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Song learning by prairie warblers: When, where, and from whom

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Abstract

Songbirds of many species acquire their songs by imitating the songs of conspecific singers. Conclusive evidence of such imitation comes from controlled laboratory studies, but such studies do not reveal when and where songbirds learn their songs under natural conditions. To determine the timing and location of song learning in a population of prairie warblers, we compared the songs of yearling prairie warblers of known hatching location to the songs of other birds in the yearlings' natal and first breeding areas. The comparisons yielded a likely model song (and model singer) for each of the song types used by the focal yearlings. We supplemented our findings from the song comparisons with inferences drawn from an analysis of local geographic variation in songs. This analysis revealed that shared song types showed no tendency to be geographically clustered within the study area. Taken together, our data suggest that prairie warblers learn their songs during the hatch year, at locations somewhat distant (mean distance 1,437 m) from their natal site, most likely as birds wander about during the post-fledging period.

KEYWORDS

birdsong, Parulidae, *Setophaga discolor*, song development, song learning

1 | INTRODUCTION

In laboratory studies of song development in oscine songbirds, birds of almost all studied species develop normal songs only if exposed to songs of other individuals of their species (Hultsch & Todt, 2004). These studies have generally shown that songbirds imitate songs or song elements to which they are exposed, thereby acquiring songs that are similar to those of the birds that served as models (Soha, 2017). However, many details of the song learning process vary among species (Beecher & Brenowitz, 2005). For example, in some species, song learning continues throughout an individual's life (open-ended learning, e.g., nightingales, *Luscinia megarhynchos*, Todt & Geberzahn, 2003), but in other species songs crystalize after a limited period of learning, after which song forms remain more or less fixed (age-limited learning, e.g., song sparrows, *Melospiza melodia*, Nordby, Campbell, & Beecher, 2002).

Although laboratory studies of song development have revealed a great deal about the mechanics and neural basis of song learning (Brainard & Doupe, 2002; Mooney, 2009), they cannot by themselves reveal how the learning process plays out in wild birds. The dynamics of song learning in the wild are instead investigated by observing the outcome of song development in free-living birds of known natal origin (e.g., Baptista & Morton, 1988; Grant & Grant, 1996; Wheelwright et al., 2008). Such studies are often aimed at determining the timing and location of song learning, and the identity of the model bird or birds (i.e., the birds from which songs were learned).

In the current study, we sought to determine when, where, and from which birds male prairie warblers (*Setophaga discolor*) learn their songs. Prairie warblers appear to be age-limited learners; birds recorded across multiple years do not substantially modify their song types or add new ones. (Between 2009 and 2019, we recorded 21 banded individuals in two different years, and recorded 7 birds in three or more different years, and did not detect any between-year song type additions or losses in these 28 birds.) We assessed prairie warbler song learning by recording the songs of males that were banded as nestlings and returned to our study site the following

year to breed. We compared the songs of the returning birds to those of other prairie warblers in the area, including the birds living near the nests of the focal birds during their hatch year, and the birds living near the sites at which the returning birds settled for breeding.

We supplemented our direct observation of the outcome of song learning with an assessment of local geographic variation of songs. Inferences about song learning can be drawn from patterns of geographic variation, particularly the pattern of song similarity among birds in an area (e.g., Nelson, Khanna, & Marler, 2001; Ranjard, Withers, Brunton, Parsons, & Ross, 2017; Vargas-Castro, 2015). Such variation is linked to the timing and location of song learning and the timing and distance of dispersal (Podos & Warren, 2007). For example, if learning in a species with age-limited learning occurs mainly early in the hatch year, such that the model birds are most likely to be parents and/or other adult birds in the vicinity of the nest, and birds do not disperse very far from the natal area prior to breeding, then breeding adults in an area would tend to share song types. If, however, birds that learn near the nest do disperse some distance before breeding, then breeding adults in an area would be less likely to share song types. If birds learn songs in the hatch year but only after first moving some distance from the nest, then the degree of song type sharing in an area will again depend on the distance between the sites of learning and breeding. If, instead of or in addition to learning in the hatch year, song learning occurs the following year at the first breeding site, then model birds are most likely to be territorial neighbors of the developing bird. In this case, neighboring birds would tend to share song types.

2 | METHODS

2.1 | Study site

Our study focused on prairie warblers present in 2009 and 2010 at the Montague Plains Wildlife Management Area (N 42°34′, W 72°31′), a 600 ha pitch pine-scrub oak barren in Franklin County, Massachusetts. The site contains a mosaic of scrub oak thickets, thinned pine forests, and powerline corridors. Most of the focal birds were captured in mist nets and color-banded for individual identification. A few focal birds were unbanded, but we were able to identify these birds by their distinctive song types and consistent presence in particular locations adjacent to the territories of banded birds. We mapped the territories of the prairie warblers in the study area (71 territories in 2009, 86 in 2010) via repeated observation of the GPS coordinates of singing males over the course of the breeding season (see Akresh, King, & Brooks, 2015 for details). We also searched for nests by observing parent behavior and conducting systematic searches (Martin & Geupel, 1993), and monitored nests every 2–4 days. We color banded nestlings when they were approximately 8 days old.

2.2 | Study species

Like the songs of many wood warbler species, prairie warbler songs fall into two categories: first category songs and second category songs (Spector, 1992). The songs in each category include multiple distinct song types, both across a population and, in some cases, within an individual (Houlihan, 2000; Nolan, 1978). In our study population, about 7% of the birds we recorded extensively used two song types within a category. The category of a song type is easily distinguishable by ear or by visual inspection of spectrograms; first category songs are composed of rapidly repeated, frequency-modulated "buzzy" elements, whereas second category songs are composed mostly of more slowly repeated tonal whistles. Songs in the two categories are used in different contexts (Houlihan, 2000), with unmated males singing predominantly first category songs, and males engaged in aggressive interactions with other males singing predominantly second category songs. In addition, prairie warblers' distinctive dawn performances, consisting of rapid singing interspersed with intense chipping, consist exclusively of second category songs (Nolan, 1978). In some other *Setophaga* species, songs of the two categories differ in patterns of geographic variation (Kroodsma, 1981), mode of cultural evolution (Byers, Belinsky, & Bentley, 2010), and mechanism of development (Byers & Kroodsma, 1992), so it is possible that these differences are present in prairie warblers as well. Given the known and potential differences between prairie warbler first category and second category songs, we assessed each song category separately.

Songs of both categories occur throughout the prairie warbler breeding season. In the period immediately following male arrival on the breeding grounds, almost all males are unmated and singing consists largely of first category songs. As females arrive and settle on territories, almost all males acquire mates (97% of the birds in our study population were mated; Akresh et al., 2015), and the proportion of first category songs decreases. As birds pass through the stages of the breeding cycle, the proportions of songs from the two categories vary, but songs of both categories occur at all stages (Houlihan, 2000; Nolan, 1978).

Individuals in their first breeding season appear to arrive on the breeding grounds with a fixed repertoire. For example, in 13 yearling male prairie warblers that we recorded regularly from arrival through the breeding season in 2009 or 2010, we detected no instances of song types lost from or added to the repertoires recorded immediately after arrival.

2.3 | Song sample

We recorded first category songs from 64 birds in 2009 (90% of the birds present), and second category songs from 49 of these birds (69%). In 2010, we recorded first category songs from 48 birds (56%) and second category songs from 39 of these birds (45%). The 2010 sample included first category and second category songs from six

birds that had been banded as nestlings in 2009 (we henceforth refer to these birds as "returning nestlings"). We banded 90 nestlings in 2009, and the six recorded returning nestlings represent all of the male nestlings that returned to the study area. Overall, 14% of nestlings banded from 2008 to 2011 returned to the study area (Akresh et al., 2015). Surveys of suitable habitat within 15 km of the study area detected very few returning nestlings (unpublished data), so we consider it possible that most returning nestlings settled within the study area.

The identity of each sampled singer was determined by observation of color bands or, for unbanded birds and instances in which a bird's bands were not seen, by the bird's location (obtained by locating the sample's GPS coordinates on our territory map). All songs were recorded between 4:15 a.m. and 9:00 a.m. with a Nagra LB solid-state recorder (48 kHZ sampling rate, 16-bit sample depth) and a Sennheiser MKH62 microphone mounted in a Telinga Pro parabolic reflector. Most sampled birds (including the returning nestlings) were recorded on multiple days between early May and late June, but some birds (8 in 2009, 11 in 2010) were recorded only once or twice. We included these birds in our analysis because we wanted to include as many as possible of the song types present in the study area.

Our song sample did not include songs from all of the males defending territories in our study area; the number of unsampled birds was larger for second category than for first category songs. However, the sampled birds included all birds near the 2009 natal locations of the six returning nestlings, and all birds near the 2010 breeding locations of the returning nestlings (i.e., all birds within 4 territorial boundaries of those locations).

2.4 | Song classification

To begin our analysis, an observer blind to the purpose and predictions of the study reviewed the recordings from each bird, viewing spectrographs (512 point FFT) of each song in Raven 1.4 (Bioacoustics Research Program, 2011) and printing an example of each distinct song form in each recorded sample. The observer also saved each printed song as a separate sound file for later analysis, provided that song recording was of high quality (sharply defined spectrograph, minimal background noise). The observer then used the spectrograph print-outs to classify the printed songs of each bird into song types (i.e., the song types of that bird, without comparison to the songs of other birds), with a type defined as a particular sequence of song elements. Within a bird, prairie warbler songs fall into a small number of clearly discrete and distinct types, so we are confident that a single observer's within-bird classification led to unambiguous and repeatable results.

To determine whether the songs of the returning nestlings matched those of any birds present in 2009 and/or 2010, we began with spectrographic cross-correlation (SPCC, Clark, Marler, & Beeman, 1987). This algorithmic procedure analyzes and compares frequency and time components of a pair of sounds, and returns a single correlation coefficient that represents the degree of similarity between the two sounds. Prairie warbler songs are composed of relatively acoustically simple elements with no harmonics and are therefore well-suited to analysis by SPCC (Khanna, Gaunt, & McCallum, 1997). To generate pairwise SPCC comparisons between the song types used by the six returning nestlings and all of the song types recorded from other birds in 2009 and 2010, we submitted our saved song files to the CORMAT module in SIGNAL 5 (Engineering Design, Berkeley, CA). The SPCC procedure used spectrographs with a 256-point FFT length and limited to frequencies between 2 kHz and 8.5 kHz (to limit the effects of background noise); frequency was normalized such that spectrographs with similar shapes but slightly offset frequencies would be scored as similar. Because different utterances of a bird's song types may not be exactly identical, our SPCC analysis included four exemplars of each song type from each bird, except for a few cases in which we had fewer than four high-quality recordings of a type.

We considered any song pairs with SPCC values of 0.7 or higher to be potential matches, and entered songs that met this threshold into a visual classification process. (For comparison, SPCC values between different examples of a song type from the same bird ranged from 0.8 to 0.92.) In the visual classification process, two naïve observers independently compared an unlabeled printed spectrograph of each eligible 2009 and 2010 song type to spectrographs of each song type from a returning nestling. For each comparison, each observer rated it as (a) a match (same elements in same order), (b) a near match (similar elements in same order, with "similar elements" defined as non-identical but with same general shape and differing by no more than roughly 10% in duration or inter-element interval [time since prior element] and/or differing in frequency by no more than roughly 100 Hz), or (c) non-matching. If, after making all available comparisons for a given returning nestling song, no song had been classified as a match, the observers were asked to identify the near-matching song that was most similar to the returning nestling song. After each observer completed the classification, the two observers discussed and resolved any discrepancies between their classifications. In cases in which the best match identified by visual classification did not correspond to the pair with the highest SPCC value, we accepted the result of the visual classification.

For one returning nestling song type, no other song met the screening criterion of an SPCC value >0.7. In this case, the observers compared the returning nestling song to all other sampled song types and selected the type they judged to be the most similar available song.

After the most similar available songs had been identified for each returning nestling, we measured the distances between the nestlings and the birds singing the similar songs. In particular, we measured (a) the distances between the natal (2009) locations of the nestlings and the 2009 territory locations of the birds singing the songs most similar to those of each nestling and (b) the distances between the first breeding (2010) locations of the returning nestlings and the territory locations of the birds singing the most similar songs. Distances were measured as Euclidean distances between territory centers, using the ruler tool in Google Earth.

To identify the song types present in 2009 (for subsequent use in our analysis of geographic variation), we followed a two-step classification procedure similar to the one we used to identify matches to the types of returning nestlings. In this case, however, the SPCC analysis compared all possible pairwise combinations of songs, and the visual comparison examined all pairs of songs that met the SPCC > 0.7 criterion. The results of the comparison were used to assign type identifiers to songs, with identifiers designed to indicate matches and near matches. For example, three matching songs might be assigned to type 7a, with a song that was near match to those songs assigned to type 7b. After this classification was complete, each song that had failed to clear the SPCC > 0.7 threshold with any other song was visually compared to each of the typed songs. None of these comparisons yielded a match, but several yielded a near-match judgment and were assigned a type number accordingly. Each of the remaining non-matching songs was then assigned its own type number. Subsequently, each bird's song types were marked on our map of bird territories.

2.5 | Geographic analysis

We analyzed the local geographic distribution of song types in 2009, to determine whether song types tended to cluster. To assess potential associations between song similarity and distance between birds, we performed Mantel tests (Manly, 1991), which compare matrices of pairwise distance and similarity measurements, yielding a single correlation statistic per comparison. We constructed a song similarity matrix by assigning each pair of males a value of 0 (no matching type), 1 (a matching type), or 0.5 (a near-matching type but no matching type). A second similarity matrix assigned a value of 1 to both matching and near-matching types, to allow a second analysis using a less-stringent definition of similarity. Geographic distance between individuals was measured as the number of territorial boundaries crossed by the most direct path between two birds. The distance between immediate territorial neighbors was assigned a value of l, the distance between neighbors once-removed a value of 2, and so on. Thus, between-bird distance was encoded in a minimum-path connectivity matrix (Sokal, 1979) intended to incorporate a distance metric that has a biologically interpretable meaning. Pairs of males that were not connected by any direct series of contiguous territories were assigned an arbitrarily high distance value of 20, as suggested by Sokal (1979).

In addition to this assessment of the overall relationship between distance and song similarity, we also assessed the contribution of individual song types to the overall microgeographic distribution of types. In particular, each song type that was sung by more than one bird was tested for evidence of spatial autocorrelation, as measured by a join-count statistic (Cliff & Ord, 1981; Sokal & Oden, 1978). Join-count statistics compare the observed number of joins (in this case, the number of territorial boundaries) separating matching songs to the number expected under a null hypothesis of random spatial distribution. Thus, the statistic can be viewed as a measure of whether a song type is more (or less) clustered in space than is expected by chance. When, as in our initial test, joins are defined as boundaries separating matching songs that occur on adjacent territories, clustering is identified relative to a conservative standard, because matches between songs on nearby but non-adjacent territories are not included. We therefore also calculated a second version of the statistic, in which joins were defined on the basis of different classes of distance between territories. We defined two distances classes, to detect (a) songs shared between territories separated by up to three boundaries and (b) songs shared between territories separated by up to six boundaries.

Mantel tests and join-count statistics were calculated using the PASSaGE software package (Rosenberg & Anderson, 2011). Calculation of join-count statistics assumed sampling with replacement. Statistical significance of Mantel correlations and join-count statistics was assessed with permutation tests (1,000 permutations). All analyses were performed separately for first category songs and second category songs.

3 | RESULTS

3.1 | Returning nestlings and model songs

We identified 12 different song types from the six returning nestlings, one first category song type (Figure 1) and one second category song type (Figure 2) from each bird. All but one of these song types was classified as a match (5 types) or near match (6 types) to a song type used by at least one of the other birds in our study area. The matches and near matches identified by visual classification were generally supported by the SPCC analysis; the song visually classified as closest available match to a returning nestling song was also the song with the highest spectrographic cross-correlation value (8 cases) or the second- or third-highest SPCC value (3 cases). The mean SPCC value for the 11 match/near-match pairs was 0.83 (range 0.78–0.88). For one returning nestling song type (the second category song of nestling 2; see Figure 2), no matching or near-matching song was identified, but two visual classification observers independently identified the same song type as the most similar type available.

Thus, we identified a plausible potential model for each of the song types acquired by the returning nestlings (see Figures 1 and 2), though in one case (the second category song of nestling 2) we had lower confidence in the model assignment. Each model song type was sung by a different model bird, with one exception; one bird provided the first category model for one returning nestling and the second category model for a different returning nestling. In two cases, potential model song types were shared by two birds; the others were used by only one sampled bird in the study area. Many of the birds singing likely model songs were present in both 2009 (the hatch year of the returning nestlings) and 2010. However, five of the likely model birds were present only in 2009 and their song types were not recorded in 2010. Thus, all of the model songs

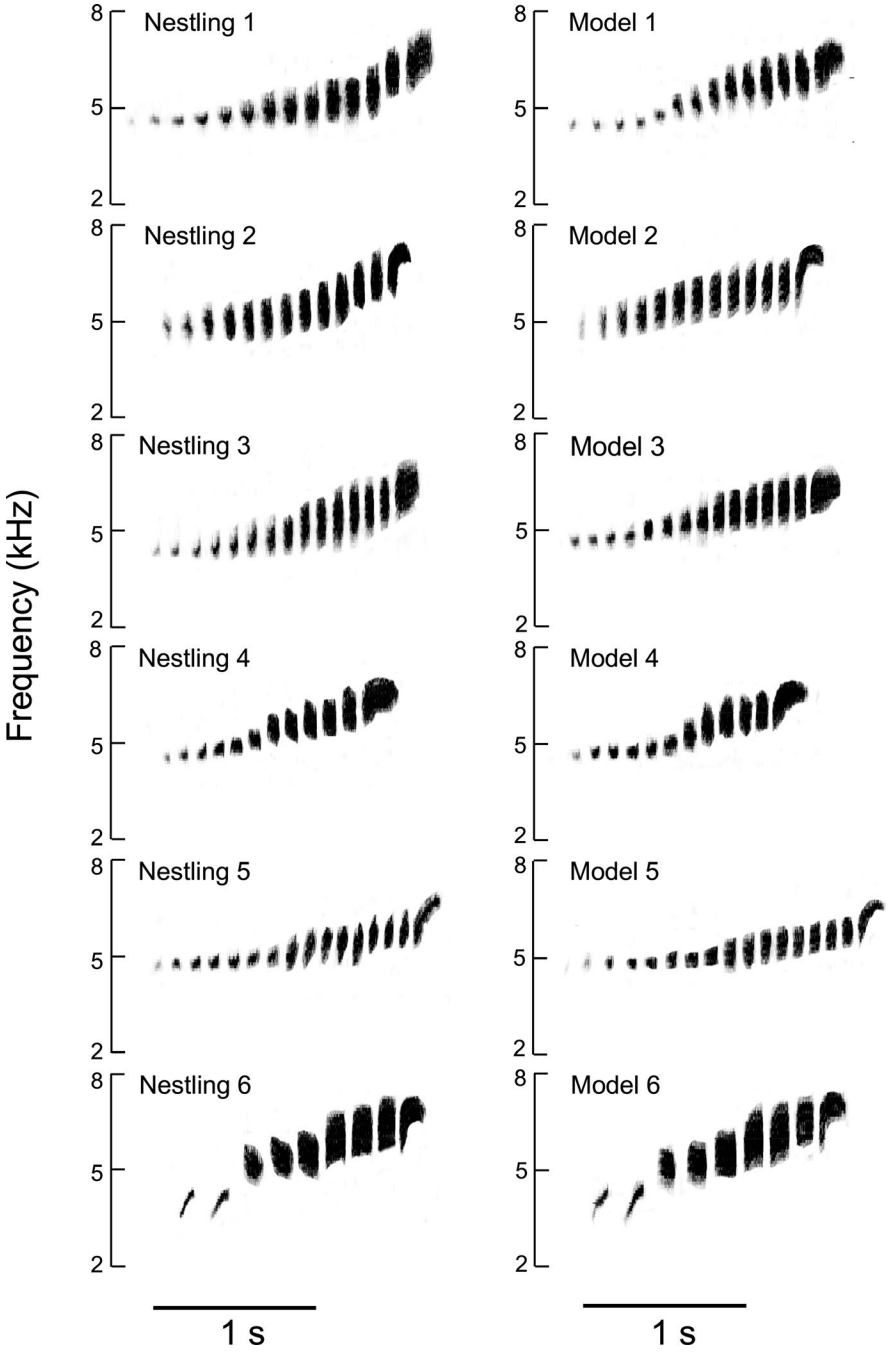

FIGURE 1 Spectrograms (512 point FFT) of the first category songs of six male prairie warblers that were banded as nestlings (left column) and the songs most likely to be the models that the returning nestlings imitated (right column). Each returning nestling song appears in the same row as its model

were detected in the study area in 2009, but only some were also detected in 2010.

The returning nestlings bred some distance from where they were hatched and from the locations of their potential model birds (Table 1). The 2010 breeding territories of the returning nestlings were all at least 550 m from their 2009 natal territories (mean distance 1,586 m, range 560–2,080 m). The 2009 singing locations of the potential model birds were not especially close to the 2009 natal territories of the returning nestlings (mean distance 1,437 m, range 600–1,980 m). The 2010 singing locations of the potential model birds were similarly distant from the 2010 breeding territories of the returning nestlings (mean distance 1,285 m, range 560–2,040 m). For scale, the mean area of a prairie warbler territory in our study area was 0.97 ± 0.45 ha (Akresh et al., 2015), so the diameter of a typical territory was about 100 m. Almost all territories directly abutted the territories of one or more other birds; in some cases, clusters of territories were separated from other clusters by areas of habitat unsuitable for prairie warblers (e.g., dense forest). In our experience, prairie warbler second category songs are audible to human listeners on a territory adjacent to that of the singer, but generally not to listeners on more distant territories. First category songs are somewhat louder and are sometimes audible two or three territories distant from the singer.

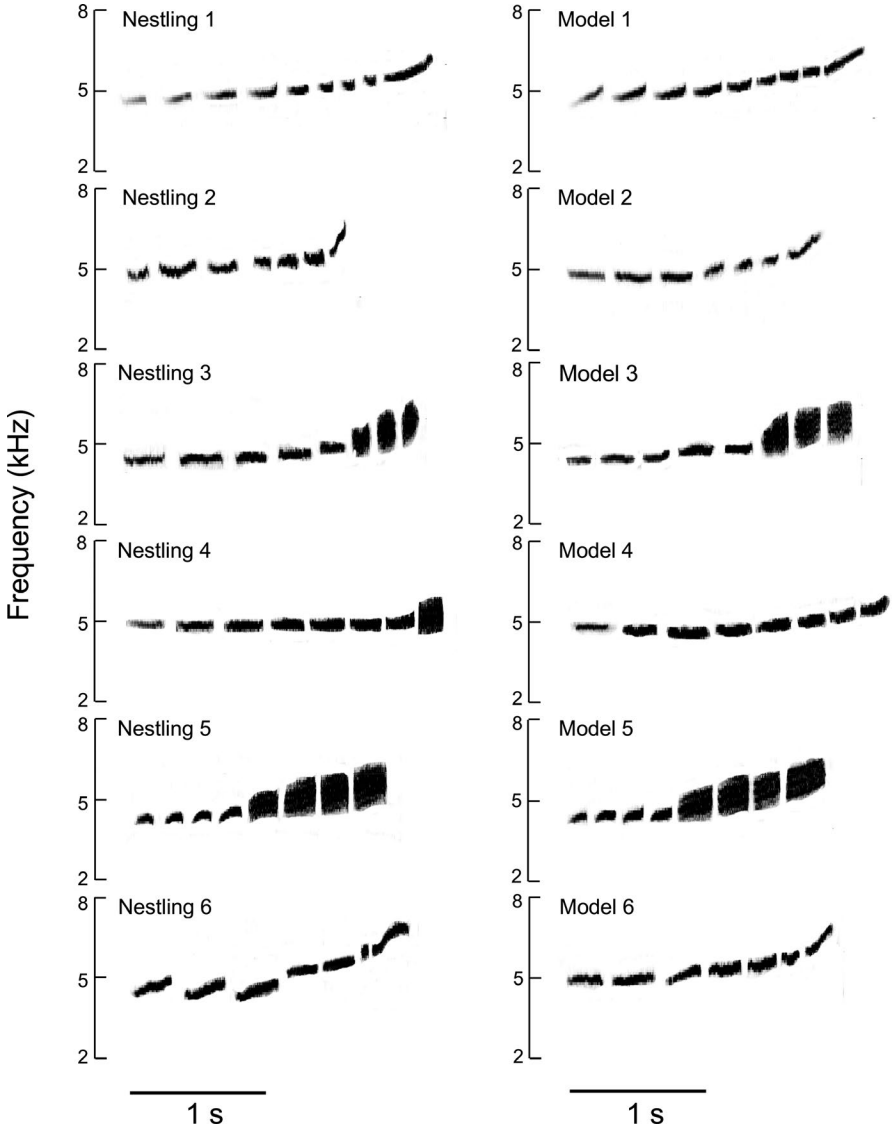

FIGURE 2 Spectrograms (512 point FFT) of the second category songs of six male prairie warblers that were banded as nestlings (left column) and the songs most likely to be the models that the returning nestlings imitated (right column). Each returning nestling song appears in the same row as its model

3.2 | Micrographic variation

Among birds recorded in 2009, we identified 45 first category song types, of which 17 were used by more than one bird. We also identified 51 s category song types, of which 13 were used by more than one bird. The mean SPCC value from comparisons of songs sung by more than one bird and assigned to the same type was 0.82 (range 0.79–0.87).

Mantel tests suggested no association between song sharing and distance between birds for first category songs, but did detect a weak negative correlation for second category songs. Mantel tests for first category songs were not statistically significant, whether based on a stricter definition of song similarity ($r = .01$, $p = .84$) or a looser one ($r = .02$, $p = .51$). Mantel tests for second category songs were, however, statistically significant for both the stricter ($r = -.12$, $p = .007$) and looser ($r = -.10$, $p = .035$) definitions.

Join-count statistics also indicate that first category song types did not tend to cluster geographically. None of the 17 shared first category song types yielded a significant join-count statistic for adjacent-neighbor joins (all $p > .17$; joins represent shared song types). Likewise, no shared first category song type yielded a significant join-count statistic for joins with neighbors up to three territories distant (all $p > .23$), or for neighbors up to six territories distant (all $p > .33$).

Join-count statistics for second category songs suggest that the weak correlation between singer proximity and second category song similarity that was detected by Mantel tests was driven mainly by a few song types that were clustered geographically, though not necessarily on adjacent territories (Table 2). Three of 13 shared second category song types yielded significant join-count statistics, one type for adjacent-neighbor joins and two types for joins with somewhat more distant neighbors.

4 | DISCUSSION

Our assessment of song similarity between returning nestlings (i.e., yearling birds known to have hatched in our study area) and other

TABLE 1 Distances separating six male prairie warblers banded as nestlings from their hatch site and from the males most likely to have served as models for the nestlings' eventual first category and second category songs

	Bird	Hatch site to breeding site (m)	Hatch site to hatch-year site of model (m)	Breeding site to hatch-year site of model (m)	Breeding site to breeding-year site of model (m)
First category	1	1,930	1,660	355	1,690
	2	1,340	880	560	630
	3	2,080	1,980	685	Model not present
	4	1,890	1,840	330	Model not present
	5	1,720	860, 1,850[a]	1,710, 630	1,720
	6	560	600	250	Model not present
Second category	1	1,930	1,740	1,490	1,520, 1,480
	2	1,340	880	615	560
	3	2,080	1,560	1,040	640
	4	1,890	1,920	105	Model not present
	5	1,720	1,830	133	Model not present
	6	560	1,190	1,560	2,040
Mean		1,586	1,437	646	1,286

Note: Mean diameter of a territory was roughly 100 m, and most territories directly abutted at least one other territory.

[a]Two birds sang the matching type in 2009. One was unbanded, so whether it returned in 2010 is unknown, but in 2010 the matching type was recorded from only one bird—the banded bird that was also present in 2009.

TABLE 2 Joint-count statistics for second category song types in a population of prairie warblers, showing expected (under a null hypothesis of no spatial autocorrelation) and actual counts of like song types on adjacent territories, within three territory boundaries, and within six territory boundaries

	Adjacent territory			≤3 territories distant			≤6 territories distant		
Type	E(JC)	JC	*p*	E(JC)	JC	*p*	E(JC)	JC	*p*
111a	0.09	1	.04**	0.27	1	.15	0.40	1	.20
113a	0.20	0	.95	0.60	3	.02**	0.91	3	.04**
104b	0.20	1	.13	0.60	3	.02**	0.91	3	.04**
105c	0.09	0	.95	0.27	0	.95	0.40	1	.21
109b	0.09	0	.95	0.27	0	.95	0.40	0	.95
117a	0.35	1	.26	0.956	1	.95	1.62	1	.89
107f	0.09	0	.95	0.27	1	.12	0.40	1	.19
108a	0.09	0	.95	0.27	0	.95	0.4	0	.95
108c	0.09	0	.95	0.27	1	.15	0.40	1	.20
114a	0.09	0	.95	0.27	0	.95	0.40	0	.95
116a	0.09	0	.95	0.27	0	.95	0.40	0	.95
122a	0.09	0	.95	0.27	0	.95	0.40	0	.95
121a	0.20	1	.13	0.60	1	.95	0.91	1	.95

Note: The three song types with statistically significant ($p < .05$) geographic clustering appear at the top of the table.

** statistically significant join-count statistics are indicated by double asterisks

singers suggests that prairie warblers acquire their song repertoires by imitating adult singers during the nestlings' hatch year. For five of the acquired song types, learning in the hatch year seems like the only possibility because the likely model birds were detected only in the hatch year. We are confident that if these birds had also been present the following year, we would have detected them, as we monitored the study area for banded prairie warblers throughout the 2009 and 2010 breeding seasons. For the other seven acquired song types, the singer of the model type was present in both years, so the returning nestlings could in principle have acquired their songs in either the hatch year or the first breeding year. Differences between birds in a population in the timing of song acquisition are not necessarily unexpected; Savannah sparrows (*Passerculus sandwichensis*), for example, may acquire songs in either hatch year or the following year (Wheelwright et al., 2008). Nonetheless, a scenario in which some of the returning prairie warblers' songs were acquired in the first breeding season is rendered less plausible by the distances separating the first breeding season locations of the

returning nestlings and the locations of their models. If the returning nestlings whose models were still present in the first breeding year had acquired their songs that year, we would expect their models' territories to be located very near or even adjacent to the returning nestlings' breeding territories, as occurs in other species that learn songs in the first breeding season, such as Bewick's wrens (*Thryomanes bewickii*, Kroodsma, 1974), chipping sparrows (*Spizella passerina*, Liu & Kroodsma, 2006), indigo buntings (*Passerina cyanea*, Payne & Payne, 1997), and a Washington population of song sparrows (Beecher, 2017). However, in the first breeding season of our returning prairie warbler nestlings, their models' territories were instead fairly distant from the those of the nestlings (an average of 1,286 m away, see Table 1), suggesting that the returning nestlings would likely have had little opportunity to hear the songs of the models in the first breeding year (though some prairie warblers do move about the study area after returning from migration but before settling on a breeding territory, and might therefore briefly encounter singing birds other than the ones they settle near).

Would the returning nestlings have had an opportunity to hear the models' songs in the hatch year? In that year, the models were distant from the natal sites (an average of 1,437 m away, see Table 1), so it is not likely that the nestlings were exposed the model songs on the natal territory. A more likely scenario is that the returning nestlings encountered their models during post-fledging movements about the study area. We observed color-banded fledglings at distances of up to 1,650 m from their nest, and Nolan (1978) documented substantial post-fledging movements by prairie warblers (e.g., movements of 500 m in a 5-hr time span). Radio-tracking studies of other wood warbler species have documented post-fledging movements that take fledglings more than 1,000 m from the nest within 30 days of fledging. For example, in that time frame, radio-tracked cerulean warblers (*Setophaga cerulea*) moved to 2.4 ± 0.7 km from the nest (Raybuck, Larkin, Stoleson, & Boves, 2020), golden-winged warblers (*Vermivora chrysoptera*) to 1,238 ± 528 m (Streby, Peterson, Kramer, & Andersen, 2015), worm-eating warblers (*Helmitheros vermivorum*) to 1,141 ± 245 m (Vitz & Rodewald, 2010), and ovenbirds (*Seiurus aurocapilla*) to 1,314 ± 174 m (Vitz & Rodewald, 2010). If our returning prairie warbler nestlings moved over similar distances, most of them would likely have been exposed to the songs of both of their models (for all six returning nestlings, the first category model and the second category model were different birds). In 5 of 6 cases, a nestling's two models were fairly close together in the hatch year (mean distance 323 m, range 30–520 m), making it reasonably likely for a wandering fledgling to have encountered both of its models. (One returning nestling was a puzzling outlier in this respect, with 1,830 m between its first category and second category models.) Overall, song acquisition during wide-ranging post-fledging movements seems like the most plausible scenario. Baptista and Morton (1988) identified a similar mode of song acquisition in a migratory population of white-crowned sparrows (*Zonotrichia leucophrys*).

The timing of prairie warbler fledging is largely compatible with a scenario of song acquisition during post-fledging movements in the hatch year. Most of the returning nestlings we studied had hatched in early- to mid-June, so their periods of post-fledging movement would have occurred while most of the male prairie warblers in the area were still singing abundantly. However, one of the returning nestlings (nestling 5) did not hatch until about July 11, so its post-fledging period did not begin until late July. By that date, the number of singing prairie warblers had declined substantially, and by early August there was very little prairie warbler singing in the study area (pers. obs). Nonetheless, nestling 5 seemingly imitated songs from two models, one of which was present only in the returning nestling's hatch year, and the other of which was present both years but was located 1.7 km distant from returning nestling 5 in his first breeding season. It thus appears that even late-hatching prairie warblers are able to acquire songs in the hatch year, despite comparatively limited exposure to adult songs. Birds of several species have been shown in laboratory studies to acquire songs they have heard only a small number of times (Deshpande, Pirlepesov, & Lints, 2014; Hultsch & Todt, 1989a, 1989b; Peters, Marler, & Nowicki, 1992; Thielcke-Poltz & Thielcke, 1960), or to acquire songs on an accelerated schedule if they hatch late in the season (Leitner, Teichel, Ter Maat, & Voigtt, 2015). Perhaps prairie warblers share these abilities.

Although our direct observations of the outcome of prairie warbler song learning are limited to a small number of birds, the pattern of microgeographic song variation in our study area suggests that our conclusions about the timing and location of song learning may apply more broadly in our study population. We found a pattern of local song variation that is consistent with a system of song development in which birds acquire songs in the hatch year at sites somewhat distant from the natal territory and do not subsequently settle near their models. In particular, we did not find the widespread clustering of song types that would be expected if most birds learn songs at the natal site and settle nearby (Lachlan & Slater, 2003), or if most birds imitate the songs of territorial neighbors in the first breeding season (McGregor & Krebs, 1982). Instead, we found that first category songs did not cluster at all and only a few second category types did. This small amount of geographic clustering could arise if a small proportion of birds settled near the territories of hatch-year models that returned to the same or a nearby territory in the subsequent year. Nonetheless, most song types that were shared by multiple birds were dispersed at random across the study area, as would occur if songs were acquired by fledglings that had dispersed in random directions from the natal territory and in the subsequent year settled in breeding locations some distance from the sites of song acquisition. The return rate of breeding birds in our study population is high, as is breeding site fidelity of returning birds; from 2008 to 2011, 72% of banded males returned to the study site, 71% of the returning birds occupied their prior-year territory, and returning birds that did change locations often did not move very far (Akresh et al., 2015). Thus, it is likely that few territorial vacancies occur each year, so that yearling prairie warblers do not usually have an opportunity to settle near the site of song acquisition.

Do developing prairie warblers tend to preferentially imitate males whose songs are especially attractive to females? An earlier investigation of singing in our study population (Byers, Akresh, &

King, 2015) suggested that females prefer to mate with males whose first category songs are lower pitched and delivered at a more rapid rate, whose second category songs are longer and have longer elements, and whose songs in both categories are performed more consistently (i.e., with less variation between renditions). However, when we calculated the average values of these song traits in each of the model songs we identified in this study, and compared those values to the average values of the traits across the entire 2009 sample of singers, we found no strong evidence that the model songs were more attractive than the average song in their song category. Among 39 comparisons of the song traits associated with female mating preference (3 traits for each of 7 first category model songs, 3 traits for each of 6 s category model songs), we found 23 cases in which the model song trait was superior to the population average for that trait, and 16 cases in which the model song was inferior (binomial test $p = .17$). Thus, our findings do not support the hypothesis that male prairie warblers with superior song performance are more likely to transmit their song types to the next generation.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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