Ethology **108,** 39—50 (2002)

ISSN 0179–1613

Adult Song Sparrows do not Alter their Song Repertoires

J. Cully Nordby, S. Elizabeth Campbell & Michael D. Beecher

Animal Behavior Program, Departments of Psychology & Zoology, University of Washington, Seattle

Abstract

To understand fully the function of vocal learning, it is important to know when, during an individual's lifetime, learning occurs. Songbirds are generally categorized into two groups with respect to their adult song learning ability. 'Open-ended' song learners are able to learn to produce new songs in adulthood, whereas 'age-limited' song learners can only acquire songs during their first year of life. Researchers have long assumed that certain oscine species are open-ended or age-limited song learners, but the evidence to date has been inadequate to test these assumptions for most species. We tested the hypothesis that song sparrows (*Melospiza melodia*) are age-limited song learners who do not alter their song repertoires in adulthood by examining the song repertoires of 24 color-banded males who were fully recorded in two, three or four different years. We compared sonagrams of the song types produced by males in different years and looked for any changes in repertoire composition (i.e. added or dropped song types). With few exceptions, males produced song repertoires that were identical in every year they were recorded. The exceptions (four males who did not produce one of their song types during one recording session) were all cases in which we believe that we missed recording a song type that a male did indeed have, not that the males dropped a song type. The finding that adult males do not alter the composition of their song repertoires provides strong evidence that song sparrows are age-limited song learners. Although it is possible that song sparrows make subtle within-song type changes across years, such changes would not necessarily constitute new song learning.

Corresponding author: J. Cully Nordby, Ecosystem Sciences–ESPM, 151 Hilgard Hall #3110, University of California–Berkeley, Berkeley, CA 94720-3110, USA. E-mail: nordby@nature.berkeley.edu

Introduction

Vocal communication is a learned behavior in a wide variety of animal groups, including birds, cetaceans, non-human primates, and humans. Brown & Farabaugh (1997) suggest that vocal learning may be adaptive because it allows individuals to share vocalizations with a particular subset of conspecifics. In order to understand fully the function of vocal learning, and of sharing vocalizations, it is important to know when, during an individual's lifetime, learning occurs.

Songbirds (oscine passerines) are generally categorized into two groups with respect to their ability to learn new songs in adulthood (Nottebohm 1984). 'Open-ended' song learners are species that are able to alter their song repertoire throughout their lifetime by adding new song types that they learn as adults (e.g. the canary *Serinus canaria*; Nottebohm & Nottebohm 1978). In contrast, species that are 'age-limited' song learners can only acquire songs within their first year of life, and their adult song repertoire remains the same throughout adulthood (e.g. the zebra finch *Taeniopygia guttata*; Immelmann 1969). For our purposes, we define 'age-limited' song learning as when a male acquires (memorizes) all of his songs during his first year of life, regardless of whether the sensitive period for song acquisition occurs during the first few months of life (e.g. zebra finches; Immelmann 1969) or continues into the bird's first spring (e.g. the marsh wren *Cistothorus palustris*; Kroodsma & Pickert 1984). The important component of this definition is that once a bird's song repertoire has crystallized, it remains fixed throughout the adult life of the bird.

Researchers have long assumed that song sparrows (*Melospiza melodia*) are age-limited song learners. Inherent in many investigations of song sparrow song is the assumption that adult males do not change their song repertoires. For example, in our studies of song type use between neighboring males (Stoddard et al. 1990, 1991, 1992a; Beecher et al. 1996, 2000), we have often used songs recorded in previous years as stimulus songs in playback experiments. Because we never have had subject birds reply with previously unrecorded song types (M. D. Beecher, pers. obs.), we too assumed that song sparrows were age-limited song learners.

One way to test the hypothesis that species are age-limited song learners that do not alter their song repertoires as adults is to record males in different years and compare the songs produced in each year. Several studies of song sparrows have included examination of whether males alter their song repertoires across years, but each has been unable to answer this question adequately. Saunders (1924) found birds singing the same repertoire on the same territory two years in a row, but these males were unmarked and he was able to follow only three males across years. Nice (1943) documented the maintenance of song repertoires across years for song sparrows in Ohio, but for only two banded males. A study of Maine song sparrows (Borror 1965) showed similar song repertoires for males in different years, but none of the birds in this study were banded and in most cases the song repertoires were incompletely recorded. Searcy et al. (1985) and Hiebert et al. (1989) recorded full repertoires of color-banded males in multiple years and

found no differences in repertoire composition, but the sample sizes in these studies were small; two and five males, respectively. Finally, Cassidy (1993) found identical song types in different years for color-banded males, but only five of 20 subjects were fully recorded in more than one year.

The purpose of this study was to test the hypothesis that song sparrows do not change their song repertoires in adulthood by examining the song repertoires of 24 color-banded males who were fully recorded in two or more different years and looking for any changes in repertoire composition (i.e. added or dropped song types). This study provides a much more powerful test of the hypothesis than the previous observations because we sampled a large number of birds that had been recorded under a common protocol and because we used a single method to compare all songs.

Methods

Study Population and Subjects

Our study site is an undeveloped park (200 ha) along Puget Sound in Seattle, WA, USA. The resident song sparrow population is sedentary, and in any given year there are 120–150 males occupying breeding territories. The average territory tenure for a bird in this population is 3 years. This site has been part of a long-term study started in 1986, and each year all males are uniquely banded (with three plastic color leg bands and one U.S. Fish and Wildlife Service aluminum band) and their song repertoires are recorded.

Subjects for the present study were 24 adult male song sparrows banded between 1986 and 1996. We recorded the song repertoires of each of these birds between 1987 and 1998 when they were between 1 and 6 years of age. All subjects were territorial and paired with a female during the breeding seasons they were present on our study site.

Song Repertoire Recording and Analysis

Song sparrows have song repertoires comprised of 5–12 different 'song types'. Each song type in a male's repertoire is a distinctive sequence of song elements, or notes, that are produced in a consistent manner. Podos et al. (1992) showed that, although males produce many variations of each of their song types (e.g. adding notes to the end of the song), the variation within song types is much less than between song types. Thus, variations of one song type are easily distinguished by eye from songs of another type.

Males sing with eventual variety, meaning they produce several songs of one type before moving on to a 'bout' of the next type (i.e. AAA…, BBB…). Also, as a male sings, he cycles through his repertoire avoiding recently sung song types. In our population, a bird will cycle through his repertoire of N song types, on average, in N + 2 song type bouts (C. R. Wilkerson, J. C. Nordby & M. D.

Beecher, unpubl. data). Males sing throughout the breeding season and occasionally during the non-breeding season as well.

We recorded each subject's adult song repertoire in two, three or four different years. Forty-nine of 53 recording sessions were made during the breeding season between early Mar. and early Jul.; the remaining four sessions were recorded in Sep., Oct. or Dec. We did not include recordings of young males made before Apr. of their first breeding season because their song repertoires were still plastic before then. Young males may selectively drop or alter song types in their repertoire before song 'crystallization' which, in our population, occurs around mid-Mar. (J. C. Nordby, S. E. Campbell & M. D. Beecher, unpubl. data). Recordings were made using Sony TC-D5M, Sony WM-D6C, or Marantz PMD221 cassette recorders and Sennheiser ME67, ME88, or MKH-816T-U directional microphones. All recordings were analysed on a Kay DSP 5500 sonagraph.

Males were included in this study if we had recorded them in two or more years and if the following two criteria were met: (1) one of the recording sessions included at least 16 consecutive song type bouts, and (2) the other session(s) included at least 10 consecutive song type bouts. Because song sparrows cycle through their repertoire in a predictable manner, recording 16 consecutive song type bouts reliably includes all song types in a male's repertoire (for rationale see Kroodsma 1982; C. R. Wilkerson, J. C. Nordby & M. D. Beecher, unpubl. data). In most instances, however, the entire repertoire is recorded in less than 16 bouts. Therefore, we relaxed the criterion for the additional sessions to 10 or more bouts, with the understanding that we may have missed recording a song type in those sessions due to undersampling. These criteria were met for 20 subjects. To increase our sample size, we included an additional four subjects for whom we had recorded only 14 or 15 consecutive song type bouts in one session, and 10 or more bouts in the additional session(s).

Some other researchers have used number of songs recorded, rather than number of song type bouts, as their criterion for recording a male's complete song repertoire (usually 200 or more songs, e.g. Cassidy 1993; Searcy et al. 1985). The number of songs a male sings within a bout can vary tremendously; for example, in the present study subject MAGO sang 527 songs in 13 song-type bouts, whereas subject BGMG sang 114 songs in 22 bouts (Table 1). We used song type bouts rather than songs to determine when we have recorded a bird's complete song repertoire and did not document how many songs were recorded in every session. For comparative purposes, we included number of songs recorded per session in Table 1 when that number was available.

To examine whether adult song sparrows modify their song repertoires between years, we compared the song types produced by each male in each year he was fully recorded. Sonagrams of all song types, including distinct variations, were made during analysis of the first recording session for each bird. For analysis of sessions recorded in subsequent years, we (JCN, SEC or a trained assistant) visually compared sonagrams of the song types produced to the sonagrams from the first session and looked for song types that may have been added or dropped.

Table 1: Subjects' age, number of song bouts, songs, song types and changes in repertoire identified in each recording session

Subject	Date recorded	Age[a] years	No. of bouts	No. of songs	No. of song types recorded	Repertoire identical?[b]
OIMR	25 Mar 92	≥ 2	15	252	5	–
	8 Mar 94	≥ 4	14	183	5	yes
BBMR	13 Jun 87	≥ 1	13	121	7	–
	9 May 90	≥ 4	26	–	7	yes
BMGB	25 Apr 89	≥ 1	14	223	7	–
	10 Mar 90	≥ 2	11	–	7	yes
BMYY	14 Apr 89	≥ 1	19	156	7	–
	17 May 90	≥ 2	16	–	7	yes
GGMG	25 Apr 87	≥ 1	16	–	7	–
	19 Jul 91	≥ 5	15	–	7	yes
IGWM	11 Jun 92	≥ 1	16	–	7	–
	22 May 97	≥ 6	31	406	7	yes
MRRB	26 Jun 87	≥ 2	25	216	7	–
	26 Apr 88	≥ 3	21	148	7	yes
OOGM	24 Jun 91	≥ 1	14	–	7	–
	4 May 92	≥ 2	10	–	7	yes
	23 Mar 95	≥ 5	14	–	7	yes
RBMC	4 Jun 91	≥ 1	21	–	7	–
	8 Apr 92	≥ 2	15	–	7	yes
	8 Oct 93	≥ 3	29	284	7	yes
	3 Mar 94	≥ 4	13	110	7	yes
RMGY	25 May 96	1	20	–	7	–
	2 Jun 98	3	50	738	7	yes
GOMB	20 Jun 96	1	22	193	8	–
	15 May 97	2	20	198	8	yes
IIAM	7 Apr 94	2	23	–	8	–
	14 Apr 98	6	34	350	8	yes
OIGM	18 Sep 93	≥ 2	26	306	8	–
	9 Mar 94	≥ 3	18	182	8	yes
RGRM	21 Apr 88	≥ 1	19	118	8	–
	10 Apr 89	≥ 2	18	236	8	yes
GGRM	24 Apr 92	1	10	–	9	–
	17 Jun 93	2	28	–	9	yes
MAGO	18 Dec 92	2	11	264	9	–
	2 Sep 93	3	13	527	8	−1 song type
	9 Mar 94	4	13	254	9	yes
	13 Apr 95	5	19	312	9	yes
MOIW	20 Apr 94	≥ 1	26	134	9	–
	17 May 96	≥ 3	14	–	9	yes
MPOX	26 Jun 87	≥ 1	14	209	9	–
	12 Apr 88	≥ 2	16	241	9	yes
ROMP	29 Apr 91	≥ 1	15	123	9	–
	8 Mar 94	≥ 4	12	143	9	yes
BAMP	10 Apr 96	1	23	364	9	–
	19 May 98	3	40	430	10	+ 1 song type

Table 1: Continued

Subject	Date recorded	Age[a] years	No. of bouts	No. of songs	No. of song types recorded	Repertoire identical?[b]
BIRM	22 May 96	≥ 1	18	–	10	–
	15 Apr 97	≥ 2	31	411	10	yes
IIOM	24 Apr 92	≥ 1	28	–	10	–
	22 May 97	≥ 6	33	159	10	yes
MGBB	5 Jun 87	≥ 2	17	133	10	–
	11 Jun 90	≥ 5	12	67	9	−1 song type
BGMG	27 May 87	1	22	114	11	–
	1 Mar 90	3	17	135	10	−1 song type

Subjects are listed in order of repertoire size.
[a]For subjects banded as adults, we list their minimum possible age at the time they were recorded.
[b]Repertoire comparisons are made relative to the first recording session.

Because the song types within each male's repertoire are quite distinct, songs of a particular song type recorded in different years can be unambiguously identified as the same type. We did not examine within-song type differences between years, only whether there were changes at the level of whole song types.

Results

Twenty-one males were recorded in two different years, one male was recorded in three different years, and two males were recorded in four different years. The maximum number of years between recording sessions for each male ranged from 1 to 5 years ($\bar{x} \pm SE = 2.3 \pm 0.3$ years). The number of song type bouts recorded in each session ranged from 10 to 50 bouts (19.8 ± 1.1 bouts). We identified the number of songs recorded in 35 of the 53 recording sessions. The number of songs per session ranged from 67 to 738 songs (241.1 ± 23.6 songs).

Twenty of 24 subjects had song repertoires that were identical in every year they were recorded (Table 1). As an example, Fig. 1 shows subject IIAM's complete repertoire of eight song types when he was 2 years old and 6 years old. The remaining four subjects had one song type each that was missing from only one recording session in one year. In two of these cases, the recording session missing the one song type contained less than 16 song bouts (13 bouts for MAGO and 12 bouts for MGBB) which is our criterion for recording a complete song repertoire. In the third case, subject BAMP sang only nine of his 10 song types in 23 consecutive bouts in the first recorded session. We know that he did not add the tenth song type after his first year, however, because we recorded that song type in his plastic song repertoire earlier in his first year. BAMP also sang that song type in a partial recording session in the year between the years we recorded our two complete sessions. In the last case, subject BGMG produced 11 song

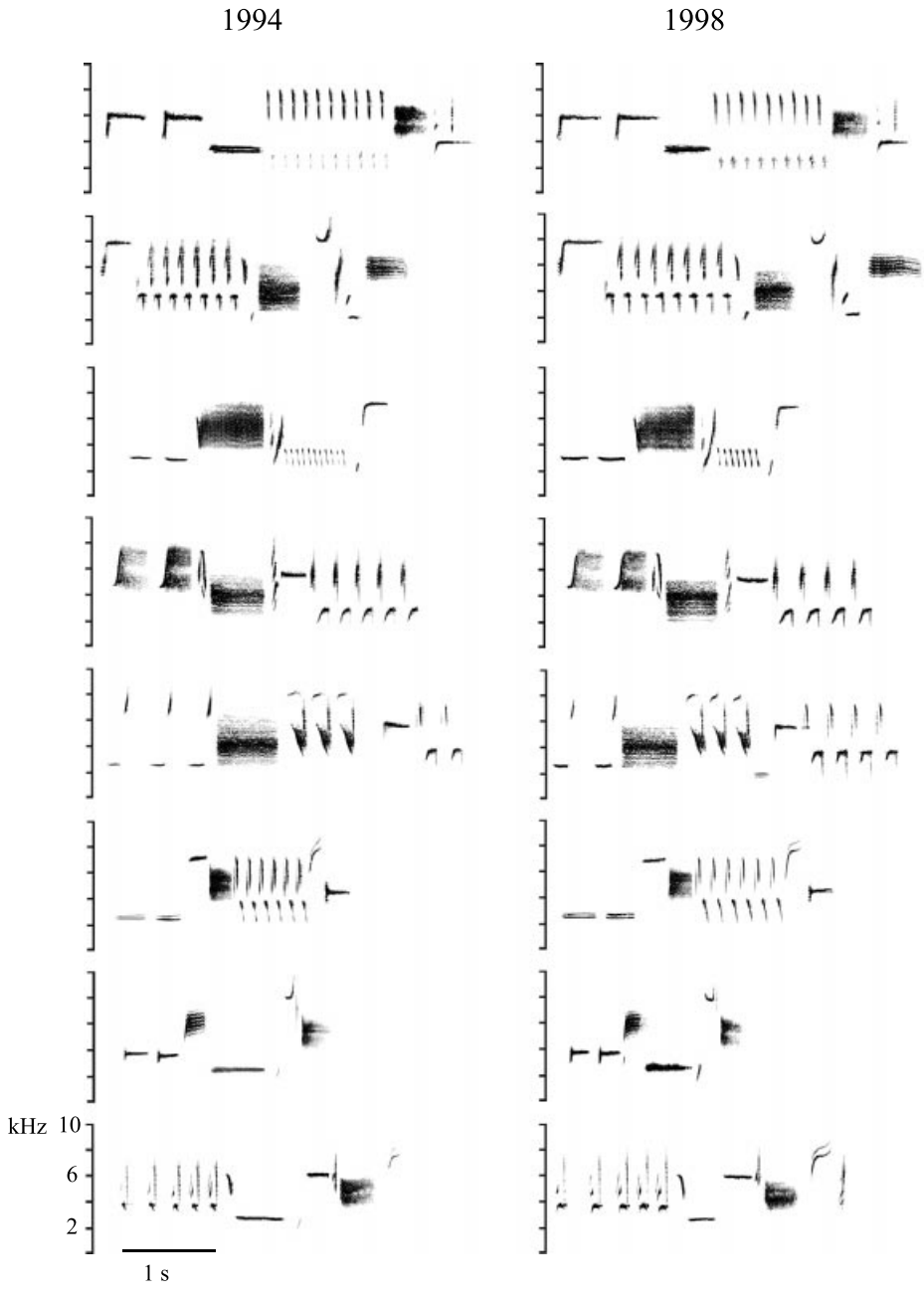

Fig. 1: Sonagrams of subject IIAM's eight song types recorded when he was 2 yr old (1994) and when he was 6 yr old (1998). Sonagrams represent the best matching variations for each song type

types in the 1987 recording session but sang only 10 of them in 17 consecutive bouts in the 1990 recording session. All four of these males had relatively large repertoires (9–11 song types vs. 5–10 song types for the remaining 20 subjects).

In addition to the 53 recording sessions included in Table 1, we recorded a total of 15 other complete sessions (i.e. ≥ 16 song type bouts) for 10 subjects in this study. These additional sessions were recorded in the same year as other sessions listed in Table 1. To shorten Table 1, we included the one session per year that had the highest number of song type bouts recorded. In each of the additional recording sessions the repertoires were complete (no missing song types) and the song types were the same as those in all other sessions. We also recorded 23 incomplete sessions (3–9 song type bouts) for 10 subjects; four of these sessions were recorded in different years from those listed in Table 1. There were no additional song types recorded in any of these sessions.

Discussion

This study confirms that song sparrows do not alter their song repertoires in adulthood. With few exceptions, males in this study produced song repertoires that were identical in every year they were recorded and song types were not added or dropped between years. Recordings of many subjects were made several years apart, up to 5, and a few subjects were recorded in three or four different years, which strengthens the conclusions of this study. The finding that adult males do not alter their song repertoires provides strong evidence that song sparrows are age-limited song learners.

The only exceptions to our finding were four males who did not produce one of their song types in one year. For two of these males we did not meet our complete recording criterion in that session (i.e. 16 consecutive song-type bouts). It is likely that in these two cases we missed recording a song type simply because we did not record enough song type bouts. In the other two cases, however, we did meet our recording criterion in the session missing a song type. We recorded 135 songs in 17 song type bouts for BGMG, who was the only male in our sample with 11 song types in his repertoire. It is possible, in this case, that our criterion for recording complete repertoires was not sufficient because this bird had a particularly large repertoire. In the last case, we recorded 364 songs in 23 song-type bouts for BAMP, who had 10 song types in his repertoire. Our recording effort in that session should have been sufficient to document his complete repertoire. We know that this male sang that missing song type in the year previous and the year following the year we recorded him. It is possible that this male, for some reason, did not cycle through his entire repertoire during the time we recorded him.

There is another possible explanation for missing song types. Although song sparrows generally cycle through their full repertoire in a limited number of song bouts, they may deviate from this pattern when countersinging with neighbors, preferring to use song types they share with a particular neighbor (Beecher et al. 1996). This could lead to a neglect of some song types over a period of time. For

all four males in this study who did not produce one song type in one recording session, we believe the parsimonious explanation for an apparent change in repertoire composition was that we missed recording a song type that they did indeed have, not that they dropped a song type. Even if these few males did in fact drop one song type in one year, it would represent only a minor change in repertoire composition. The amount of change in repertoire composition across years in open-ended song learners is much greater. For example, great tits (*Parus major*) alter their repertoires by 32–46% per year (McGregor & Krebs 1989). Furthermore, a male dropping a song type, rather than adding a song type, is not an example of song acquisition. Therefore, such a finding would still be consistent with the hypothesis that song sparrows are age-limited song learners.

Because we have studied this phenomenon in one particular population, we may have missed certain natural scenarios under which a song sparrow would change his repertoire. In particular, a bird that moves to a new territory might do so. It is extremely rare for a male in our population to change territories as an adult. In our 15 years studying the population in Seattle, we have documented a male moving territories perhaps three times. In no case have we noted a subsequent change in the composition of that bird's repertoire. However, it is almost assured that each of our present 24 subjects had a different set of neighbors in each of the years he was recorded. The average territory tenure in our study population is 3 years, so a male will have, on average, one or two new neighbors each year, and sometimes more. This in fact is the scenario under which most open-ended learners change their song repertoires (e.g. great tits; McGregor & Krebs 1989). So, while the focal males in our study may not have changed territories, they certainly interacted with new males singing different songs each year and yet we still find that their repertoires do not change.

Although song sparrows do not learn to produce new songs as adults, they can memorize new songs as adults. Numerous studies have shown that males in the wild recognize their neighbors by song (Stoddard et al. 1988, 1990, 1991, 1992a; Beecher et al. 1996, 2000). In many of these studies the neighbor-pairs used as subjects were new neighbors, and at least one of the males in the pair was an adult, so those older males must have memorized their new neighbor's songs when they were adults. Also, Stoddard et al. (1992b) demonstrated that adult males are not constrained by memory limitations. Using an operant conditioning method, they showed that male song sparrows were capable of learning and discriminating concurrently between 64 unfamiliar song types.

The question of whether a species is an open-ended or an age-limited song learner can be difficult to answer and has been adequately tested in relatively few species. The difficulty in confirming that a species is an open-ended song learner comes from having to verify that a song produced for the first time later in life was in fact acquired when the bird was an adult. The alternative explanation is that song acquisition is restricted to the first year of life and the new songs were memorized early but only produced for the first time in later years. Studies in the field or in the laboratory have provided strong evidence that several species are open-ended song learners, including the Natal robin *Cossypha heuglini* (Farkas

1969), the canary (Nottebohm & Nottebohm 1978; Güttinger 1979), the saddleback *Philesturnus carunculatus* (Jenkins 1978), the great tit (McGregor & Krebs 1989), the European starling *Sturnus vulgaris* (Eens et al. 1992; Chaiken et al. 1994), the American redstart *Setophaga ruticilla* (Lemon et al. 1994), and the village indigobird *Vidua chalybeata* (Payne & Payne 1997).

To confirm that a species is an age-limited song learner one must follow known males across multiple year and verify that their song repertoires do not change. Many species are thought to be age-limited song learners, but this assumption has been validated in only a small number of species, including the chaffinch *Fringilla coelbs* (Thorpe 1958), the cardinal *Cardinalis cardinalis* (Lemon 1965; Lemon & Scott 1966), the zebra finch (Immelmann 1969), and the marsh warbler *Acrocephalus palustris* (Dowsett-Lemaire 1979). The assumption that most mimetic species are open-ended song learners should also be confirmed, as highlighted by Dowsett-Lemaire's (1979) study of marsh warblers. She showed that, unlike other mimetic species, marsh warblers, who are remarkable mimics incorporating the songs or calls of up to 84 other species in their song repertoires, are nevertheless age-limited song learners.

One of the main difficulties in identifying a species as an age-limited or open-ended song learner is the labor-intensive method of documenting full song repertoires, especially in species with multiple song types. It is even more difficult, or perhaps impossible, to document within-song type variation fully for a species. In song sparrows, for example, Podos et al. (1992) found that males continued to produce new song type variations even after extensive recording (up to 900 songs) and that most variations (70%) were produced very infrequently. They argue that song types, rather than song variations, are the unit of memory, and that each type has a large, but restricted, degree of variation. In the present study, we did not address potential within-song type changes across years. It is possible that song sparrows could favor different variations of their song types in different years, or perhaps even deliver a subtle song variation that had not previously been produced. However, such changes across year in within-song type variation would be minor and would not necessarily indicate adult song learning (i.e. new song acquisition).

Whether vocal learning occurs early in life or continues throughout adulthood, it is a learning mechanism that, in many species, allows individuals to share vocalizations with one another. In several bird species that are open-ended song learners, adult males change their song repertoires in a way that increases song sharing with new neighbors (e.g. great tits, McGregor & Krebs 1989; saddlebacks, Jenkins 1978). In species that are age-limited song learners, males can also share songs with their territorial neighbors by preferentially learning the songs of these males during song development (e.g. song sparrows, Nordby et al. 1999).

If it is advantageous to share vocalizations with one's neighbors, then it might seem that birds with a restricted learning period would be at a disadvantage after their first year. However, this is not necessarily the case because, after their first year, males become the song 'tutors' from whom the next generation of males

learn their songs. Thus, for example, in our study population of song sparrows, the amount of sharing that a male has with his neighbors does not decrease over his lifetime despite the fact that he has, on average, one or two new neighbors each year (M. D. Beecher & S. E. Campbell, unpubl. data). However, whether song tutoring is an active process on the part of the adult designed to maintain song sharing with neighbors remains an open question.

Acknowledgements

We thank the many people who have spent many hours over the years recording in the field, including Michelle Elekonich, Chris Hill, Cynthia Horning, Dan Markiewicz, Patti Mulligan, Troy Smith, Philip Stoddard, Cynthia Wilkerson and Mary Willis. We also thank the staff of Discovery Park for generously hosting our field work. Ofer Tchernichovski, Steve Nowicki, Brendan Reeves and an anonymous reviewer provided valuable comments on the manuscript. This study was supported by grants from NSF to M. D. Beecher. Financial support was provided to J. C. Nordby by personnel training grant (T32 DC00033) from the National Institute on Deafness and Other Communication Disorders, National Institutes of Health, and the University of Washington, Department of Speech and Hearing Sciences and also by the San Francisco Estuary Institute.

Literature Cited

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. 1996: Repertoire matching between neighbouring song sparrows. *Anim. Behav.* **51,** 917—923.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000: Song type matching between neighbouring song sparrows. *Anim. Behav.* **59,** 21—27.

Borror, D. J. 1965: Song variation in Maine song sparrows. *Wilson. Bull.* **77,** 5—37.

Brown, E. D. & Farabaugh, S. M. 1997: What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. In: Social Influences on Vocal Development (Snowdon, C. T. & Hausberger, M., eds). Cambridge Univ. Press, Cambridge, pp. 98—127.

Cassidy, A. L. E. V. 1993: Song variation and learning in island populations of song sparrows. PhD Thesis, Univ. British Columbia, Vancouver.

Chaiken, M., Böhner, J. & Marler, P. 1994: Repertoire turnover and the timing of song acquisition in European starlings. *Behaviour* **128,** 25—39.

Dowsett-Lemaire, F. 1979: The imitative range of the song of the marsh warbler *Acrocephalus palustris*, with special reference to imitations of African birds. *Ibis* **121,** 453—467.

Eens, M., Pinxten, R. & Verheyen, R. F. 1992: Song learning in captive European starlings, *Sturnus vulgaris*. *Anim. Behav.* **44,** 1131—1143.

Farkas, T. 1969: Notes on the biology and ethology of the Natal robin *Cossypha natalensis*. *Ibis* **111,** 281—292.

Güttinger, H. R. 1979: The integration of learnt and genetically programmed behaviour: a study of hierarchical organization in songs of canaries, greenfinches and their hybrids. *Z. Tierpsychol.* **49,** 283—303.

Hiebert, S. M., Stoddard, P. K. & Arcese, P. 1989: Repertoire size, territory acquisition and reproductive success in the song sparrow. *Anim. Behav.* **37,** 266—273.

Immelmann, K. 1969: Song development in the zebra finch and other estrildid finches. In: Bird Vocalizations: Their Relation to Current Problems in Biology and Psychology (R. A. Hinde, ed.). Cambridge Univ. Press, London, pp. 61—74.

Jenkins, P. F. 1978: Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav.* **26,** 50—78.

Kroodsma, D. E. 1982: Song repertoires: problems in their definition and use. In: Acoustic Communication in Birds: Song Learning and its Consequences (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, New York, pp. 125—146.

Kroodsma, D. E. & Pickert, R. 1984: Sensitive phases for song learning: effects of social interaction and individual variation. *Anim. Behav.* **32,** 389—394.

Lemon, R. E. 1965: The song repertoires of cardinals (*Richmondena cardinalis*) at London, Ontario. *Can. J. Zool.* **43,** 559—569.

Lemon, R. E. & Scott, D. M. 1966: On the development of song in young cardinals. *Can. J. Zool.* **44,** 191—197.

Lemon, R. E., Perrault, S. & Weary, D. 1994: Dual strategies of song development in American redstarts, *Setophaga ruticilla*. *Anim. Behav.* **47,** 317—329.

McGregor, P. K. & Krebs, J. R. 1989: Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour* **108,** 139—159.

Nice, M. M. 1943: Studies in the life history of the song sparrow II. The behavior of the song sparrow and other passerines. *Trans. Linn. Soc. N. Y.* **6,** 1—328.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 1999: Ecological correlates of song learning in song sparrows. *Behav. Ecol.* **10,** 287—297.

Nottebohm, F. 1984: Birdsong as a model in which to study brain processes related to learning. *Condor* **86,** 227—236.

Nottebohm, F. & Nottebohm, M. E. 1978: Relationship between song repertoire and age in the canary, *Serinus canarius*. *Z. Tierpsychol.* **46,** 298—305.

Payne, R. B. & Payne, L. L. 1997: Field observations, experimental design, and the time and place of learning bird songs. In: Social Influences on Vocal Development (Snowdon, C. T. & Hausberger, M., eds). Cambridge Univ. Press, Cambridge, pp. 57—84.

Podos, J., Peters, S., Rudnicky, T., Marler, P. & Nowicki, S. 1992: The organization of song repertoires of song sparrows: themes and variations. *Ethology* **90,** 89—106.

Saunders, A. A. 1924: Recognizing individual birds by song. *Auk* **41,** 242—259.

Searcy, W. A., McArthur, P. D. & Yasukawa, K. 1985: Song repertoire size and male quality in song sparrows. *Condor* **87,** 222—228.

Stoddard, P. K., Beecher, M. D. & Willis, M. S. 1988: Response of territorial male song sparrows to song types and variations. *Behav. Ecol. Sociobiol.* **22,** 124—130.

Stoddard, P. K., Beecher, M. D., Horning, C. L. & Willis, M. S. 1990: Strong neighbor-stranger discrimination in song sparrows. *Condor* **92,** 1051—1056.

Stoddard, P. K., Beecher, M. D., Horning, C. L. & Campbell, S. E. 1991: Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behav. Ecol. Sociobiol.* **29,** 211—215.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C. 1992a: Song-type matching in the song sparrow. *Can. J. Zool.* **70,** 1440—1444.

Stoddard, P. K., Beecher, M. D., Loesche, P. & Campbell, S. E. 1992b: Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour* **122,** 274—287.

Thorpe, W. H. 1958: The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis* **100,** 535—570.

Received: April 10, 2001

Initial acceptance: May 29, 2001

Final acceptance: August 16, 2001 (J.-G. Godin)