllables in courtship songs (Ciaburri & Williams, 2019). One possibility is that short syllables resulting from homoplasy are less distinctive and more likely to be lumped together during hierarchical clustering, causing their persistence to be overestimated by the logistic regression.

Several limitations to this study should be highlighted. Firstly, our model is largely agnostic about guided variation and other internal transformative processes (Mesoudi, 2017). Setting a maximum number of possible syllables to reflect physiological constraints may have indirectly captured some of these processes, but researchers applying these methods in more complex and domain-general cultural systems should carefully consider this issue. Secondly, our clustering process had a subjective component, in that we chose parameter values that yielded results consistent with previous studies. Since hierarchical clustering leads to a nested structure, different parameter values for the tree cut change only the scale of the data, and the transmission biases we modelled should lead to similar population level patterns regardless of scale. Finally, physiological and cognitive constraints likely limit the phonetic space within which house finches can innovate, leading to widespread homoplasy over long periods of time (Roginek et al., in press) that poses a challenge for the reconstruction of the evolutionary history of syllable types (Ju et al., 2019). While we explicitly accounted for homoplasy in our simulations by pulling innovated syllables from a limited number of types, we cannot rule out the possibility that it may have influenced the results of our logistic regression.

The importance of cultural traits in conservation is increasingly recognized among scientists (Brakes et al., 2019; Caro & Sherman, 2012; Keith & Bull, 2017; Laiolo & Jovani, 2007; Whitehead, 2010) and policy makers (United Nations Convention on Migratory Species, 2017). For songbirds that culturally transmit mating signals, researchers are concerned about the negative effects of population decline and habitat fragmentation on song diversity (Briefer et al., 2010; Hill & Pawley, 2019; Holland et al., 1996; Laiolo & Tella, 2005, 2007; Ortega et al., 2014; Pang-Ching et al., 2018; Paxton et al., 2019; Petrusková et al., 2010; Sebastián-González & Hart, 2017). Reduced song diversity has been linked to decreased population growth (Laiolo et al., 2008), leading some researchers to suggest that song diversity may be a useful assessment tool for threatened populations of songbirds and cetaceans (Garland et al., 2015; Laiolo, 2008; Pérez-Granados et al., 2016; Rivera-Gutierrez et al., 2010). To use song diversity as a metric for population

viability, researchers need to better understand how population diversity results from individual level processes such as innovation and biased transmission (Greggor et al., 2017). An over-reliance on conformity bias, for example, could slow recovery by reducing effective variation, whereas novelty bias could quickly spread innovated syllables through the population (Barrett et al., 2019). If researchers using song diversity for population assessment assume that cultural transmission is neutral, which is unlikely to be realistic in most cases (Barrett et al., 2019), they may underestimate long-term population viability. Future studies can use our agent-based modelling framework to better understand how cultural transmission and population declines influence song diversity in wild populations.

Data and Code Availability

The agent-based model used in this study is available as a new R package called 'TransmissionBias' on GitHub (https://github.com/masonyoungblood/TransmissionBias). The GitHub repository includes a standard ODD protocol description of the model, along with an 'example' subfolder that has our processed syllable data and analysis scripts. The unprocessed song recordings are available upon request.

Author Contributions

This study was developed and written by both M.Y. and D.L. Statistical analysis, modelling and software development was performed by M.Y.

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Appendix

Table A1

The number of syllable types and cluster validity indices for each value of deep split, calculated using the 'clValidpackage' (Brock et al., 2008)

Deep split	N	Silhouette	Dunn	Connectivity
0	13	0.093	0.0027	7168
1	36	−0.030	0.0023	12 380
2	114	0.018	0.0020	20 797
3	596	0.071	0.0020	34 602
4	1646	0.084	0.0020	44 967

For all three indices, higher values correspond to higher-quality clustering. We used a deep split value of 3 because it yielded results more consistent with previous research and had only slightly lower values of the silhouette and connectivity indices and an identical Dunn index, which appears to outperform the silhouette index when hierarchical clustering is used with real data sets (Arbelaitz et al., 2013).

Table A2

The observed summary statistics from 1975, 2012 and 2019

	1975	2012	2019
Proportion of syllables that appeared once	0.0094	0.0054	0.010
Proportion of most common syllable type	0.059	0.052	0.045
Number of syllable types	410	517	384
Simpson's diversity index	0.98	0.99	0.98
Shannon's diversity index	4.86	4.98	4.68
Pielou's evenness index	0.81	0.80	0.79
Exponent of fitted power-law function	9.17	108.81	1.96

Table A3
The 10 most important summary statistics used by the random forests to estimate each parameter, identified using the Gini impurity method

	1	2	3	4	5	6	7	8	9	10
N_B	2012 (6)	2012 (2)	2019 (6)	1975 (6)	2012 (4)	1975 (4)	1975 (5)	2019 (2)	2012 (1)	2019 (4)
N_S	2012 (1)	2012 (7)	1975 (7)	2012 (3)	2019 (7)	2019 (3)	2019 (5)	1975 (3)	2012 (5)	2012 (6)
μ	2019 (1)	1975 (1)	2012 (3)	2012 (1)	2019 (3)	1975 (3)	2012 (5)	2019 (5)	2012 (6)	1975 (6)
D	2019 (6)	1975 (6)	1975 (2)	2019 (2)	1975 (4)	2012 (6)	2012 (2)	2012 (1)	1975 (5)	2019 (4)
p_{att}	1975 (5)	2012 (5)	1975 (4)	2012 (4)	2019 (2)	2012 (2)	2019 (5)	1975 (3)	2012 (1)	2019 (4)
α	1975 (2)	2012 (2)	1975 (4)	2019 (2)	2019 (4)	2012 (4)	2019 (5)	1975 (5)	2019 (6)	2012 (5)
v	2019 (6)	1975 (2)	1975 (6)	1975 (4)	2019 (2)	2012 (6)	2012 (2)	2012 (4)	2012 (1)	1975 (5)

The summary statistics are numbered as they appear in the Methods: (1) the proportion of syllables that only appear once; (2) the proportion of the most common syllable type; (3) the number of syllable types; (4) Simpson's diversity index; (5) Shannon's diversity index; (6) Pielou's evenness index; (7) the exponent of the fitted power-law function to the progeny distribution.
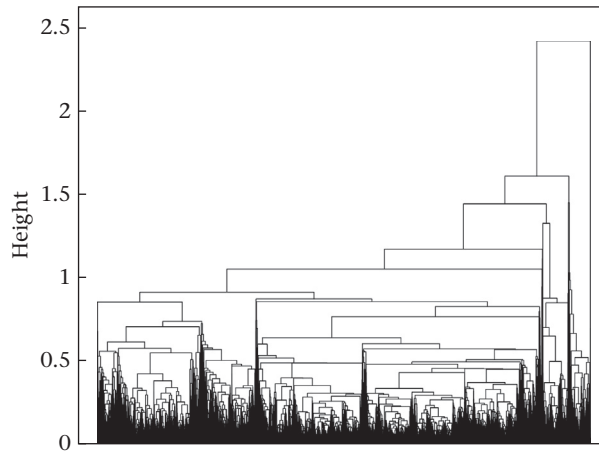

Figure A1. A dendrogram showing the results of the hierarchical clustering. The clusters could not be labelled because the number of syllable types exceeded the maximum colour limit of R.
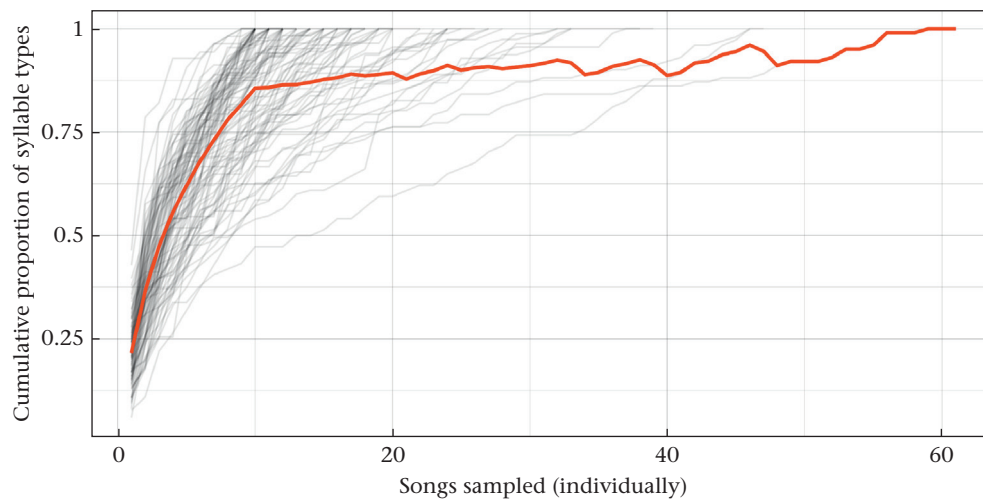

Figure A2. The cumulative proportion of syllable types (*Y* axis) detected with each additional song sampled (*X* axis) for the 106 birds from whom we had at least 10 recorded songs. The red line is the average value, which crosses 75% around eight songs.
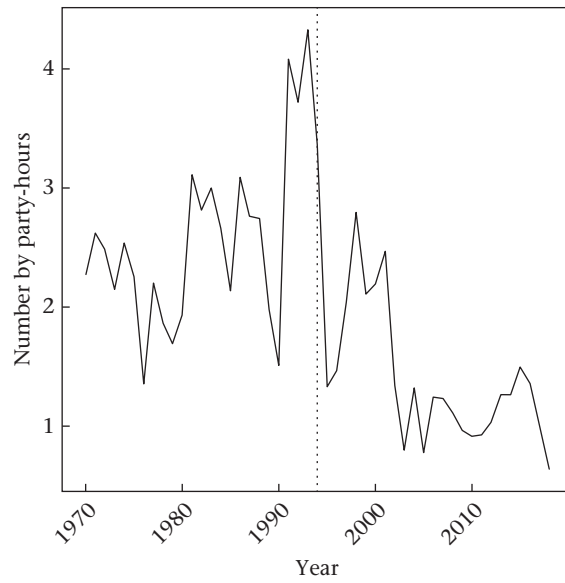
Figure A3. Average number of house finches encountered per party-hour in western Long Island (Brooklyn, Queens and Nassau County). The dotted line indicates 1994, the year in which conjunctivitis was first detected in the eastern range (Dhondt et al., 1998).
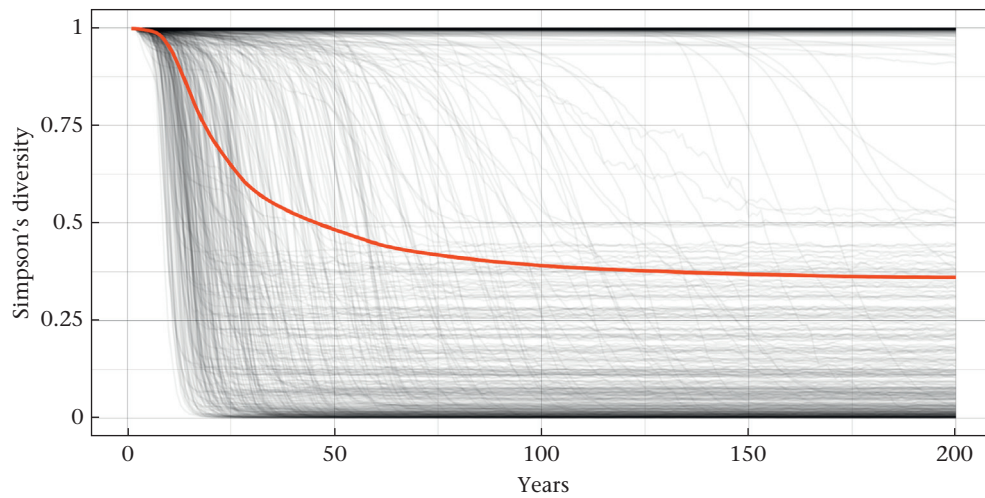

Figure A4. The Simpson's diversity index for 500 burn-in iterations. The red line is the mean Simpson's diversity index across all iterations in that year.
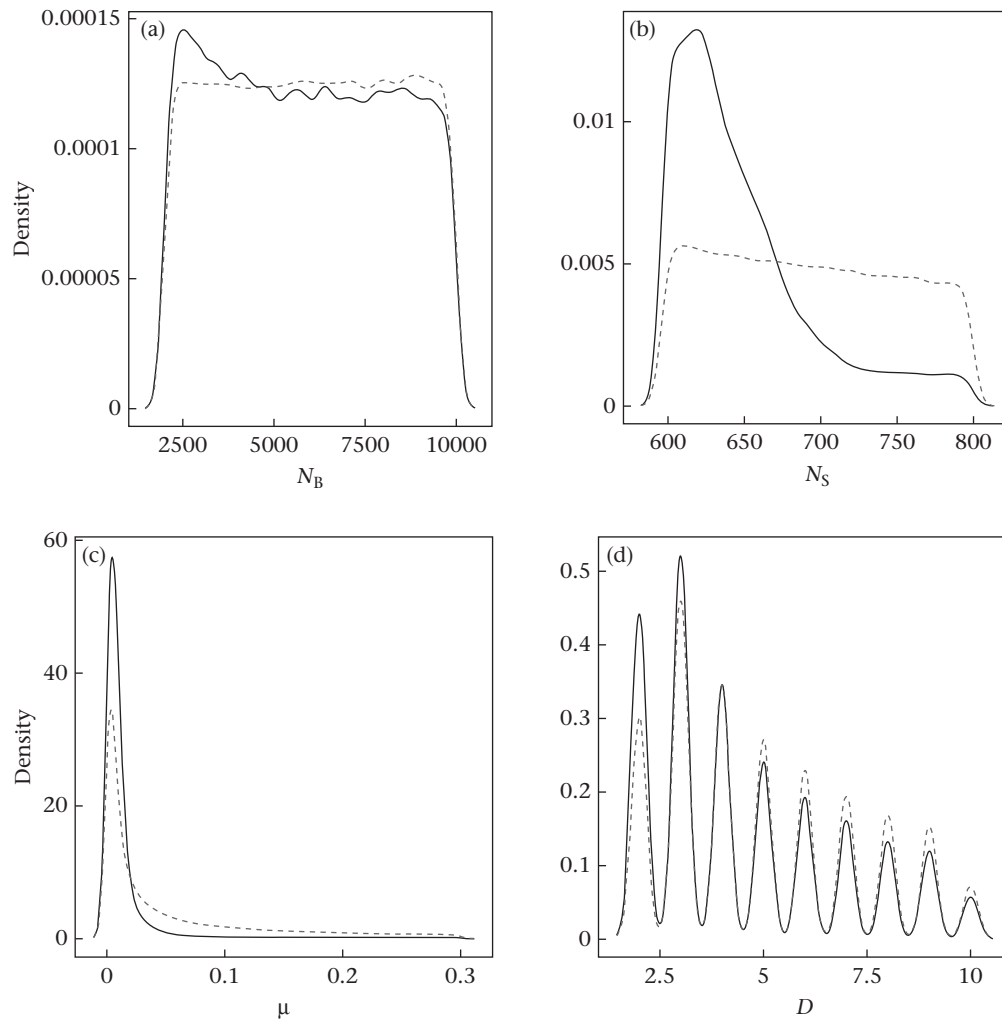
Figure A5. The prior (dotted lines) and posterior (solid lines) distributions for the four dynamic parameters in the agent-based model unrelated to transmission biases.