Correlation of song learning and territory establishment strategies in the song sparrow

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ABSTRACT In a field study, we show that a young song sparrow (*i*) selects his songs from three or four older birds who have neighboring territories, (*ii*) preferentially learns song types that these tutor neighbors share, and (*iii*) ultimately sets up his territory next to, or replaces, one of these tutor neighbors. The consequence of this song learning strategy is that the young bird's song repertoire represents the "logical intersection" of the song repertoires of his tutor neighbors. We argue that this repertoire is optimally designed for mimicry (sounding like your neighbors) and for communication between neighbors (song sparrows address or reply to a neighbor with a song they share with that neighbor).

Song learning in passerine birds is a selective process in which the young bird retains in his final, adult repertoire only a fraction of the many song types to which he is exposed (1). Despite considerable theoretical interest in the design and function of song repertoires (2–6), however, little is known about the variables determining which of the "tutor" songs are selected for the song repertoire, other than that conspecific songs are preferred over heterospecific songs. To test the hypothesis that social variables are the key determinant of song selection, we studied song learning in a free-living population of song sparrows (*Melospiza melodia*).

In this study, we tested a model of song learning derived from three sets of observations. First, in many (but not all) songbird species, birds share their song types with neighbors, with the resemblances in some cases being so close as to suggest that one bird learned the song type from the other (7). Second, young male song sparrows, starting in the summer of their hatching year, "float" on the territories of several adjacent territorial males and eventually (usually by the following summer) try to set up a territory in this floater range (see refs. 8 and 9; unpublished observations). Third, in song sparrows (and many other songbirds) the early part of a bird's life (especially his second and third months) is critical in the formation of his song repertoire (10). Since we have never observed a male song sparrow to add or drop a song type between his first breeding season and subsequent years, we assume that a young song sparrow's repertoire crystallizes sometime in his first year of life, possibly as early as his hatching summer. Putting these observations together, we hypothesized that during this floater period the young bird learns the song types of some or all of the territorial males in his floater range. To test this hypothesis, we attempted to trace the song tutors for a sample of young male sparrows from our study population.

In this paper, we follow conventional usage and call the bird from whom the song was learned the tutor (the learner is the student). We do not mean to imply by these terms that the older bird actively teaches the younger bird (although he may) or that the younger bird is a passive learner (indeed our evidence suggests quite otherwise). A field study such as ours

has one major disadvantage and one major advantage for the study of song learning. The disadvantage is that we cannot identify a bird's tutors with the certainty that we can in the laboratory. Nevertheless, we should not overestimate the difficulty of tutor assignment in the field compared to the laboratory, since in the final analysis the method of identifying tutors is the same in both cases: one identifies tutors on the basis of the similarity of the song types of student and potential tutor. The compensating advantage of the field approach is that it permits deductions about song learning strategies, for in the field the young bird is free to select his tutors, to interact with them normally, and to choose where he will set up his territory. As we shall see, laboratory and field approaches give different results, and if we are to understand song learning it will be necessary to carefully evaluate these differences.

METHODS

Study Population and Subjects. Our study site is an undeveloped 3-km^2 park bordering Puget Sound in Seattle, Washington. The population is resident (nonmigratory), and typically there are ≈150 males on territories in a given year. Birds disperse into and out of the study population from surrounding areas. The present experiment is part of a long-term study (since 1986). We selected 14 birds of known age whose histories we knew in detail. Each of the 14 subjects was identified as a first-year bird because we had either (*i*) banded him in the nest, (*ii*) netted him as a juvenile (identifiable by an incompletely pneumatized skull and juvenile plumage), or (*iii*) netted him in fall or winter as a young adult in an area where all adult males had been banded.

Song Analysis. Complete song repertoires (all song types) of the subjects and potential tutors were recorded in the field and analyzed on a Kay DSP-5500 sonograph. A song sparrow sings his song types with "eventual variety" (i.e., A A A . . . B B B . . . etc.) and in free singing appears to use the different types interchangeably and with approximately equal frequency (but see below). Although a song sparrow sings variations on each type (11–13), this intratype variation is small compared to intertype variation; moreover, types are clearly defined by the eventual-variety style of singing. The complete repertoire (all song types) of a song sparrow could be obtained in 2–5 hr of recording. Most birds (subjects and potential tutors) were recorded on at least 2 days, and many were recorded in 2 or more years.

Our method of analysis was based on the observation made early in our long-term study that, if our records were complete, we could invariably match a song type of a young bird to a very similar song in the repertoire of one or more older birds. In our analysis, we have identified the older bird with the most similar rendition of the type (complete with idiosyncratic features not seen in other renditions of the type) as the young bird's "probable tutor" for that type. Examples

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Ecology: Beecher *et al.*

Proc. Natl. Acad. Sci. USA 91 (1994)   1451

are shown in Fig. 1. We searched for song tutors by comparing the subject's songs to those of all older birds in the study population who were on territory in the subject's hatching year. The search was carried out blindly with respect to geography, because in theory a bird and his tutor could have widely separated final territories.

Our scheme for evaluating song similarity is based on our field song-matching assay (14) and our laboratory perceptual assay (15–18), and it takes account of the intratype variation mentioned above. A bird was identified as a tutor if one (or more) of his song types was more similar to one of the young bird's song types than that of any other potential tutor. In some cases, two older birds had versions of a song that were highly and equally similar to the young bird's. In such a case, neither one of the older birds was identified as the tutor on the basis of that song type. If one of them was identified as a tutor on the basis of other song types, however, the first song type would enter into subsequent calculations of "tutor-shared" vs. "tutor-unique" types. This technique is conservative and may exclude some older birds who had some impact on the young bird's final repertoire, but it is essential to avoid circularity. The final sample for the present analysis consists of 14 birds hatched between 1986 and 1990.

RESULTS

We could identify one or more probable tutors for each of the bird's 7–11 song types (or all but one, birds 3 and 7). Examples of the close resemblances between tutor's and student's versions of a type are shown in Fig. 1. The vast majority of learned songs were faithful renditions of a song type as sung by one or more of the bird's tutors: 29% were renditions of unique songs of a single one of the bird's tutors, 71% were renditions of shared (similar) types of two or more of the bird's tutors. Of the shared types learned, 53% resembled one of the tutor's versions of the type most closely, 32% blended features of two or more tutors' versions of the type, and 15% resembled two or more tutors' versions equally well (this occurred when tutors' versions were highly similar). A small percentage (4%) of the learned songs were hybrids of two dissimilar song types: in all cases, these hybrid songs were constructed from two song types of the same tutor. We have never found a clear example of a bird hybridizing a song type from one singer with a dissimilar song type from a different singer. An example of an intrasinger, intertype hybrid song is shown in Fig. 2.

When the subject's entire repertoire is considered, in no case does one single tutor have the closest match for every song type. Instead, in every case, three or four tutors were required to account for the subject's 7–11 song types. Again, an older bird was not classified as a tutor unless at least one of his song types matched one of the subject's song types better than that of any other tutor. We then examined the geographical relationships of these tutors (identified purely on the basis of song similarity) among themselves and to the subject. In every case, the three or four tutors turned out to have been contiguous neighbors in the summer of the young bird's hatching year. Moreover, in every case, the young bird's territory in the following spring (first breeding season) turned out to be within or adjacent to the territorial boundaries of these tutor neighbors; 71% of these tutors were still present at that time. For the seven birds whose tutors were
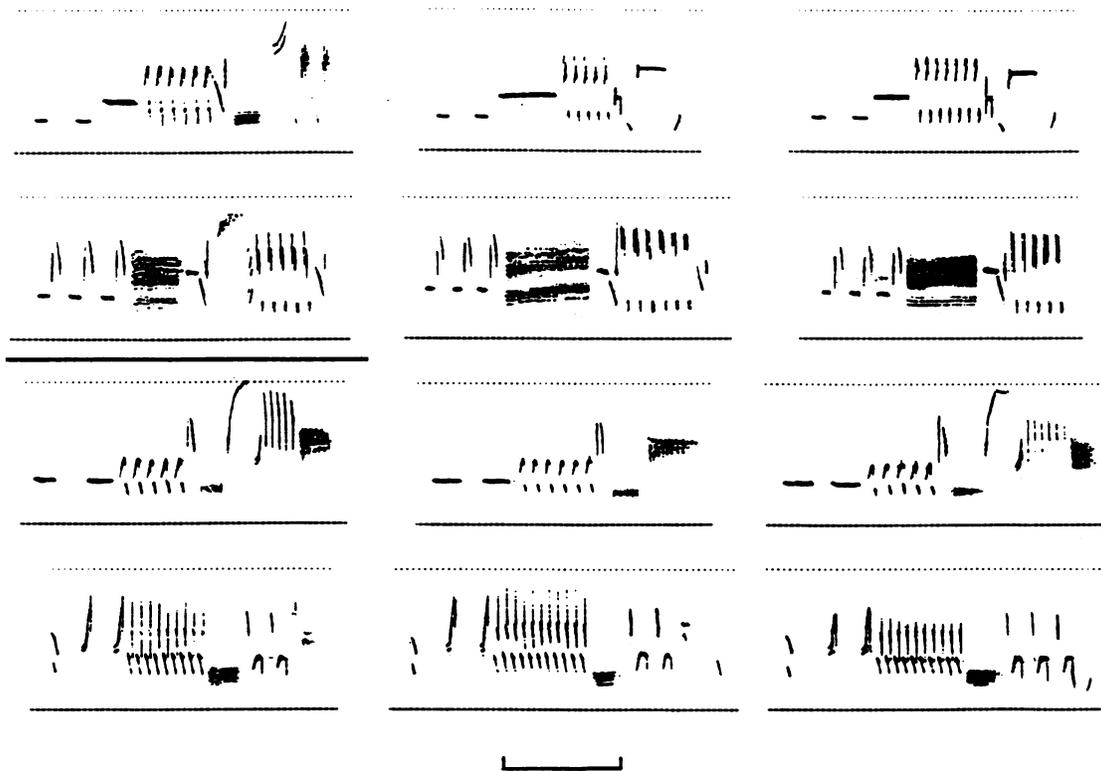

FIG. 1. Four of the nine song types of bird 8 are shown in the middle column. Left and right columns show the matching song types of three of his four tutors (left column contains two song types of tutor A and two of tutor B; right column contains four song types of tutor C). These song types represent just under half of the total song repertoires of these birds. Note that song types not shown include those unique to a particular tutor and those shared by three or more tutors. In some cases, the young bird's version of the song type was closer to that of one tutor or the other. For example, his renditions of the top two song types were more like that of the tutor to the right. Note that song classification was based on several versions of each song type from each bird and therefore on more than is shown in this figure. This is a key point, for song sparrows vary their song types from one occasion to another, and song types therefore are song classes. Endings are most variable and therefore are the least diagnostic of type. Examples of song variants are shown in ref. 12. Frequency markers at bottom and top of each sonogram, 0 and 10 kHz; time marker, 1 sec; bandwidth, 117 Hz.
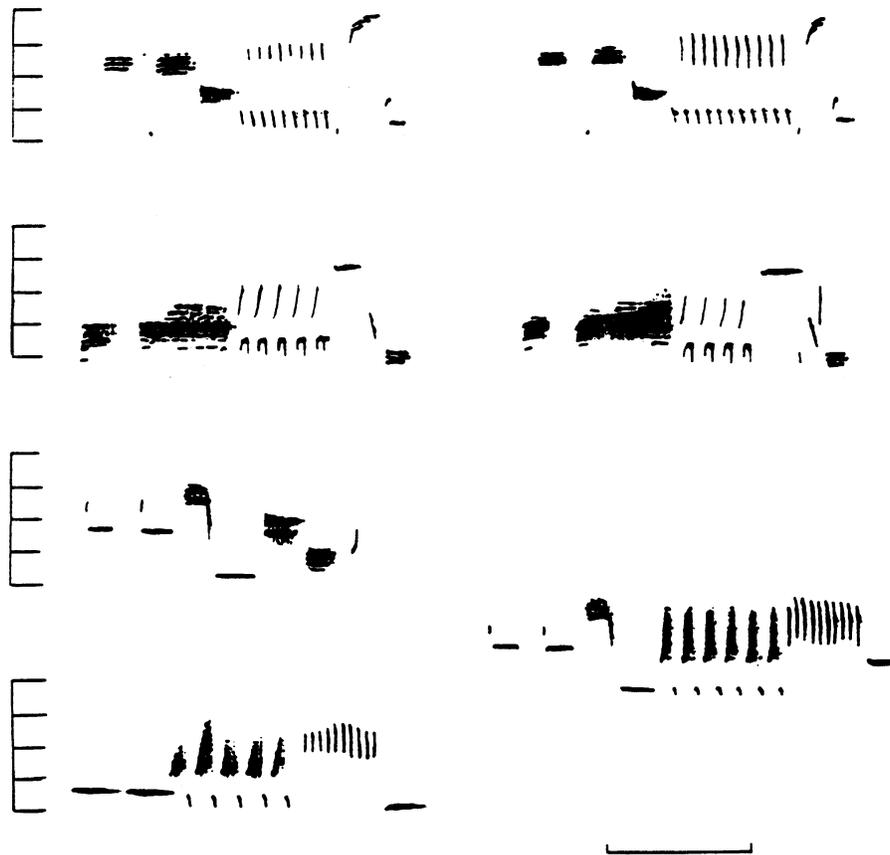
FIG. 2.   Three of the eight song types of bird 9 are shown in the right column, along with four song types of tutor 1 (his primary tutor) in the left column. The top two songs of bird 9 are straightforward copies, but his third song is a hybrid of two song types of the tutor (the first four elements of the tutor's third song type, and all but the first two elements of the tutor's fourth song type). As noted in Fig. 1, song classification was based on several versions of each song type from each bird and therefore on more than is shown in this figure. Frequency scale, 2–10 kHz in 2-kHz steps; time marker, 1 sec; bandwidth, 117 Hz.

all present the following spring, the bird settled next to the primary or secondary tutor (the two tutors from whom the bird learned most of his songs). For the seven birds who had one or more missing (deceased) tutors the following spring, the bird settled closest to or in the territory of one of these departed tutors (and adjacent to one or more of the other tutors). These findings are consistent with our hypothesis that the young bird's tutors are the resident males of his floater territory.

Since the young bird may become territorial at any point between August of his hatching year and the next June, we may ask whether presence of the tutor in this period is a factor in determining how many of the tutor's songs are learned. Of the 48 tutors, 71% survived the winter and were present the next spring in the subjects' first breeding season. Subjects learned no more songs from tutors present in the subject's first breeding season than they did from tutors not present (2.6 vs. 2.3 songs per tutor; 2.7 vs. 2.8 if we count only the first 3 tutors). This suggests that song learning was essentially complete by the bird's first spring and is consistent with the laboratory finding that most songs are learned in the bird's first months of life (10).

Once we had identified the probable tutors of each of our subjects, we looked for characteristics that might distinguish tutor songs the bird learned from those he did not learn. We classified each of the song types in a tutor group as tutor shared (two or more of the subject's tutors had similar versions of the song) or as tutor unique. The classification was done without knowledge of which of the tutor songs had been learned. It is shown in Table 1 that each of the 14 subjects was more likely to learn song types shared by his tutors than song types unique to particular tutors ($P = 0.0001$,

sign test; means $= 6.07$ vs. 2.57 songs or 70% vs. 30% of the repertoire). This learning preference for tutor-shared types occurred even though shared types were less common than unique types (mean 7.2 shared vs. 12.4 unique song types per tutor group). Overall, the 14 subjects learned 84% of the 101 shared songs and only 21% of the 174 unique songs. It is possible that the learning preference for tutor-shared types is due to a dosage effect: the subject is exposed to a unique type from only a single tutor in the tutor group, whereas if the type is shared by, say, two tutors, he is exposed to it twice as often on average. To test the simple dosage hypothesis, we weighted each shared song type by the number of tutors singing it. By this hypothesis, this frequency-weighted percentage of shared types learned by the bird should equal the percentage of unique types learned by the bird. For all 14 subjects, the weighted percentage of shared types learned was still higher than the percentage of unique types learned (see Table 1, column sh × f; $P = 0.0001$, sign test).

DISCUSSION

Bird song has become a major model system for the study of learning in vertebrates, owing to several decades of innovative laboratory studies and the recent discoveries concerning the neurobiology of the song system (e.g., see refs. 19 and 20). To the extent that a laboratory study fails to replicate the essential conditions of the natural song-learning context, however, it may give an incomplete or partially misleading view of song learning (see, e.g., refs. 21 and 22). Our field study provides a different picture of song learning from that provided by laboratory studies to date. In particular, our field study suggests at least three important rules of song learning

Ecology: Beecher *et al.*

Proc. Natl. Acad. Sci. USA 91 (1994) 1453

Table 1. Learning preferences for tutor-shared and tutor-unique song types

| Bird | Hatch year | Song types | Tutors | Song types learned/song types in subject's tutor group | | | Subject's territory in first breeding season* |
				Shared	Unique	sh × f	
1	1986	11	3	3/3	8/22	3/7	Adjacent to tutor 2
2	1986	9	4	6/6	3/19	6/15	Adjacent to tutor 2
3	1987	8	4	4/5	3/17	4/10	Adjacent to tutor 1
4	1989	11	4	7/10	4/13	7/21	Replaced tutor 3
5	1989	8	4	6/8	2/14	6/19	Replaced tutor 4
6	1989	11	3	7/7	4/17	7/14	Replaced tutor 2
7	1989	8	4	5/5	2/11	5/11	Replaced tutor 3
8	1990	9	4	7/11	2/13	7/24	Replaced tutor 3
9	1987	8	3	8/8	0/5	8/21	Adjacent to tutors 1, 2
10	1988	8	4	8/12	0/8	8/29	Adjacent to tutors 1, 4
11	1986	9	3	8/8	1/4	8/18	Replaced tutor 3
12	1988	7	3	5/6	2/10	5/13	Adjacent to tutor 2
13	1990	7	3	5/6	2/9	5/13	Replaced tutor 3
14	1990	9	4	6/6	3/12	6/18	Adjacent to tutor 1
Mean		8.78	3.57	6.1/7.2 (84%)	2.6/12.4 (21%)	6.1/16.4 (37%)	

Song types are classified as tutor shared (sung by two or more of the tutors in the bird's tutor group) or tutor unique (sung by only one of these tutors). The denominator of sh × f is the sum of the shared types, where each is weighted by the number of tutors singing it (e.g., if there were six shared types, two of which were sung by three tutors and four of which were sung by two tutors, this number would be 14).

*Geographical relationship of bird to his tutors (nearest neighbor or tutor he replaced) in his first territorial spring (see text for additional details). Tutors are ranked in terms of their degree of influence on the subject's song repertoire.

not predicted by laboratory song-learning studies. First, song sparrows copy songs precisely. We find only two exceptions to the rule of faithful copying: (*i*) the bird often blends two different tutors' versions of the same song type and (*ii*) occasionally hybridizes two different song types of the same tutor. This rule and its exceptions can be summarized by saying that the young bird preserves type and/or tutor. In contrast, laboratory studies have found that song sparrows often combine elements from different song types even when they are presented in nonoverlapping periods and/or are from different singers. It is important to note that these cross-type and cross-singer hybrid songs have been obtained with both tape tutors (10, 23) and multiple, live tutors (M.D.B., S.E.C., and J. M. Burt, unpublished study).

Second, song sparrows preferentially copy song types shared by tutors. Laboratory studies have not revealed this song-learning phenomenon because they have generally used tape tutors and because, to simplify the task of identifying the model or tutor for the subject's learned song, they have avoided using shared (similar) song types.

Third, our field study indicates that the young song sparrow samples several tutors, and most likely this means active sampling: territories are sizable and the young bird would probably have to move from tutor to tutor to get an adequate hearing of each. The few laboratory studies using multiple live tutors have not addressed the question of active sampling (24–26).

Although the features of song learning revealed by our field study have not been suggested by laboratory studies to date, it should be quite possible to design a laboratory study that manipulated the variables we have identified: the young bird would be permitted to move between several, spatially separated tutors, who shared some but not all of their song types. Presumably, this experiment would replicate the pattern of results of our field study. In summary, these are that the young bird constructs his song repertoire by (*i*) sampling the repertoires of three or four older tutor neighbors, (*ii*) preserving, within limits, the identity of both the song type and the song tutor, and (*iii*) preferentially learning types shared among these tutors. This song-learning strategy functions to maximize the number of songs the bird shares with his neighbors—not only his tutor neighbors but also the younger

birds who will eventually replace his original tutors, for they will have learned many of the same songs.

There is evidence in a single song-type species, the indigo bunting, that younger birds who copy the song type of an older neighbor are more successful than those who do not (27). Although this correlation between song sharing and reproductive success may be purely incidental, we suggest four possible advantages to sharing songs with neighbors. First, song sharing may provide an advantage to a young bird in competitive interactions. The advantage may accrue through mimicry (the young bird is confused with older established residents; ref. 28) or through some other mechanism (hypotheses in refs. 29–31). A long-term mimicry advantage in our population is unlikely, however, given our finding that long-term neighbors can recognize one another on the basis of a single song type (32, 33). Second, song sharing may provide an advantage in our population to a young bird in cooperative interactions with neighbors. A recent study by Beletsky and Orians (34) has shown that in red-winged blackbirds, males with familiar neighbors have greater breeding success than males with unfamiliar neighbors. As they point out, this effect may favor cooperative behavior in this and other similar species. We would add that it may also favor communication signals that encode familiarity. A third possible advantage, perhaps relating to the second one, has been suggested by our recent experiments (M.D.B., P.K.S., S.E.C., and C. L. Horning, unpublished data). We have found that a song sparrow will reply to a neighbor song by singing a song type he shares with that neighbor; we call this repertoire matching. Finally, a fourth possible advantage is suggested by studies indicating a role for females in shaping song repertoires in song sparrows— namely, that females might prefer the common song types of a neighborhood (35, 36).

It might be argued that the high degree of song sharing we find in our population ($\approx$40%, measured between any two neighbors) is unusual and may occur only in a resident (nonmigratory) population. For example, song sharing between neighbors is evidently lower in the migratory population of song sparrows studied in Ontario, Canada, by Kramer and Lemon (37). We would point out, however, that there does not have to be less song sharing in a migratory popu-

lation than in a resident population. Sharing will be high in any population where birds remain in (resident population) or return to (migratory population) the area where they learned their song types. There is considerable evidence that in most songbird species birds learn their songs after dispersal from the natal area; evidence is also accumulating that, in migratory species, first-year breeding males return to the area to which they dispersed in their hatching summer, presumably where they learned their song types (review in ref. 38; see also ref. 39).

Finally, our results and speculations suggest another view of song repertoires. Song repertoire size has generally been viewed as a sexually selected trait, and virtually all such theories to date have implied strong directional selection pressure on number (or at least diversity) of song types. We suggest that, at least in some species, it may be sharing of song types with several neighbors, rather than the number of types *per se*, that is the target of selection. If this view is correct, it may explain one of the more difficult observations for the view that repertoire size *per se* is under selection: in most species repertoire size is rather small (usually <10 types, often <5), despite no obvious costs or counterselection pressures. By learning only shared types, song sparrows wind up sharing more song types with more neighbors than they would if they learned all (or most) of the tutor song types: unique types would be shared with only one tutor, and then only until he died or moved. If song sparrows could learn new song types as adults, then there would be less of an advantage to preferentially learning shared types when younger, for a bird could simply learn the songs he needed when his new neighbors appeared. Song sparrows evidently learn all their song types relatively early in their first year, however, and our argument assumes this as a constraint. It now appears that in a number of species, unlike in song sparrows, the male has the ability to replace an old song type with a new song type of a new neighbor in his first breeding season and perhaps even in later breeding seasons. It may be significant that these species, in which the repertoire is not finalized early in life, turn out to be ones with small song repertoires (one to three song types; see refs. 40–43).

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