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House finches learn canary trills

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ABSTRACT

We analyse data from a cross-fostering experiment in which house finches were fostered by canary parents. Some individuals received canary song input, while others received no input, after a period of masking noise. We compare audio recordings of songs by these individuals to each other and to species-typical house finch and canary songs. Canary-tutored house finches learn to trill as part of their song. Since trills are not present in typical house finch song, naturally occurring song patterns underestimate what a species is capable of learning and producing. These results highlight a potential avenue for the origin of novel syntax in songbirds.

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Introduction

Vocal production learning is an uncommon trait in animals but is known in parrots, songbirds, hummingbirds, whales and dolphins, bats, seals, elephants and humans (Janik and Slater 1997; Jarvis 2006). The vocal learning programme, or the way environmental and inherited factors interact to shape vocal development, varies widely among species and has been most extensively studied in songbirds (Podos et al. 2009; Woolley 2012). An important component of any vocal learning programme is the underlying vocal flexibility: the range of sounds an organism is capable of memorising and producing. Experimental tutoring studies are particularly important in the study of vocal flexibility because they allow researchers to test subjects on a range of sounds beyond those typically produced by the focal species. Focusing on birdsong, examples of acoustic models in such studies are manipulated songs where one or a few variables can be modified against the background of otherwise species-typical song (e.g. Podos 1996; Lahti et al. 2011); songs or other sounds of untutored or otherwise unusual individuals (e.g. Fehér et al. 2009); chimeric models where elements of the songs of multiple individuals are combined to produce a novel stimulus (e.g. Soha and Marler 2000); and songs of geographically or genetically distinct individuals or even heterospecifics (e.g. Marler and Peters 1988; Munding and Lahti 2014). Such atypical song models allow researchers to place the species-typical range of vocal learning and production in the broader context of what is possible given the cognition and physiology of the species. Then, questions

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can be addressed as to why the actualised or naturally observable range is more narrowly specified. The results of such studies can be relevant not only to cognition and development of bird song but to gene–environment interaction, cultural evolution, speciation and even the macroevolutionary diversification of major song features.

Here, we present an experimental study of vocal learning flexibility in the house finch (*Haemorrhous mexicanus*), a common North American passerine. Native to the American southwest and northern Mexico, the house finch was introduced to New York in the 1940s and has since spread nearly throughout the continental United States (Hill 2002; Ju et al. 2019). House finches are considered non-territorial (Hill 1993). Colouration is sexually dimorphic, with males having partially red (or orange) plumage while females are brown. Nesting is semi-colonial (Thompson 1960), and both males and females provision nestlings (Badyaev and Hill 2002). House finch song is a moderately complex warble consisting of a sequence of discrete and variable elements (often called ‘syllables’) delivered over a duration of 2–3 s (Mundinger 1975). Syllables are usually frequency-modulated pure tones but can also be ‘buzzes’ or broadband noisy signals. Each bird generally has a repertoire of 2–4 song types and 18–32 unique syllables (Mundinger 1975; Pytte 1997). House finch song varies between geographic regions, with birds on the East Coast having a more stereotyped song, more syllable sharing and lower syllable repertoire size (Mundinger 1975; Bitterbaum and Baptista 1979; Pytte 1997). Unusual for temperate, non-territorial songbirds, both males and females sing (Mundinger 1975; Kornreich et al. unpublished data). Males appear to sing more often (Mundinger 1975; Bitterbaum and Baptista 1979). Male and female songs are similar in acoustic structure and complexity, although the female song is higher in mean frequency and lower in frequency bandwidth (Kornreich et al. unpublished data).

House finch song most likely involves vocal production learning, as every oscine passerine bird that has been subject to experimental testing has been shown to do so. Indirect evidence also suggests song learning in house finches: in addition to population variation, individuals can modify their song to counteract temporary environmental disruptions (Garcia et al. 2009), and they have been reported to mimic heterospecific song in the wild (Baptista 1972; Payne et al. 1998). Also, several studies have shown greater song similarity, especially in syllable composition, between individuals that are geographically closer, at least when the comparisons are conducted within a short (<5 km) range (Mundinger 1975; Bitterbaum and Baptista 1979; Tracy and Baker 1999; Ju 2015). However, no published work has tested the biases and extent of learning in house finches. Here, we compare song from house finches that were tutored with canary song, house finches that received no meaningful acoustic input and house finches that had exposure to species-typical song.

Cross-fostering has been utilised frequently to test for vocal learning and the extent of learning permissivity because it replaces species-typical acoustic input with that of another species (Owren et al. 1992; Zann 1985). The cross-fostering protocol has an advantage over tape-tutoring of providing the subjects with a social environment, even if atypical, during development (Immelmann 1975; Rowley and Chapman 1986). Following this developmental exposure, features of subjects’ song that are retained in species-typical form can be concluded not to require vocal learning from a specific vocal model for their development; song features that differ from the species-typical or are more variable suggest that vocal learning might be important, although one must also take into

are not typical of house finch song, allowing us to test for flexibility particularly in the area of syntax.

This study is an analysis of data collected by PCM and LW from 1971 to 1974. The data are limited and unbalanced, and some portions have been lost over time. Nevertheless, we present results of the remaining clear data because they represent the only experimental test of vocal learning in house finches to date.

Methods

We analysed acoustic recordings of 16 house finches, each of which belonged to one of three experimental groups based on their rearing conditions: (1) cross-fostered by canaries and permitted to hear their songs (*canary-tutored*); (2) cross-fostered by canaries but prevented from hearing canary songs throughout fostering by acoustic masking (*noise/quiet reared*); and (3) raised naturally in the wild (*wild-tutored*). Of the wild-tutored birds, some were captured as juveniles and kept in captivity with each other and recorded in the lab, whereas others were raised naturally in the wild and recorded in the wild. For simplicity and because we are more interested in how the canary-tutored and noise/quiet-reared house finches relate to wild-tutored house finches, we combined the juvenile-captured and wild-recorded house finches into one group. We found no differences between these two subgroups in song organisation, and there were only minor differences between a random forest model with the two groups separated and a random forest model with the two groups combined. These differences did not have an effect on the overall results. We also analysed the songs of the canary foster parents. See [Table 1](#) for individuals, their sexes and numbers of songs analysed. Other recordings besides those analysed here were excluded for unclear or missing information or for poor recording quality.

Cross-fostering experiment

The house finches to be cross-fostered were reared from eggs collected from the wild (Rye and Merrimack, NY) or from an aviary at The Rockefeller University, both in the summer of 1972. To ensure that the birds received no meaningful acoustic exposure post-hatch, all house finches were hatched and reared in sound-attenuation chambers (sound attenuation between the interior of adjacent chambers was 80–130 dB). The sex

Table 1. Study subjects and numbers of songs analysed.

Group	Individual	Sex	Songs	Group	Individual	Sex	Songs
Canary	O16	♀	10	House finch: juvenile captured	B1–74	♂	62
	OGW	♀	5		B6–74	♀	9
	Peg	♀	18		C5–74	♀	8
	Red	♂	36	House finch: field recordings	F1	♀	2
	Y17Y37	♂	33		M1	♂	2
	Y20	♂	14	M2	♂	2	
House finch: canary tutored	A5	♀	13	House finch: noise/quiet reared	M3	♂	2
	B1	♂	100		A6	♀	5
	C6	♂	39		B5	♀	28
	D2	♀	23		D3	♀	59
	D5	♂	41		D4	♀	64

was not known before being placed into the experimental groups. Five eggs were placed in the canary-tutored group. Of those five, three were male and two were female. Four eggs were put in the noise/quiet-reared group, three of which were siblings (individuals B-5, D-3 and D-4). All noise/quiet-reared individuals turned out to be female.

The canaries used for fostering were Belgian Waterslager canaries from an inbred strain purchased from a Belgian breeder. The breeder and strain were chosen because the population had little between-individual variability in song. Recordings of three males and three females were analysed. A comparison of individual model and copy songs is not possible because some of the songs of the canary foster parents are missing. Nevertheless, all of the canaries came from the same inbred stock and had similar initial acoustic exposure.

Recordings of crystallised song of many of the cross-fostered house finches are missing, although printed spectrograms are available for some individuals. We compared the printed spectrograms to the available recordings and compared pre-crystallised and crystallised song recordings where both were available. Song duration and the number of song variants differed between late plastic and crystallised song, so we did not analyse these two acoustic parameters. No other parameters differed over developmental time.

All nine of the captive-reared house finches were fostered by canaries, even if they did not receive meaningful acoustic input. All individuals were also exposed to a period of 100-dB white noise during rearing (details below). The white noise served to mask auditory input while not causing long-term damage (Marler et al. 1973). The canary-tutored group was exposed to white noise as a partial control for potential stress caused by the white noise in the other captive-reared birds. The stress associated with white noise, however, is reported to be much less than that associated with cochlear removal and may be minimal (Crino et al. 2013). The white noise was produced by a Grayson-Stadler noise generator (Model 455C), amplified by a Lafayette amplifier (Model PA645A) and broadcast through two to three 5-inch speakers attached to each chamber. Siblings were kept together until 1–2 months of age and were separated before they began to produce subsong.

Each house finch was administered 10 mg pellets of testosterone propionate in late January, early March and mid-April of their first year to ensure high levels of testosterone throughout vocal development. This partially compensated for the high number of females in the sample, as well as the possible decrease in motivation as a result of social isolation or acoustic masking. The high number of females in the data set, and the fact that the noise/quiet-reared group had only females, is not ideal. In many temperate zone songbird species, only the male produces song. However, female house finches do sing in the wild (Mundinger 1975). Female song was present in seven of the nine recording stations in Mundinger's (1975) analysis, and they sang the same song types as the males. Bitterbaum and Baptista (1979) also found that female house finches injected with testosterone sang and produced song similar to that of males: females had fewer song variants and syllable repertoires, but the acoustic structure of the syllable and syllable sequencing were not different. A study of New York recordings from the time period of the present study produced similar results (Kornreich et al. unpublished data).

The noise/quiet-reared group consisted of four house finch females, which did not receive any tutoring during rearing, with white noise being played until they were isolated at 31–38 days. Once they were moved into individual quiet chambers, they

were able to hear only their own vocalisations. Three siblings (D-3, D-4 and B-5) had noise removed before being isolated (noise ended at day 31 and they were not moved until day 34). If the foster parents did sing, the birds may have experienced temporary deafness associated with chronic noise (Ryals et al. 1999); nevertheless, this situation limits specific conclusions from these members of the noise/quiet-reared group.

The canary-tutored house finch group was exposed to white noise from hatching until 30–33 days old, at which point the noise was ended and the birds were able to hear their canary fosters. The male canaries were administered 10 mg pellets of testosterone propionate to ensure song output. Both foster parents sang during rearing. All canary-tutored house finches heard song from both male and female canaries, except for one house finch individual (C-6) that was not exposed to female canary song. After 60–68 days post-hatch, all the house finches were isolated in quiet acoustic chambers.

The house finches were recorded by a voice-actuated Tandberg tape recorder (Model 15–21, 3¾ ips). Voice actuation was disabled when it was found to cut off the beginning of many songs. From the end of March, each individual was continuously recorded for 2-h sessions every 2–4 days.

All birds had ad libitum access to water and were provided a diet of millet, niger thistle seed, rape, lettuce, fruit (apple and orange slices) and, during the rearing season, egg food.

Recording of wild-tutored house finches

In July 1973, three wild house finch juveniles (two females and one male, with estimated hatch dates of mid-May to early June) were captured and placed together in a chamber and recorded from approximately 120 days of age in August until song crystallisation in late May of 1974. The birds had acoustic contact with each other until at least March of 1974, and acoustic masking was not used.

Because the wild juvenile captives involved only three individuals, and to ensure that crystallised song features of the captives were broadly similar to those of wild individuals, songs from four adult individuals from the time period and region of the study were included in the analysis. These were one female and three males, recorded by PCM on David's Island, New York, in June 1972. Songs were recorded using a Nagra III (3/4 ips) with a Sennheiser 804 microphone.

Song analysis

We define 'syllable', following Tchernichovski et al. (2000), as a continuous sound with any amount of silence on both sides. We define 'song' as a sequence of more than four syllables with less than 0.4 s between syllables, a broad definition intended to be as inclusive as possible when dealing with two different species, acoustically masked and then isolated (noise/quiet-reared) birds and cross-fostered birds. In Praat (Boersma and Weenink 2016), the 'Annotate: To TextGrid (silences)' function was used for automatic annotation, i.e. to find and label songs (minimum silent interval = 0.4 s, minimal sounding interval = 0.001 s, silence threshold settings variable depending on signal-to-noise ratio). One of us (DCM) proofread and occasionally corrected the automatic annotation when it failed to capture the whole song or captured background noise.

We used the software package FinchCatcher (Ju 2016), which was designed for house finch syllable analysis according to spectral shape-related features (e.g. Ju et al. 2019), to create a syllable inventory for each bird. For each song, DCM manually adjusted amplitude, filter and interval settings to divide the song into syllables. Syllables were then classified by frequency and spectral shape characteristics as seen on a spectrogram. For each individual bird, DCM labelled every syllable with a letter and cross-checked each new syllable with those that were previously labelled. Similar to Pytte (1997), DCM labelled syllables as the same type if he found continuous variation between them and different types if he found consistent discrete differences. For every syllable in the data set, FinchCatcher calculated 10 acoustic measures: mean fundamental frequency (F0), maximum and minimum F0, F0 range (the difference between the minimum and maximum F0), start and end F0, F0 slope (average frequency change), duration, concavity (the number of changes in the sign of the slope of frequency over time: Ju et al. 2019) and frequency–time excursion length (the total frequency modulation over time: Podos et al. 2016; Ju et al. 2019).

Using these data, we used a Random Forest classification algorithm (Breiman 2001) to test which canary-tutored house finch syllables would be classified with canary syllables. Using the *randomForest* package (Liaw and Wiener 2002) in R (R Core Team 2017), we used wild-tutored house finch and canary syllables to train the classification model (500 trees built with 3 parameters dictating each bifurcation of a tree). We used 435 syllables from each group to ensure that the numbers of syllables were equal between canaries and wild-tutored house finches. We found 435 syllables for wild-tutored house finches and then selected a random subset of the same number of canary syllables. We tested the model on all syllables produced by every canary-tutored and noise/quiet-reared house finch.

We also analysed several features at the whole-song level: number of syllable types, percentage of syllables that were trilled, trill length, trill rate, maximum trill rate and sameness likelihood. Trills are defined as the same syllable repeated in sequence; trill length is how many syllables are repeated before switching to another syllable type; and trill rate is the number of syllables produced per second. Trill rate was measured for each unique syllable type in each bird's inventory that repeated three or more times consecutively. Trill rate was measured as the time from the energy peak of the first syllable to the energy peak of the last syllable of a trill, divided by the number of inter-syllable silences. Sameness likelihood is the probability that a syllable will be followed by a syllable of the same type. For each syllable–syllable transition, we gave a binary score of 0 or 1, depending on whether the transition was between the same or different syllable types. We divided the sum of binary scores by the total number of syllable transitions in the song to get the overall sameness likelihood score: e.g. AABB = $\{1, 0, 1\} = 2/3 = 0.667$.

We collapsed measurements for each individual to the median value, so for each acoustic parameter, each individual is represented by one data point. We used the *shapiro.test* to check for normality. Because of the small sample sizes in each group, and because much of the data were non-normal, we used non-parametric tests, median values and interquartile ranges, unless otherwise stated. When comparing two groups, we used *wilcox.test* in R *stats* package (R Core Team 2017). When comparing more than two groups, we used the *kruskal.test* function in R *stats* to perform a Kruskal–Wallis (K-W) rank-sum test. For *post-hoc* comparisons, we used *pairwise.wilcox.test* with the Benajmini

and Hochberg (1995) false discovery rate method ($p.adjust.method = 'BH'$) to correct for multiple comparisons. For group comparisons, we used the mean rather than the median for concavity and trill length because for these two variables floor effects (high frequency of 0 values) made the median unreliable.

Results

The wild-tutored house finches and the Waterslager canaries sang typically for their species and breed, respectively (Figure 1). Compared to the canaries, wild-tutored house finches sang consistently at higher frequencies and sang longer syllables (Table 2).

Among the three house finch groups, within-group variation at the syllable level was high and obscured between-group variation. While median scores differed for some acoustic parameters, interquartile ranges overlapped for every acoustic variable (Table 2). Canary-tutored and noise/quiet-reared individuals were at the low end of the wild-tutored house finch range for frequency slope and for complexity of syllables as measured by the number of syllable types and changes in concavity within a syllable. The canary-tutored house finches were also at the low end of the wild-recorded house finch range for frequency range and syllable complexity as measured by frequency excursion. All five canary-tutored house finches sang trills in a manner similar to canaries (Figure 2). The four noise/quiet-reared house finches sang songs with some repeated syllables, though not extensively trilled (Figure 3).

The random forest classification of wild-tutored house finch and canary syllables yielded an out-of-bag estimated error rate of 3.91%: 3.44% for canary syllables and 4.3% for wild-tutored syllables. Tested against this model, the majority of the syllables sung by canary-tutored and noise/quiet-reared house finches were classified with wild-tutored house finch syllables (Table 3). All noise/quiet-reared individuals had over 70% of their syllables classified with wild-tutored house finches. The majority of the syllables of one canary-tutored house finch was classified with canary syllables, whereas nearly half of the syllables of another canary-tutored house finch were classified with canary syllables (Table 3).

Canaries, canary-tutored house finches, noise/quiet-reared house finches and wild-tutored house finches were different with respect to the extent and speed of syllable repetition, including the likelihood that a syllable would be the same as the syllable that preceded it (sameness likelihood: K-W = 19.565, $df = 3$, $p = 0.0002$), trill length in number

Table 2. House finch and canary syllable-level measures.

	Canary	House finch		
		Canary tutored	Noise/quiet reared	Wild tutored
Unique syllables	16.5 (± 10.25)	8 (± 6)	10 (± 4)	21 (± 12.5)
F0 (Hz)	2079 (± 874.7)	3289 (± 484.4)	3452 (± 695.5)	3614 (± 283.4)
Start F0 (Hz)	2062 (± 796.9)	3000 (± 937.5)	3281 (± 1383)	3750 (± 281.2)
End F0 (Hz)	2062 (± 632.8)	3375 (± 187.5)	3562 (± 656.2)	3562 (± 187.5)
Minimum F0 (Hz)	1688 (± 796.9)	3000 (± 750)	2719 (± 609.4)	3000 (± 281.2)
Maximum F0 (Hz)	2438 (± 703.1)	3562 (± 375)	3938 (± 609.4)	4312 (± 46.88)
F0 range (Hz)	843.8 (± 468.8)	562.5 (± 375)	1125 (± 93.75)	1125 (± 562.5)
Duration (ms)	29.33 (± 16.67)	77.33 (± 45.33)	129.3 (± 75.33)	93.33 (± 31.33)
Slope	4.167 (± 3.094)	1.881 (± 0.89)	1.654 (± 0.845)	3.031 (± 1.548)
Concavity ^a	0.59 (± 0.315)	0.28 (± 0.83)	1.21 (± 0.73)	1.65 (± 0.98)
Excursion	0.135 (± 0.074)	0.176 (± 0.049)	0.325 (± 0.085)	0.298 (± 0.23)

^aMedian of the means for individuals.

Median group values (median of individual medians) with interquartile ranges in parentheses.

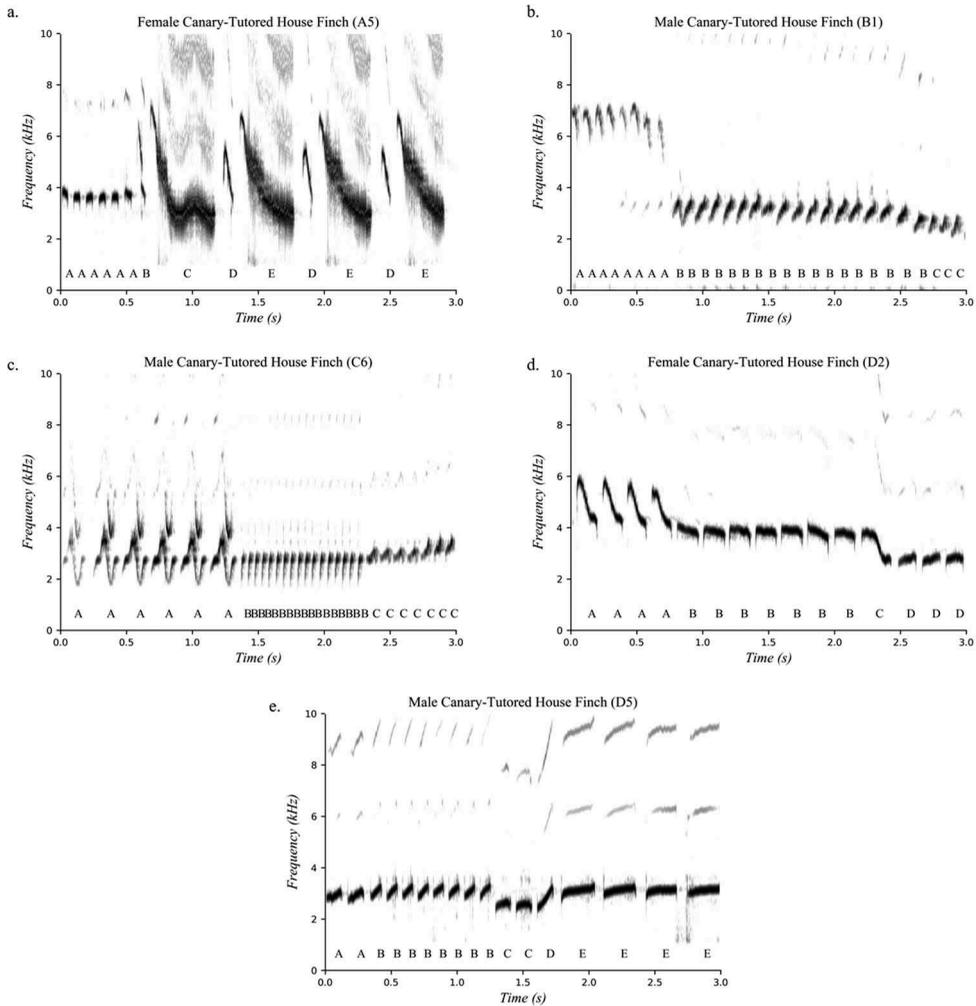


Figure 2. Representative spectrograms of canary-tutored house finches. In every case, they produced trills.

of syllables (K-W = 18.77, $df = 3$, $p = 0.0003$), trill rate (K-W = 15.4, $df = 3$, $p = 0.001$) and maximum trill rate (K-W = 14.612, $df = 3$, $p = 0.002$). Comparing specific groups (see [Table 4](#) for p -values, corrected for multiple comparisons), several differences are evident.

Canaries vs. house finches

Canaries had a higher sameness likelihood and trill length than all house finch groups. Canaries also had a higher trill rate than noise/quiet-reared and wild-tutored house finches, but their higher trill rate than canary-tutored house finches fell short of significance.

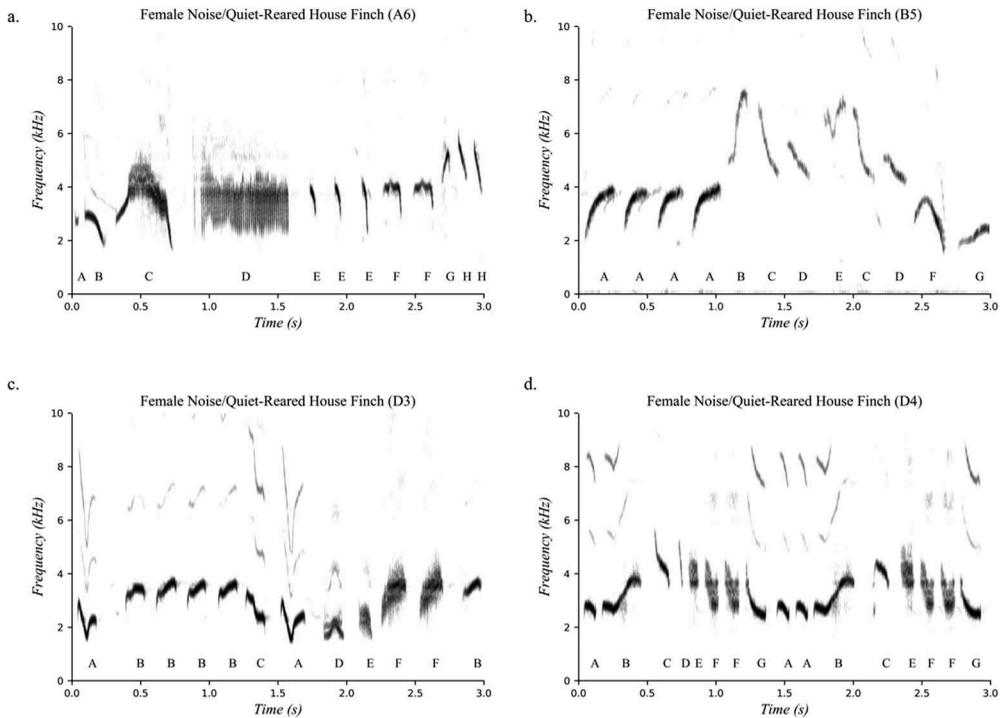


Figure 3. Representative spectrograms of noise/quiet-reared house finches (individuals reared by canaries but prevented from hearing their vocalisations).

Table 3. Random forest classification of house finch syllables.

Group	Per cent classified as house finch ^a
Noise/quiet reared	A6 – 92.22
	B5 – 83.14
	D3 – 78.90
	D4 – 74.34
Canary tutored	A5 – 87.03
	B1 – 62.25
	C6 – 52.98
	D2 – 85.00
	D5 – 13.04

^aRemaining syllables in all cases were classified as canary. This is despite the fact that the analysis did not enforce classification; i.e. syllables could have remained unclassified.

Canary-tutored house finches vs. other house finches

The canary-tutored house finch group had a higher sameness likelihood and trill length than both noise/quiet-reared and wild-recorded house finches. Trill rate was higher in canary-tutored than in wild-recorded house finches, with noise/quiet-reared house finches being intermediate and significantly different from neither.

Table 4. Group medians and p -values for comparisons at the song level.

		Noise/quiet HF	Wild HF	Canary
Sameness likelihood				
Canary-tutored HF	0.77 (± 0.1)	$p = 0.016^*$	$p = 0.008^{**}$	$p = 0.009^{**}$
Canary	0.94 (± 0.03)	$p = 0.011^*$	$p = 0.007^{**}$	-
Wild HF	0.059 (± 0.07)	$p = 0.009^{**}$	-	-
Noise/quiet-reared HF	0.4 (± 0.03)	-	-	-
Trill length				
Canary-tutored HF	6.7 (± 3.18)	$p = 0.019^*$	$p = 0.01^{**}$	$p = 0.01^{**}$
Canary	18.6 (± 2.57)	$p = 0.0143^*$	$p = 0.01^{**}$	-
Wild HF	2.0 (± 0.4)	$p = 0.066$	-	-
Noise/quiet-reared HF	2.9 (± 0.52)	-	-	-
Trill rate				
Canary-tutored HF	10.5 (± 5.42)	$p = 0.19$	$p = 0.035^*$	$p = 0.078$
Canary	13.3 (± 3.68)	$p = 0.038^*$	$p = 0.016^*$	-
Wild HF	0 (± 2.51)	$p = 0.110$	-	-
Noise/quiet-reared HF	5.65 (± 3.75)	-	-	-
Max. trill rate				
Canary-tutored HF	11.5 (± 3.77)	$p = 0.413$	$p = 0.013^*$	$p = 0.013^*$
Canary	31.5 (± 9.84)	$p = 0.309$	$p = 0.013^*$	-
Wild HF	0 (± 2.51)	$p = 0.138$	-	-
Noise/quiet-reared HF	5.78 (± 11.2)	-	-	-

All p -values have been adjusted based on a Benjamini–Hochberg procedure for multiple tests. *Significant at the $p = 0.05$ level; **significant at the $p = 0.01$ level.

Noise/quiet-reared vs. wild-tutored house finches

Noise/quiet-reared house finches had a higher sameness likelihood than wild-recorded house finches, but their higher trill length and rate did not reach significance.

Only one song of one house finch, in any group, had a trill rate above 20 syllables per second. The noise/quiet-reared individual A6 produced a song with a trill rate of 41 Hz, even higher than typical canary trills. This trill is an outlier in several respects: the longest exemplar is only 169 ms, it is in the upper range of the house finch frequency spectrum (7078 Hz), it is in the lower range of syllable duration (11 ms) and it has a higher syllable duration coefficient of variation than any other trill in the four groups (A6 trill $C = 0.55 \sim$ Overall = 0.12 ± 0.14). This outlier is the reason why noise/quiet-reared and canary maximum trill rates are not statistically significant. If removed, the interquartile range of the noise/quiet-reared maximum trill rate falls from 11.2 to 3.47. Without the outlier song, canaries and noise/quiet-reared house finches are statistically different (adjusted $p = 0.014$), but noise/quiet-reared and canary-tutored house finches still are not.

Canary-tutored house finch songs appeared similar to those of Waterslager canaries when the latter's trill rate was below 25 Hz and had a dominant frequency above 2 kHz (Figure 5).

Discussion

We present the first experimental evidence that house finches learn their songs. Typical house finch song is produced with very little repetition of syllables. Without meaningful acoustic input during development, however, house finch songs repeat syllables, perhaps owing to impoverished learning opportunities, although other interpretations are possible. Their incongruity with species-typical song in sequencing is consistent with acoustic isolation experiments performed in other songbirds (Konishi 1965; Fehér et al. 2009). A stronger line of evidence for vocal production learning comes from the trilling of house

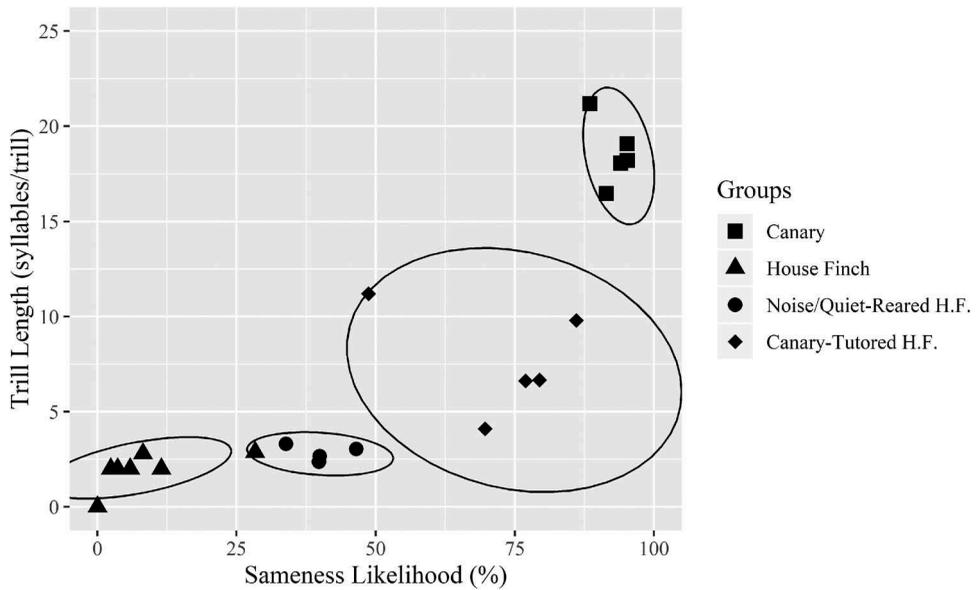


Figure 4. Plot of trill length (sequences of repeated syllables), by sameness likelihood. Ellipses are 90% confidence interval. One canary (O16) is removed from the graph because of a very high median length of trill (64.4 syllables/trill). Songs of canary-tutored house finches are intermediate between those of wild-tutored house finches and canaries.

finches tutored by canaries. Although acoustically isolated house finches did repeat syllables, only the canary-tutored individuals produced long strings of repetitions (Figure 4). Trilling is not a feature found in most house finch song, and when it is present, it is at a slower rate and the trills are much shorter. All canary-tutored birds in this study trilled, and some of the trills closely resemble canary tutor songs. Nevertheless, our conclusions could be more specific and stronger if the study had included house finches reared in the lab and tutored with other house finches, for direct comparison to the canary-reared birds.

Comparisons among the treatment groups in this study indicate a coordinated operation of inherited and learned features in the development of house finch song. Heterospecific learning is evident in several results. The trilling by canary-tutored house finches included a higher occurrence (sameness likelihood) and extent (trill length) of syllable repetition, as well as a faster vocal delivery of the sequences (trill rate), than typical wild house finches. In addition, a minority (though in one individual a majority and in another nearly a half) of canary-tutored house finch syllables were classified as canary syllables. Nevertheless, even in song features that were learned from canary tutors, learning did not result in a completely canary-like form, as shown for instance in the separation of the treatment groups in Figure 4. In the present study, all house finches, regardless of experience, sang longer syllables, at higher frequencies, in fewer trills, with lower syllable repetition than canaries, in species-typical fashion. Neither acoustic isolation, canary-tutoring, nor capturing as juveniles resulted in any acoustic parameter differing significantly from wild-recorded house finches, although the variation in many of these parameters is high. Most syllables sung by house finches either tutored

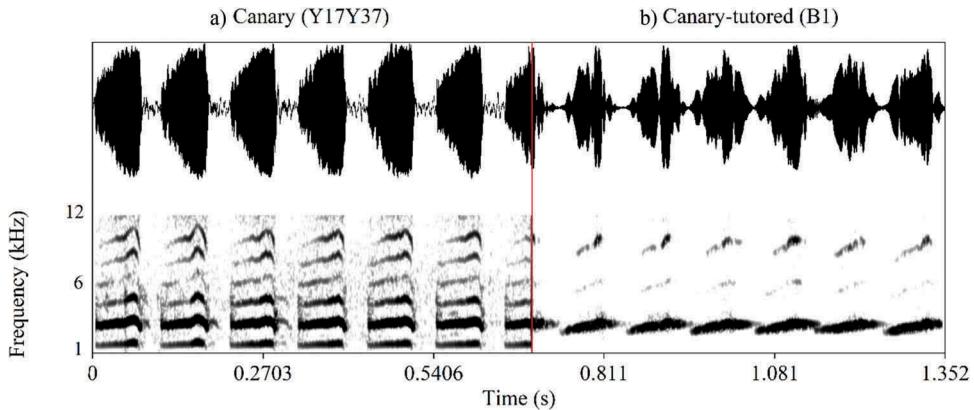


Figure 5. Example of a similar trill type between (a) a canary (trill rate = 9.24 Hz, F_0 = 1680 Hz) and (b) a canary-tutored house finch (trill rate = 9.3 Hz, F_0 = 3130 Hz). The fundamental frequency of the canary-tutored house finch corresponds roughly to the second harmonic of the canary. The canary presented was not the tutor of the house finch, but many trills and syllable types were shared among the canaries.

by canaries or reared without audible tutors were classified as house finch rather than canary syllables. Thus, several house finch song features are substantially inherited, and their expression is robust to varied experience. In sum, tutoring of house finches exclusively by canaries results in what can be described as house finch–canary song hybrids.

Learning song features from heterospecifics has been demonstrated experimentally in several other songbird species that do not typically do so in the wild, such as song sparrows (*Melospiza melodia*), swamp sparrows (*Melospiza georgiana*), white-crowned sparrows (*Zonotrichia leucophrys*), zebra finches (*Taenopygia guttata*) and Bengalese finches (*Lonchura striata*) (Marler and Peters 1977; Clayton 1989; Marler 1997; Soha and Marler 2000; Kelley et al. 2008). A particularly similar result to the present study was found by Clayton (1989) in zebra finches, which when tutored with phrase-repeating Bengalese finches learned to repeat phrases, although not to the extent that Bengalese finches do.

House finches likewise are rarely known to utilise this ability in the wild, although Baptista (1972) reported a single wild individual mimicking a white-crowned sparrow song, and Payne et al. (1998) reported a small group of house finches singing canary tours. PCM has also recorded house finches imitating the northern cardinal (*Cardinalis cardinalis*) in two disjunct populations (unpublished data). Even if unusual or unsung in the wild, the permissiveness or flexibility of a vocal learning programme can be indicative of avenues by which vocal novelty can evolve. For instance, a perennial question in songbirds and other vocal learners is how novel forms of syntax (patterns of ordering elements) can arise (Suzuki et al. 2018). In birds, one of the most striking syntactical differences is between species that trill and those that do not, and yet, closely related species can vary in this regard. For instance, despite the predominance of trilled song in the canary, its sister species the serin (*Serinus serinus*) sings a song with sequential elements involving few syllable repetitions (Cardoso and Mota 2004). The present study's

finding that house finches will trill under a specific tutor regime demonstrates their capacity for syntactical change by ‘cultural mutation’, i.e. with a change to their social environment alone.

Despite producing trills, the canary-tutored house finches did not produce accurate canary songs. Limitations on or departures from faithful mimicry of atypical song models are in line with previous work on several species, including swamp sparrows and canaries. When exposed to trill rates faster than the species-typical range, swamp sparrows can fail either to produce all of the notes in the song or to maintain the trill rate or rhythm (Podos 1996). Lahti et al. (2011) found that swamp sparrows also did not faithfully imitate artificially modified trill rates when those rates were slower than normal; instead, they elevated the input rate to a more species-typical range. When canaries that have been bred to produce either low-frequency or high-frequency song are hybridised and back-crossed, and all exposed to the same mixture of high- and low-frequency elements (tours), each bird mimicked tours in breed-typical ranges according to their genotypes (Mundinger 1995; Mundinger and Lahti 2014). In general, departures from faithful mimicry in vocal development have been explained as the result of inherited learning biases (including the learning template hypothesis Konishi 1964; Marler 1970; Marler and Sherman 1983), vocal tract or other performance constraints (Podos 1996) and developmental stress (Nowicki et al. 1998; MacDougall-Shackleton and Spencer 2012). These proximate explanations map on to a range of ultimate explanations, from being non-functional or even maladaptive to functions relating to reproductive isolation and sexual selection. Here, especially since the departures from accurate canary song mimicry by house finches were in the direction of typical house finch song, inherited species-specific factors likely contributed to the observed patterns. Inherited patterns can be cognitive (including tendencies to attend to, memorise and produce the sounds) or else could be rooted in other features such as body size and vocal tract (including beak) morphology.

Vocal learners can compensate via various means for failures to accurately mimic models. For instance, when presented with atypically fast songs, swamp sparrows can maintain trill rate by inserting breaks in the song or deleting syllables; or else they can maintain syllable structure by reducing trill rate (Podos 1996). The particular house finch and canary songs illustrated in Figure 5 suggest a compensation mechanism that (to our knowledge) is hitherto unexplored in birds. That canary song has a fundamental frequency around 1.7 kHz, which is near or just below the house finch productive and auditory range (Dooling et al. 1978). The second harmonic of the canary song, however, is within the house finch range; and at least one canary-tutored house finch, B1, appears to have matched its fundamental with the canary’s second harmonic. A higher-pitched individual matching its fundamental with the second harmonic of a lower-pitched individual is a strategy that is often employed in human music (known as ‘octave equivalence’) (Hoeschele et al. 2012). Research with octave perception in avian species has so far failed to find an effect (Hoeschele et al. 2013; Wagner et al. 2019).

In addition to previously mentioned shortcomings of this study related to sample sizes, imbalanced design and missing data results would have been clearer and more interpretable if an additional experimental group had included lab-reared house finches tutored by conspecifics. Moreover, Waterslager canaries have been artificially selected to sing a low-pitched song, whereas other canaries, such as Borders, have a similar song

structure to Waterslagers but more closely matched to the frequency range of house finches. Training house finches on Border canary song would control for frequency and test the limits of house finch trilling and syllable copying. The prediction following from this study is that house finches would mimic Border song more accurately than Waterslager song. Another project that could address questions raised by this study is a cross-generational tutoring experiment. Fehér et al. (2009) used isolate zebra finches (*Taeniopygia guttata*) as tutors of another generation, used the latter as tutors in turn and so on, discovering that song became more like the wild type in each successive generation. Such reconstruction of typical song from an isolate ‘reset’ may be possible in house finches as well since we now know that they can produce a rough song structure and basic elements in the absence of social learning.

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Data availability statement

The data described in this article are openly available in the Open Science Framework at [DOI:10.17605/OSF.IO/TPA6U](https://doi.org/10.17605/OSF.IO/TPA6U).

Disclosure statement

No potential conflict of interest was reported by the authors.

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