

## REPertoire TURNOVER AND THE TIMING OF SONG ACQUISITION IN EUROPEAN STARLINGS

by

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(With 3 Figures)  
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### Summary

In order to establish unambiguously whether a reputed open-ended learner, the European starling, could memorize new songs in adulthood, we exposed hand-reared male starlings to a series of either live conspecific tutors or tape recordings of conspecific song over a period of 18 months, and isolated them from any other exposure to conspecific song. The song motifs produced by the birds were compared with those of their tutors or training tapes to infer the time of motif memorization. We found that the starlings continued to memorize and produce new song motifs, both within and between breeding seasons, up to the age of at least 18 months. Not all the new motifs in the repertoires had been recently memorized; in some cases there was an apparent lag of a year and a half between memorization and production. There were no significant differences between live-tutored and tape-tutored groups in the timing of learning or in the rate of repertoire turnover (55-92% new motifs in each repertoire sample), although, as we have reported previously, live-tutored birds imitated a greater number of motifs and developed larger repertoires.

### Introduction

Oscine songbirds learn the details of their songs by memorizing and reproducing those of adults. In some species, the process of song memor-

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ization is restricted to a brief period in early life, usually around the time of fledging (song sparrow, *Melospiza melodia*: MARLER & PETERS, 1987; swamp sparrow, *M. georgiana*: MARLER & PETERS, 1988; zebra finch, *Taeniopygia guttata*: IMMELMANN, 1969; BÖHNER, 1983; EALES, 1985; CLAYTON, 1987; chaffinch, *Fringilla coelebs*: THORPE, 1958) or when the birds set up breeding territories in the following spring (Indigo bunting, *Passerina cyanea*: PAYNE, 1981). In contrast, certain species are thought to retain the ability to learn new songs throughout their lives (mockingbird, *Mimus polyglottos*: LASKEY, 1944; canary, *Serinus canaria*: NOTTEBOHM & NOTTEBOHM, 1978; NOTTEBOHM *et al.*, 1986; saddleback, *Philesturnus carunculatus*: JENKINS, 1977; European starling, *Sturnus vulgaris*: FEARE, 1984; ADRET-HAUSBERGER *et al.*, 1989; great tit, *Parus major*: MCGREGOR & KREBS, 1989; EENS *et al.*, 1992a, b; nightingale, *Luscinia megarhynchos*: WISTEL-WOZNIAK & HULTSCH, 1993). Although there is convincing evidence that these birds continue to produce new songs in adulthood, it is not clear whether such repertoire changes reflect continuous acquisition of new songs.

Repertoire changes in adulthood could arise from the memorization of new songs at the time of production, or from the reinstatement of songs previously discarded from the repertoire. The latter possibility is consistent with patterns of song learning described for some species. Swamp sparrows, for example, routinely retain the memory of a song for up to eight months before producing copies (MARLER & PETERS, 1981, 1982a). They also produce many more song types during the early stages of song development than eventually appear in their crystallized repertoires (MARLER & PETERS, 1982b). Field sparrows (*Spizella pusilla*) retain songs that match those of their territorial neighbors and discard other song types (NELSON, 1992). Given such examples of delayed production and selective attrition of memorized songs, the timing of song acquisition, in the sense of memorization, cannot be directly inferred from the timing of song production. Thus it is not known whether song acquisition in apparently "open-ended" learners is continuous or whether it is restricted to particular phases of the life cycle or year. These questions are of special interest in that they provide the critical behavioral background for comparative studies of the neural bases of song learning and the limits of behavioral plasticity (*e.g.* NORDEEN & NORDEEN, 1990; NOTTEBOHM, 1991; BOTTJER & JOHNSON, 1992). They can be decisively answered only in

controlled experiments where the time of exposure to specific acoustic stimuli is known.

In this study we investigate the time course of song acquisition and production in a presumed open-ended learner, the European starling. We have shown that starlings imitate vocalizations they hear during their first year (BÖHNER *et al.*, 1990). Here we ask whether the readiness to acquire new song material varies over the first 18 months and trace changes in the repertoire as new material is added.

For several species, exposure to live tutors has been shown to extend the acquisition phase beyond the boundaries established in tutoring studies employing tape-recorded song (marsh wrens, *Cistothorus palustris*: KROODSMA & PICKERT, 1984; white-crowned sparrows, *Zonotrichia leucophrys*: BAPTISTA & PETRINOVICH, 1984). In view of these findings, we report results for both tape-tutored and live-tutored groups.

## Methods

### 1. Subjects.

Twelve male starlings were collected from the wild at 8 to 10 days after hatching and hand-reared in a group. Exposure to song during the first 10 days (a period when singing is in any case at a low in starling colonies) has no effect on subsequent song development in any songbird for which relevant data is available (marsh wren: KROODSMA, 1978; swamp sparrow: MARLER & PETERS, 1981; zebra finch: EALES, 1985; song sparrow: MARLER & PETERS, 1987; nightingale: HULTSCH & KOPP, 1989). When the young starlings reached independence at 36 days of age, before they began to sing, they were visually and acoustically isolated from one another and assigned randomly to the live-tutored or tape-tutored condition. The six birds in the live-tutored group were tutored individually with live conspecifics and the six in the tape-tutored group with tape-recorded vocalizations. Except for the tutoring sessions for the live-tutored birds, each subject in both live-tutored and tape-tutored groups remained in visual and acoustic isolation from conspecifics for the duration of the study.

### 2. Live tutoring.

Each subject in the live-tutored group was housed in a separate room and shared its cage (75 × 35 × 73 cm) with a different adult male tutor during each six-week tutoring session. The tutors had been captured from the wild in at least their second year; each had a unique repertoire of song motifs which remained stable throughout the tutoring period. The mean number of song motifs in the tutors' repertoires was 70.7 ± 6.9. To ensure consistent singing, tutors were implanted with subcutaneous silastic capsules of testosterone (*i.d.* 0.058 mm, *o.d.* 0.077 mm, length 25 mm).

### 3. Tape tutoring.

Each subject in the tape-tutored group was housed in a cage (46 × 46 × 33 cm) placed inside a soundproof chamber and heard tape-recordings of starling vocalizations for one hour each morning and evening during the 6-week tutoring sessions. Different sets of training

stimuli were used for each 6-week session. The stimuli for each session included two starling songs, one recorded in the field and another recorded in the laboratory from one of the live tutors. The songs were presented in random order in mixed bouts of 3 to 7 songs separated by intervals of 4 to 13 seconds, modeled after natural singing patterns. The total number of starling song motifs presented on the tapes were 85, 91, and 44 for the first, second, and third tutoring sessions, respectively. The tapes contained additional material originally designed to address questions about selectivity in vocal learning; this included starling calls and whistles, several artificially rearranged starling song motifs, and two songs, about 1 second each, of a brown-headed cowbird, *Molothrus ater*. Eighteen instances of each training stimulus were presented on each tape. To reduce the likelihood of habituation within a training session, three different training tapes were prepared in which the same stimuli were presented in different arrangements. The tapes were rotated so that the birds heard all three versions before returning to the first. The tapes were played on a Tandberg Series 15 tape recorder at 9.5 cm/s through Realistic 40-1909B speakers placed in each chamber. The sound pressure level was set by ear to approximate that of a live singing bird.

#### 4. Tutoring schedule.

The tutoring schedule was identical for the live-tutored and tape-tutored groups (Fig. 1). Each bird was exposed to conspecific songs during three 6-week training sessions. The first began when they were in their second month (36-39 days) old, the second when they were 3 months (94-97 days) old, and the third when they were 10-11 months (296-333 days) old. Three of the six live-tutored birds were given an additional six-week training session starting at 18 months (527-564 days) of age. All birds were kept on a natural photoperiod, adjusted weekly, for Dutchess County, N.Y. (42 degrees N). To confirm that the birds came into breeding condition and molted on a normal schedule, bill color, an indicator of circulating levels of testosterone (WITSCHI & MILLER, 1938; GWINNER, 1975), was scored weekly according to the method described by WYDOSKI (1964) and BALL & WINGFIELD (1987), and the progress of the juvenile molt was scored weekly according to the system described by NEWTON (1966).

#### 5. Song sampling and analysis.

Each of the subjects was tape-recorded for 45 minutes each week from the start of training until 9 months after hatching, and every other week thereafter. If an insufficient song sample was collected during the 45-minute recording, we continued to record the bird over the next week. Recordings were made on Marantz model PMD 221 cassette recorders at

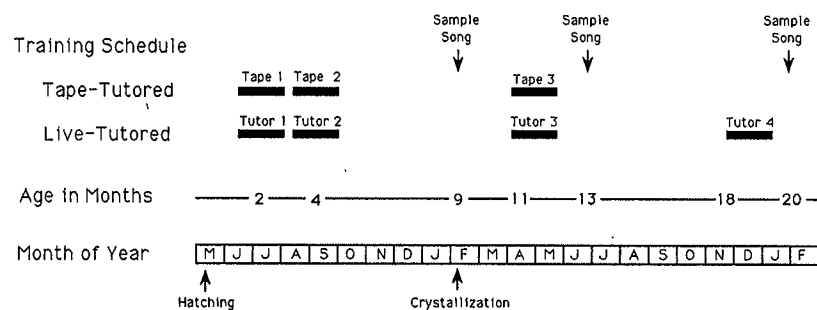


Fig. 1. Tutoring schedule.

4.75 cm/s, with Panasonic WM-2298 dynamic microphones. Tutors were recorded before and after each tutoring session.

Recordings were processed on a real-time spectral analyzer (Princeton Applied Research Spectrum Analyzer, Model 4512; see HOPKINS *et al.*, 1974) with a Cymograph camera (Grass Instruments, Model C4R).

A typical starling song lasts about 50 seconds and consists of an uninterrupted sequence of distinctive 0.5 to 1-second-long motifs (ADRET-HAUSBERGER *et al.*, 1989; EENS *et al.*, 1989; CHAIKEN *et al.*, 1993). By plotting cumulative curves for the occurrence of new motifs over time, we have determined that 15 minutes of continuous singing (with silences over 6 seconds edited out) is sufficient to capture the entire repertoire of motifs (CHAIKEN *et al.*, 1993). Similar estimates have been obtained in field investigations (HINDMARSH, 1984; ADRET-HAUSBERGER & JENKINS, 1988; EENS *et al.*, 1991, 1992b). Thus the analyses are based on edited 15-minute samples.

By comparing consecutive recordings, we determined that the subjects' repertoires had achieved their highest degree of stability, with the maximum number of imitations, by February, when the birds were 9 months old. Singing rates remained high and song structure stable until the end of summer. For the analyses reported here, we used song samples recorded in February (when the birds were 9 months old), June to July (when the birds were 13 months old), and, for the three live-tutored birds given a fourth tutoring session, the following January to February (when they were 20 months old).

Fifteen-minute samples of tutor songs were taken immediately before and after tutoring sessions and compared. Tutor repertoires did not change over the six-week tutoring periods.

Spectrograms of the subjects' songs were compared by eye with those of their tutors or those on the tape-recordings (see Fig. 2). Two observers compiled libraries of the subjects' motifs displayed beside any "model" motifs to which they bore a resemblance. Four independent observers rated the degree of similarity between model and copy on a scale from 1 (poor copy) to 5 (good copy). Copies with median ratings of 3 or more were counted as imitations.

## Results

Figure 3 shows the sources of motifs in the repertoires of the live-tutored and tape-tutored starlings at each sample period. The time at which imitated motifs were memorized is inferred from the time at which each bird was exposed to the live tutor or tape recording producing that motif.

### 1. Song acquisition in adulthood.

The results demonstrate that starlings are capable of memorizing as well as producing new motifs up to at least the age of 18 months. All of the live-tutored birds and 4 of the 6 tape-tutored birds imitated motifs presented in each of the tutoring sessions (Fig. 3).

The live-tutored birds copied a mean ( $\pm$  SD) of  $25.3 \pm 8.2$  of the motifs to which they were exposed at 2-4 months,  $12.0 \pm 7.6$  of the motifs to which they were exposed at 11-12 months, and  $7.3 \pm 3.1$  of the motifs to

which they were exposed at 18-19 months (based on the first repertoire sample taken after each tutoring session). The tape-tutored birds copied an average of  $2.5 \pm 2.4$  of the motifs to which they were exposed at 2-4 months, and  $4.3 \pm 5.7$  of the motifs to which they were exposed at 11-12 months.

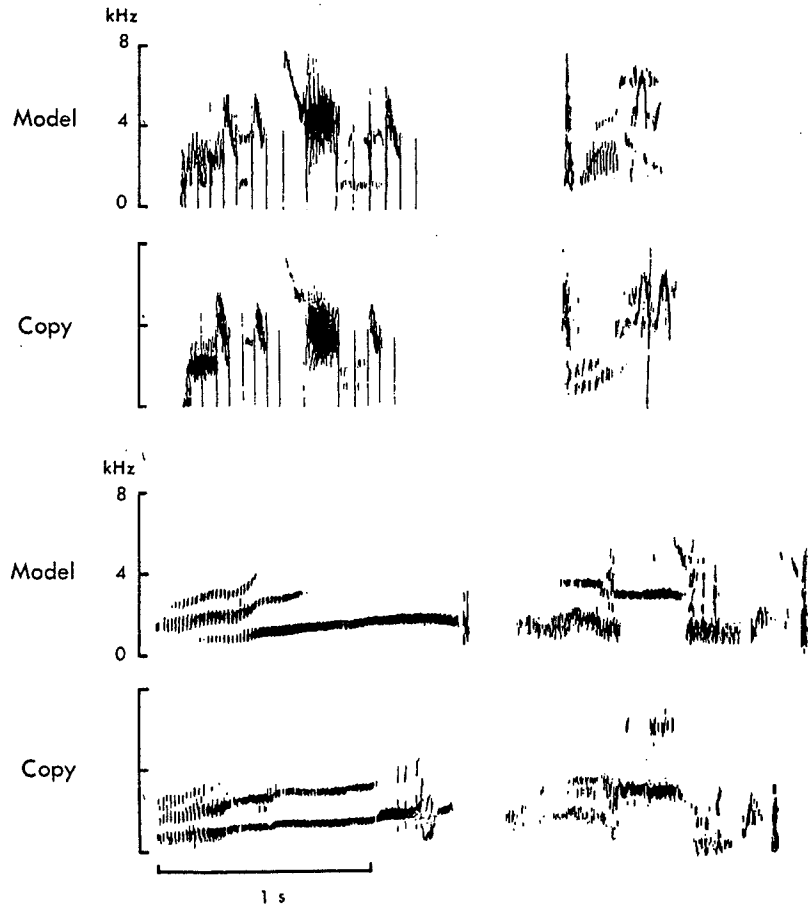


Fig. 2. Model motifs from live tutors (row 1) and tape recordings (row 3), shown above imitations produced by live-tutored (row 2) and tape-tutored (row 4) males. Median ratings for these imitations, on a scale from 1 (poor) to 5 (good), were (left to right) 5 and 3 for the live-tutored males, 5 and 4 for the tape-tutored males.

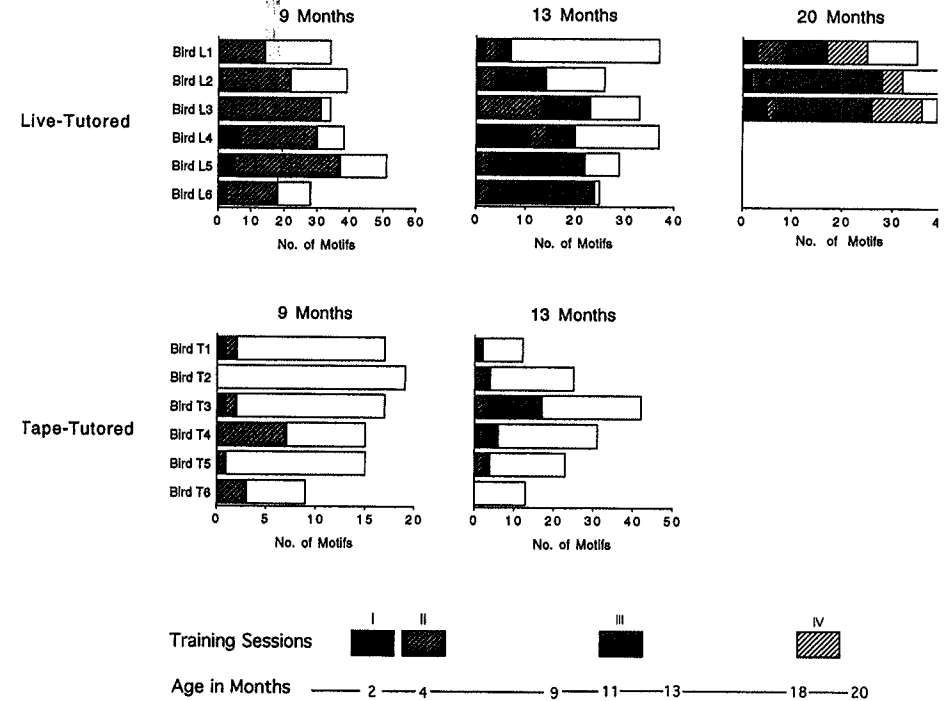


Fig. 3. Sources of motifs in the repertoires of live-tutored and tape-tutored male starlings at 9, 13, and 20 months after hatching. The patterned segments on the bar graphs indicate motifs acquired during the training session (below) with the corresponding pattern. The open segments on the bar graphs indicate motifs that could not be traced to a tape or tutor; most of these motifs were presumably improvised, but a small proportion (0-4 motifs per bird) were identified as imitations of other sounds in the environment.

## 2. Rate of repertoire turnover.

While new motifs were added to the repertoire, some old motifs were dropped. The rate of repertoire turnover was defined as the percentage of new motifs in the repertoire that had not been present in the previous sample. Turnover ranged from 55 to 92 percent (Table 1). There was no significant difference in rate of turnover between live-tutored and tape-tutored groups at 13 months (Mann-Whitney,  $p < 0.13$ ). The rate of turnover declined slightly from 13 to 20 months for the three live-tutored birds that received a fourth tutoring session.

TABLE 1. Repertoire turnover

From 9 to 13 months after hatching				
Subject	# Motifs at 9 Mo	# Motifs at 13 Mo	# Same at 9 & 13 Mo	% New at 13 Mo
Live-Tutored				
L1	34	37	12	83.3
L2	39	26	5	80.8
L3	34	33	13	66.7
L4	34	37	7	81.1
L5	51	29	3	89.7
L6	28	25	2	92.0
Mean	36.7	31.2	7.0	82.2
SD	7.8	5.3	4.6	8.9
Tape-Tutored				
T1	17	12	2	83.3
T2	19	25	10	60.0
T3	17	42	8	57.1
T4	15	31	4	87.1
T5	15	23	6	73.9
T6	9	13	5	61.5
Mean	15.3	24.3	5.8	70.5
SD	3.4	11.3	2.9	12.8
From 13 to 20 months after hatching				
Subject	# Motifs at 13 Mo	# Motifs at 20 Mo	# Same at 13 & 20 Mo	% New at 13 Mo
Live-Tutored				
L1	37	35	11	68.6
L2	26	33	15	54.5
L3	33	39	9	76.9
Mean	32.0	35.6	11.7	66.7

The rate of turnover tended to be higher for imitated motifs than for motifs that could not be assigned to a training tape or tutor, although the trend was not significant (Table 2).

### 3. Delayed production of memorized motifs.

Some imitations were first detected many months after the tutoring session in which they were memorized. The most striking example was provided by live-tutored bird #3. No motifs copied from #3's first tutor

TABLE 2. Turnover in imitations

From 9 to 13 months after hatching					
Subject	# Imit at 9 Mo	# Imit at 13 Mo	# Imit Same at 9 & 13 Mo	% Imit (Nonimit) New at 13 Mo	
Live-Tutored					
L1	15	7	5	28.6	(76.7)
L2	22	14	2	85.7	(75.0)
L3	31	23	10	56.5	(70.0)
L4	28	20	5	75.0	(88.0)
L5	37	22	2	90.9	(85.0)
L6	19	24	1	95.8	( 0.0)
Mean	25.3	18.3	4.2	72.1	(65.9)
SD	8.2	6.6	3.3	25.5	(33.0)
Tape-Tutored					
T1	2	2	0	100.0	(80.0)
T2	0	4	0	100.0	(52.4)
T3	2	17	2	88.2	(76.0)
T4	7	6	0	100.0	(84.0)
T5	1	4	2	50.0	(78.9)
T6	3	0	0	.	(61.5)
Mean	2.5	5.5	0.7	87.6	(72.1)
SD	2.4	6.0	1.0	21.7	(12.4)
From 13 to 20 months after hatching					
Subject	# Imit at 13 Mo	# Imit at 20 Mo	# Imit Same at 13 & 20 Mo	% Imit (Nonimit) New at 20 Mo	
Live-Tutored					
L1	7	25	4	84.0	(30.0)
L2	14	32	14	56.3	( 0.0)
L3	23	36	8	77.8	(60.7)
Mean	14.7	31.0	8.7	72.7	(32.2)

were found in song samples taken at 9 and 13 months, but 5 such motifs were present in the sample taken at 20 months. This represents an 18-month lag between song memorization and production. The two other birds in this group also sang imitations of their first tutors for the first time at 20 months.

As a measure of delayed imitation, we counted the number of new motifs in each bird's repertoire that were copied from a tutor or tape other than the one to which the bird had been most recently exposed. Live-tutored birds sampled at 13 months, about a month after exposure

