

Untutored song, reproductive success and song learning

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Abstract. Female zebra finches, *Taeniopygia guttata*, from one population were given a choice between males from their own population reared in aviaries, males from a different population reared in aviaries, or males from their own population reared without adult song tutors. Aviary-reared males from the same population as the females had higher reproductive success than did untutored males from the same population or aviary-reared males from a different population. Saliency as a song model was related to the song type of the adult male as well as to the total number of young the adult male fledged. All male offspring copied significantly more syllables from their fathers' songs than from others' songs, but the sons of untutored males were the least likely to copy syllables from males other than their father. Young males copied qualities characteristic of untutored song both from their fathers and from other males. Although untutored song was associated with inferior reproductive success, it was accepted by young males as a valid song model.

Many passerine songbirds, if raised with no access to adult song models, develop a song that differs from the songs of birds raised with conspecific singing adults (Thorpe 1958; Marler & Tamura 1964). This song type has been labelled 'isolate' or 'autogenous', but is more appropriately termed untutored song (although the conditions and mechanisms that give rise to this type of song vary widely, a common feature is the lack of a song tutor). Zebra finch, *Taeniopygia guttata*, males raised without access to a song model develop songs that have some characteristics of normal zebra finch song: they are initiated by a string of introductory notes and include approximately four to 12 stereotyped syllables, many of which have the normal harmonic structure (Price 1979; Morrison 1991). However, untutored song differs from normal song both in the acoustic structure of syllables and in their organization (e.g. Fig. 1). Syllables in untutored song are high in frequency, include upsweeps, and often consist of trains of clicks. Normal zebra finch song consists of a chain of syllables with few or no internal repeats; this song is repeated with only minor variations to make up a bout (Sossinka & Böhner 1980). Untutored song often includes strings of repeated syllables or syllable complexes (Fig. 1), and the stereotypy of syllable order can be decreased.

Untutored song can be interpreted as reflecting the process whereby a young male, deprived of a

normal song model, generates those sounds his vocal tract can produce and then rejects or includes these sounds in his song (as well as arranging them within the song) according to how well they fit an 'innate template' for his species' song (Konishi 1965; Marler & Sherman 1983). This process differs from normal song learning in that there is no attempt to match a model, since none has been acquired. If untutored song reflects the properties of a species-specific innate template (and not a developmentally crippled neural system for song), it may be acceptable (1) to conspecific females choosing mates or (2) to young males choosing song models, despite the differences from normal song, because of the species-specific characteristics that are retained. Although this proposition has never been tested directly, Searcy et al. (1985) found that untutored song was less effective than normal song but more effective than heterospecific song in eliciting responses from territorial males and caged females.

Young males' preference for song models from their own species (Thorpe 1958; Marler & Peters 1977; Dooling & Searcy 1980) was instrumental in forming the 'innate template' theory, but song models need not be conspecifics. When young zebra finches are reared by Bengalese finches, *Lonchura striata*, or strawberry finches, *Estrilda amandava*, and hear only the songs of their foster parents, they are able to reproduce elements of the heterospecific

song accurately (Immelmann 1969; Price 1979). Similarly, males cross-fostered between the two subspecies of zebra finches learn the songs of their foster fathers (Clayton 1990). However, when a conspecific model is present, the social effects of cross-fostering are overridden, presumably by genetically encoded instructions for recognizing song: zebra finches raised by Bengalese finches in the same aviary as breeding zebra finches learn zebra finch song, especially if zebra finch and Bengalese finch broods are present at the same time (Immelmann 1969). Although they never sing, females also appear to learn about song. When tested using playbacks, females respond preferentially to the songs of males with which they were reared (Miller 1979; Clayton 1990). Stephen Clark (personal communication) used playbacks to show that normally-reared adult females that approach and solicit copulation upon hearing the songs of normally-reared adult males respond to the songs of males reared in isolation as if they were heterospecific songs, largely ignoring them.

Young zebra finches raised in group aviaries will copy songs from males other than their fathers (Williams 1990). Using this environment, we simultaneously evaluated the ability of untutored song to serve as a sexual signal to females and as a model for song learning by males.

METHODS

Subjects

We used zebra finches, small (10 g) colonial nesters originally from Australia and Timor, that were derived from captive populations. Nine females were hatched and reared to adulthood in a group aviary at The Rockefeller University Field Research Center in Dutchess County, New York. Nine males, three from each of three conditions, were used: (1) Field Center males, hatched and reared to adulthood in the same colony as the females but a different group aviary; (2) Untutored males, hatched in sound-attenuation chambers (Industrial Acoustics) at the Field Center and reared in isolation in those chambers, and (3) Manhattan males, hatched and reared to adulthood in an aviary at Hunter College in New York City (different stock from the other birds). The two aviaries at the Field Center were derived from the same stock, but individual birds from one aviary

had never been in physical contact with birds from the other aviary. All colony-reared birds were removed from their natal aviaries before they bred. The untutored males were produced by three aviary-reared pairs breeding in separate acoustic-isolation chambers. Fathers were removed after the first egg hatched, and clutches were reared by the mothers until day 36, when the mother and all female siblings were removed from the chamber. The males used in this study remained in their separate chambers, along with either one or two male siblings, until their songs were recorded at about day 105. One adult was then replaced in the chamber, and the young males remained in this group for 4–6 months, when they were removed and placed in single-sex group cages adjacent to females for 90 days. Before being used in our study, untutored males were tested with a female that was not used in the experiment, and all courted readily. All birds were between 6 and 12 months old at the start of the study (zebra finches are sexually mature at 90 days). None had bred previously, and siblings were not given the opportunity to compete with each other for mates. The study was run between February and December 1989. After 4 months, one of the Field Center males sickened and was replaced by another of similar background.

Three aviaries (1.5 × 1 × 2 m) were set up, each containing three females, one male from each category, many perches, three nestboxes, and nesting material, grit, cuttle bones, food and water *ad libitum*. When hatchlings or fledglings were present in the aviary, eggs and a vitamin supplement (Avia) were also made available. The aviaries were placed near each other in a room that was maintained on a 14:10 h light:dark cycle. Although birds in an aviary could see and hear those in the other aviaries, it has previously been shown that young males only learn songs from adults in the same cage; males that are visible and audible in adjacent cages do not serve as song models (Böhner 1983). Although we cannot rule out the possibility that breeding activity in one aviary affected activity in neighbouring aviaries, we did not observe birds attending to individuals outside their own aviary (with the one exception of group long-calling, when all birds within hearing range joined in).

Daily observations were used to determine which birds were paired, which birds occupied which nestbox, and the status of all breeding efforts. For this purpose, all adults were colour-banded. Care

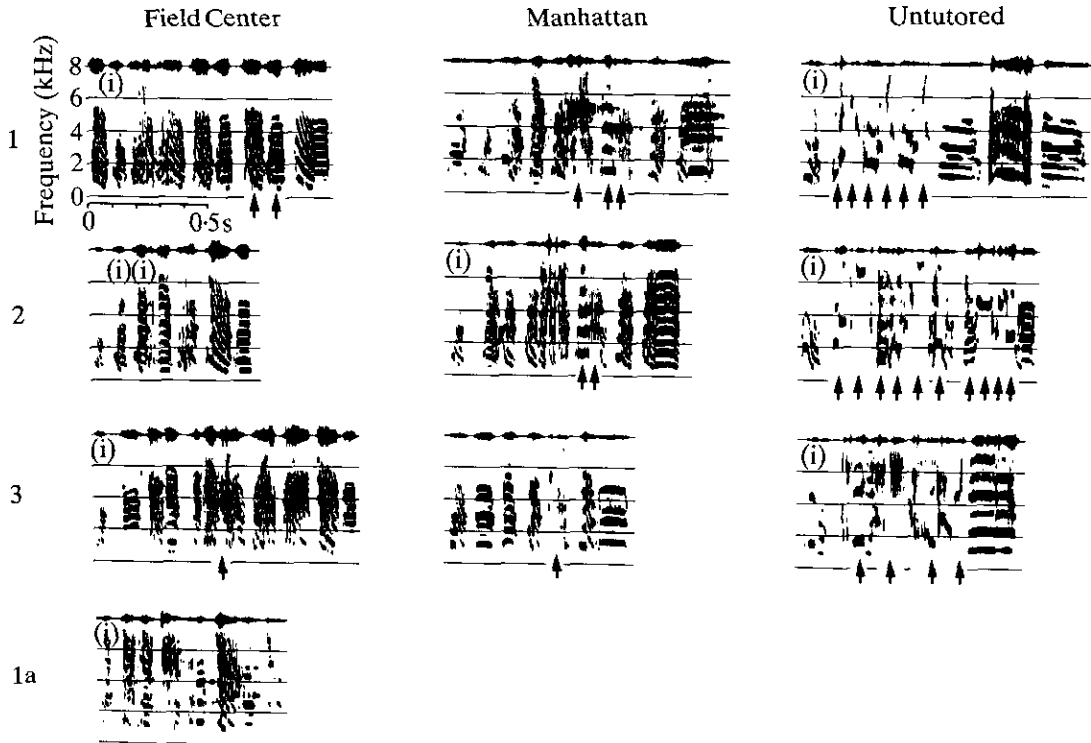


Figure 1. Songs of Field Center, Manhattan and Untutored males. Songs are designated by song type and by the aviary the male occupied. All songs conform to the standard zebra finch song structure of a series of introductory notes (i) followed by a stereotyped sequence of syllables with multiple harmonics (Sossinka & Böhner 1980). Arrows denote syllables that were judged to be 'untutored-like' (see Methods for criteria). Because syllables were defined operationally as the independent units copied by young males (or, if no copying occurred, units of sound separated by more than 5 ms of silence), males that were copied more often have more (and shorter) syllables. We used the length of syllables as well as the number of syllables in comparing song copying.

was taken not to use red or orange band colours (see Burley 1981, 1986) on any of the males, and no one colour was systematically assigned to a song type. Young were banded before fledging and allowed to remain in the aviary in contact with all three males (and their song types) until the young males were 90–110 days old, when they reached sexual maturity and song had crystallized (Immelmann 1969; Price 1979).

We considered all young to be the offspring of the pair that hatched and reared them. Extra-pair copulations resulting in offspring have been described in zebra finches housed in aviary conditions (Birkhead et al. 1988), and we cannot rule out the possibility that some young were not the offspring of the adult males occupying their natal nestbox. However, the numbers of mis-attributed young are likely to have been low; we did not observe any extra-pair copulations

(we did see intra-pair copulations), perhaps because the relatively small size of the aviaries allowed the paired male to interfere with extra-pair courtship.

Song Recording

Adult males were recorded before they were put into the aviaries; the songs of all adult males used in the study are shown in Fig. 1. The young birds were recorded after being removed from the aviaries at 90 days. For song recording, a male was placed in a sound-proof, transparent Lucite chamber measuring $0.75 \times 0.75 \times 0.5$ m and partially lined with acoustic foam, from which he could see but not hear females. A microphone (Marantz EC-7) was placed inside the chamber, and song was recorded, using a Marantz PMD 201 cassette-recorder, onto Maxell C60 tapes. All songs recorded and analysed

were 'directed' songs given as part of courtship, which are slightly faster in tempo and less likely to be incomplete than are 'undirected' songs (Sossinka & Böhner 1980).

Song Analysis

Songs were digitized at 22 kHz onto a Macintosh II computer using a MacRecorder digitizer and SoundEdit software. Sonagrams were generated using 128 point FFTs with the SoundEdit package (Farallon), yielding results visually similar to sonagrams made with a Kay Sonagraph using the 300 Hz filter.

Syllables in the young males' song models were identified and matched to those of the three potential models by visually determining the closest fit between the syllables of the young male and those of the available tutors. Matches were unambiguous, and were scored separately by each of the three authors (inter-observer agreement was greater than 95%). In cases with no clear match, syllables were scored as improvised.

We defined syllables operationally, as the sound units that were copied independently from the adults' songs (Williams & Staples 1992). This definition corresponds to the motor units of song defined by Cynx (1990). Our method tends to define more (and shorter) syllables in the songs of males that are copied more often, so we also used time as a measure for determining the amount of song copied. Measurements of syllable and song length were obtained using SoundEdit (1-ms resolution). Because a previous study has shown that a syllable and the silent interval preceding it are copied as a single unit (Williams & Staples 1992), syllable length was measured from the end of one syllable to the end of the next syllable.

Syllables within the adult tutors' songs were categorized as 'untutored-like' if they fulfilled any of the following criteria: (1) frequency modulation was upward; (2) the lowest frequency apparent on the sonagram was higher than 1.7 kHz; (3) the syllable consisted solely of clicks; or (4) the syllable was repeated within a song. These syllable characteristics can occur in normal song but are common in untutored song. Untutored-like syllables are identified in Fig. 1 and the distribution of such syllables in the three types of songs is summarized in Table I. The distribution of untutored-like syllables differed significantly among the groups of males.

Statistical Analysis

Although the birds in different aviaries could see and hear each other, each aviary was a discrete unit for the purposes of song learning as young male zebra finches only learned from adults with which they had physical contact (see also Böhner 1983; Williams 1990). Each young male based his song on the models available in his natal aviary, and each song was treated as an independent unit. We tested potential aviary and sibling effects using linear models (SuperANOVA, Abacus) with type III sum of squares, a conservative method that removes the effects of all other factors in a model before testing the factor in question. Descriptive statistics, *t*-tests, and non-parametric statistics were computed manually or with StatViewII.

RESULTS

Male Background and Pair Formation

We used the times to first egg laying (in a nest), first hatch, and first fledge as indicators of the period needed for pair formation. Alternative indicators such as association or nest-building were more ambiguous in describing pair formation: we have observed males caged singly building nests, and if two pairs had been formed in one aviary, the status of the third potential pair was often uncertain (by default, the two individuals spent time near each other and in the unoccupied nestbox).

Although the Field Center males appeared to form pairs more readily, the numbers for each category of male were low (the replacement male was excluded from analysis: aviary-reared $N=6$; untutored $N=3$), and none of the differences among indicators of pair formation reached significance, by song type, rearing type, or lineage (see Table II).

Male Background and Reproductive Success

The numbers and rates with which each male produced clutches, eggs, hatchlings, fledglings, and male offspring are also shown in Table II. Males of different song types had different success in producing fledglings ($\chi^2=6.08$, $df=2$, $P<0.05$) and male fledglings ($\chi^2=6.17$, $df=2$, $P<0.05$). Field Center males produced both a disproportionate number of fledglings (48.2% of the total) and male fledglings (67.9% of the Field Center males' offspring were males).

Table 1. Untutored characteristics in the songs of males from different backgrounds

	Breeding males												P	
	Field Center				Manhattan				Untutored					
	1	1a	2	3	Total	1	2	3	Total	1	2	3		Total
Upswept syllables per song	0	0	0	0	0	0	0	0	0	1	1	0	2	<0.05
High syllables per song	0	1	0	1	2	2	1	0	3	3	8	2	13	<0.01
Click syllables per song	0	0	0	0	0.5	1	1	1	3	2	1	2	5	<0.001
Repeated syllables per song	2	0	0	0	0	0	0	0	0	3	0	0	3	>0.5
Total 'untutored' syllables (s) per song (s)	0.30	0.08	0	0.05	0.43	0.11	0.08	0.17	0.36	0.65	0.81	0.65	2.11	<0.001
Total length of song (s) per song (s)	1.11	0.85	0.66	1.23	3.85	0.97	0.77	1.14	2.88	1.27	1.23	0.87	3.37	>0.6
'Untutored'/total syllables	0.27	0.09	0	0.04	0.11	0.11	0.10	0.15	0.13	0.51	0.66	0.75	0.63	<0.01

The number of untutored-like syllables (according to the criteria in the Methods) was tabulated for each male used in the study. Males are designated by the aviary they bred in; male 1a replaced male 1 midway through the study. A linear model, using type III sums of squares and including as an additional factor the length of the song (except for comparisons of total song length), was used to determine whether the distribution of untutored-like song characteristics was random.

Table II. Reproductive success of males from three backgrounds

	Breeding males												P				
	Field Center				Manhattan				Untutored								
	1	1a	2	3	Total	1	2	3	Total	1	2	3		Total	Song	Rearing	Lineage
First egg	9	13	177	81	89±49	6	13	173	173	64±55	153	178	20	127±54	>0.4	>0.3	>0.3
First hatch	23	26	229	187	146±63	25	190	197	197	137±56	200	192	281*	224±28	>0.3	>0.1	>0.4
First fledge	43	47	250	209	167±63	46	212	303†	303†	187±75	222	212	303†	246±29	>0.4	>0.2	>0.9
Clutches	2	2	2	2	8	4	2	1	1	7	2	2	0	4	>0.5	>0.2	>0.7
Eggs	10	8	8	12	38	17	15	9	9	41	16	10	—	26	>0.3	>0.05	>0.2
per clutch	4.6	4.4	3.5	5.6	4.8±0.5	3.4	4.6	6.9	6.9	5.9±0.9	7.9	4.6	—	6.5±1.0	>0.3	>0.3	>0.5
Hatchlings	8	8	6	11	33	13	7	4	4	24	13	7	—	20	>0.1	>0.1	>0.5
per clutch	2.6	4.4	1.5	5.6	4.1±0.6	3.3	2.5	6.1	4	3.4±0.7	6.7	3.4	—	5.0±0.9	>0.3	>0.2	>0.5
Fledglings	4	7	6	11	28	12	4	0	0	16	9	5	—	14	<0.05	>0.3	>0.5
per clutch	2.2	4.3	1.5	5.6	3.5±0.6	2.3	2.5	4.0	—	2.3±0.7	6.3	2.3	—	3.5±0.9	>0.3	>0.2	>0.1
Males fledged	2	6	3	8	19	7	1	—	—	8	6	3	—	9	<0.05	>0.2	>0.2
per clutch	1.1	4.2	0.3	4.4	2.4±0.6	1.2	1.3	1	—	1.1±0.4	5.1	1.2	—	2.3±1.0	>0.1	>0.5	>0.05

Mean ± SE for each individual male (totals and where applicable, for each clutch), and totals by male type. Differences among groups by song type, lineage, and rearing conditions were evaluated using Kruskal-Wallis or Mann-Whitney *U*-tests for timing data and by χ^2 for data on clutches. Field Center male 1a (the replacement male) was excluded from the total pairing data but included in the data on clutches.

*The bird that did not produce any hatchlings was given the number of days the aviaries were maintained for breeding + 14 (281) as the number of days to hatching.

†Birds that did not produce fledglings were given the number of days the aviaries were maintained for breeding + 36 (303) as the number of days to fledging.

Table III. Song copying is affected by factors unrelated to song type

Variable	df	Syllables copied from	
		Father	Other
Number of brothers	1	2.79 (0.11)	2.76 (0.11)
Number of siblings	1	3.22 (0.08)	2.58 (0.12)
Number of cohort	1	0.48 (0.49)	43 (0.52)
Father's total no. of fledglings	1	11.63 (0.002)	6.65 (0.02)
Aviary	2	12.68 (0.0001)	6.19 (0.006)

How the number of syllables copied from fathers and other males was affected by five factors that were inter-dependent but unrelated to the fathers' songs was determined using an analysis of covariance. *F*-statistics and associated probabilities are shown. The number in the cohort included all young born within 2 weeks of each other in the same aviary. The father's total number of fledglings included all young fledged during the course of the experiment. The results for the amount of time copied from fathers' and others' songs were nearly identical to these results, and are not shown. Residual *df* = 29.

Although the Untutored males' deficit in production of young may have been the result of later initiation of breeding and thus fewer clutches and eggs (Table I), neither the difference between number of clutches by rearing condition ($\chi^2 = 1.26$, *df* = 1, *P* > 0.2) nor that between the number of eggs ($\chi^2 = 3.47$, *df* = 1, *P* < 0.05) reached significance. The Field Center males' advantage in producing young does not appear to have been related to any single factor, but to slight advantages in all aspects of pair formation and breeding.

Song Length

Although sons of Untutored males had slightly shorter songs (9.0 syllables, 0.96 s) than the sons of Field Center males (10.1 syllables, 0.99 s) or Manhattan males (10.5 syllables, 1.12 s) the differences among groups were not significant ($F_{2,33} = 1.34$, *P* > 0.25 for syllables, $F_{2,33} = 0.864$, *P* > 0.4 for seconds). Song length and number of syllables were similar to those in the songs of wild-reared birds (0.6–1.1 s, seven to 14 syllables) as shown in Zann (1990).

Reproductive Success and Salience as a Song Model for Sons

In testing for the effect of song type on song learning, it was important first to determine how effects such as the number of young birds present during the sensitive period for acquisition affected the choice of a song model. We considered five such

factors for each young male in the study: (1) the number of brothers; (2) the number of siblings; (3) the number in the age cohort within the natal aviary; (4) the total number of young that the father fledged during the course of the study; and (5) the identity of the natal aviary. Many of these factors are related, so we used an analysis of covariance to test their effects upon choice of song model. The father's total number of fledglings, as well as the aviary, had significant effects upon both the number of syllables copied from the father and the number of syllables copied from other adult males (Table III). In one of the aviaries, only the Field Center male produced fledglings and only his song was copied by the eight males he produced, a strong contribution to the aviary effect. Fathers that fledged more young over the course of the experiment were copied significantly more often by their sons. This effect might have been due to the presence of older sons serving as corollary song models. However, with a single exception (one older brother could have influenced three younger siblings), broods were spaced more than 2 months apart, and adult sons were removed before they could influence their younger brothers.

Factors Affecting Choice of a Song Model

As a group, young males copied more syllables from their fathers than from other males (Fig. 2a; $t = 2.50$, *df* = 35, *P* < 0.05). Syllables derived from the fathers' songs also represented a larger temporal proportion of the sons' songs ($t = 2.09$,

$df=35$, $P<0.05$). Adults other than fathers only served as song models if they fledged young during the study. One Manhattan and one Untutored male, housed in the same aviary, did not produce fledglings. The eight sons of the Field Center male in that aviary (no. 3) effectively had only their father as a song model, and only copied syllables from him; they were excluded from analysis of non-father sources for song. When the 28 males that were exposed to two or more valid song models were considered, the significant difference in rate of copying from fathers and other males disappeared, both for syllables copied (Fig. 2b; $t=0.913$, $df=27$, $P>0.3$) and for the amount of time copied from songs ($t=0.616$, $df=27$, $P>0.5$). Young males exposed to more than one breeding male copied equally from their fathers and other song models.

Song Type and Salience as a Song Model

Sons of Untutored males copied more syllables from their fathers and fewer syllables from other males than did the sons of Field Center and Manhattan males (Fig. 2c). The difference in copying from other males was significant ($F_{2,23}=3.827$, $P<0.05$) when tested using a linear model that also included the two factors (aviary and the father's total number of young) shown previously to affect song copying. Untutored males appeared to have been more prominent song models for sons of other males (Fig. 3), but this difference was not significant ($F_{2,23}=0.457$, $P>0.05$).

Improvisation

Seventeen syllables were scored as improvised. No improvised syllables were produced by the sons of the Field Center male in aviary 3 which was the only effective song model in his aviary (a significant result, $\chi^2=4.85$, $df=1$, $P<0.05$). These young males produced different songs only by copying different portions of their father's song and rearranging syllable order. Of the 17 improvised syllables, five were sung by the sons of Untutored fathers, four by the sons of Manhattan fathers, and eight by the sons of Field Center fathers (Fig. 4). When the numbers of young and effects of aviary and father's total number of offspring were taken into account, the difference in distribution of improvised syllables among sons of different types of fathers was not significant ($F_{2,23}=0.335$, $P>0.7$). However, the sons of Manhattan males included longer improvised components within

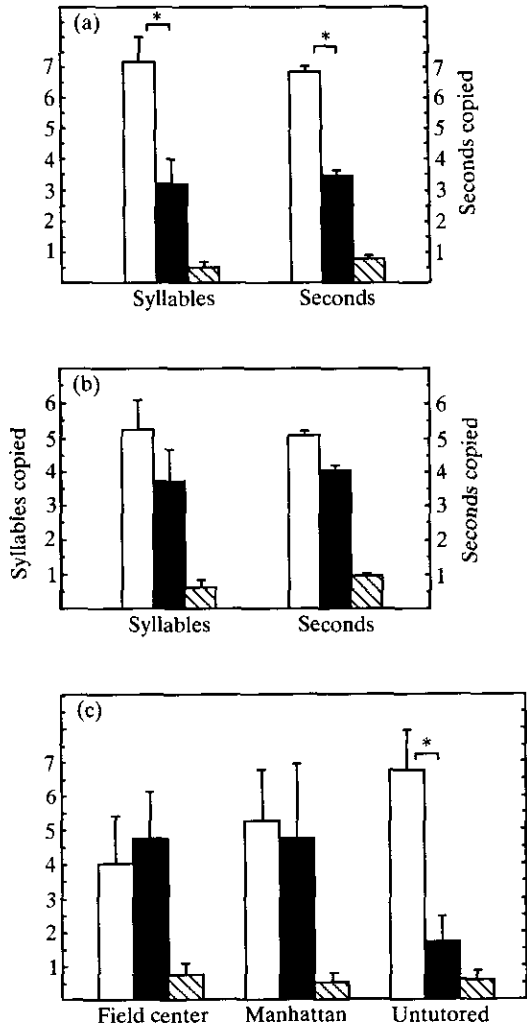


Figure 2. Sources for songs of young male zebra finches. The mean (\pm SE) number of syllables (and seconds) young males copied from their fathers (\square), other adult males (\blacksquare), and those improvised (hatched) for (a) all 32 young males, (b) the 28 young males that were raised in aviaries containing more than one effective song model (i.e. an adult male that fledged young), and (c) grouped by the father's song type, the 28 young males that had more than one effective song model. *Significant differences (t -test, $P<0.05$) between the amount of song copied from fathers and other adult males.

their songs than did the sons of Field Center and Untutored males ($F_{2,23}=4.67$, $P<0.02$).

Characteristics of Untutored Song Were Copied

Characteristics of untutored song, as we defined them, can be described as having two aspects:

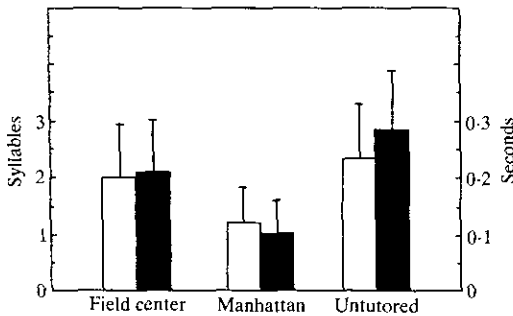


Figure 3. Song types of non-father tutors. For the 28 young males that had more than one effective song tutor, the mean (+SE) number of syllables (□) and seconds (■) copied from each of the three song types (after excluding the portions of the song copied from the father).

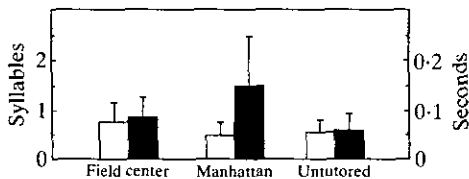


Figure 4. Father's song type and improvisation by young males. For the 28 young males that had more than one effective song tutor, the mean (+SE) number of syllables (□) and seconds (■) improvised. Young males are grouped by their father's song type.

(1) syllables with distinctive phonology, and (2) internal repeats of syllables. Sons copied a significantly larger proportion of syllables with untutored-like phonology from within their fathers' songs ($\chi^2 = 4.34$, $df = 1$, $P < 0.05$). However, when young males copied from adults other than their fathers, they copied syllables with untutored-like phonology in the proportions that they occurred within the models' songs ($\chi^2 = 0.008$, $df = 1$, $P > 0.09$). Internal repeats in untutored song were also copied by young males. Syllables were copied at a rate proportional to their representation within the adult model's song ($\chi^2 = 0.16$, $df = 1$, $P > 0.5$), with doublets in the adult's song appearing as doublets in the young males' songs.

The characteristics of untutored song were either maintained or increased in the young males' songs. Sons preferentially copied syllables with non-standard phonology from their own fathers' songs, but untutored-like syllables were treated no differently than standard syllables when copied from other males' songs. Young males also did not produce a normally structured zebra finch song

by either systematically reducing the number of repeats or failing to copy repeated syllables.

DISCUSSION

When aviary-reared Field Center females were given a choice among aviary-reared Field Center males, Manhattan males and Untutored males (Field Center males raised in isolation), aviary-reared Field Center males had the greatest reproductive success. It is possible that rearing in isolation may have effects on social behaviour that make untutored males less competent in forming pair bonds. However, the untutored males used in this study were isolated from song models, not from conspecifics, and were housed communally for several months before attempting to breed. They also courted females readily, were not disproportionately targets of male aggression, and two of the three Untutored males reared young, indicating that they were socially competent. Based on our observations, we believe that females competed for the most desirable males, and that females bred less readily and less often with the less desirable males. Evidence for female mate choice in zebra finches includes the demonstration that, in behavioural tests, females show preferences for different males' songs (Miller 1979; Clayton 1990) and leg band colours (Burley 1986). The lower reproductive success of males singing untutored songs matches Stephen J. Clark's results showing that oestradiol-treated females display more often to playbacks of normal zebra finch song than to playbacks of untutored songs (personal communication). We believe that this is the first study to show that females' playback preferences are related to males' reproductive success.

Intriguingly, the Field Center males produced proportionately more sons as well as more offspring. This result recalls Burley's (1981) study reporting that males wearing 'attractive' band colours had more sons, presumably to maximize the number of 'attractive' offspring. If our results reflect the same phenomenon, Field Center males may have achieved their success by rearing more of their hatchling sons, the mechanism suggested by Burley (1985) for her population's skewed sex ratios.

Reproductive success was related to success in transmitting a song model. Two factors contributed to this relationship. On average, young males

copied approximately half of their songs from their fathers, with improvisation and other models contributing the remainder. Hence, males with more sons were copied more often than their one-third representation in the aviary's song population. In addition, social cues related to reproductive success may have enhanced adult males' salience as song models. Even though non-breeders sang frequently, only males that fledged young served as song models, perhaps because male-fledgling interactions are important in the choice of a song model (Immelmann 1969; Williams 1990).

An adult male's song type also affected his salience as a model for young males. Sons of Untutored males copied more from their fathers and less from others than did the sons of aviary-reared males. Clayton (1987) found that males prefer secondary models with songs similar to that of their primary model. As the untutored songs are not similar to either the Field Center or the Manhattan songs, sons of Untutored males might have rejected the songs of other males as secondary models, and therefore may have copied more of their songs from their primary models. However, two lines of evidence indicate that young males did not perceive a distinct difference between untutored and normal song: untutored song was copied as much if not more often than other song types by the sons of aviary-reared males, and Untutored males' sons did not reject their fathers' songs in favour of normal zebra finch song as did young zebra finch males fostered on Bengalese finches (Immelmann 1969). The preference for untutored song was specific to untutored-like syllables, which were copied more often from untutored song than were standard zebra finch syllables. Untutored song appears to have had positive attributes for young males choosing a song model.

Acoustic qualities of song appeared to affect females' choice of mates and young males' choice of song models differently in our study. There are two possible lines of explanation for this difference: (1) the effects of familiarity and (2) differences in the manner in which males and females perceive or process song.

Although female zebra finches do not sing (Arnold 1975), they do learn about song and form preferences based on auditory experience and social cues (Miller 1979; Silcox & Evans 1982). The Field Center males' songs were the most similar to songs familiar to the females, and familiarity may be related to attractiveness and therefore to the

Field Center males' greater reproductive success. However, the young males heard all three song types as juveniles and also learned syllables from all of the song types, so familiarity cannot account for their preference for untutored song as a model.

Genetic guidelines for song learning, as postulated by the 'innate template' theory, may have given untutored song its special salience as a song model for young males. Such genetic guidelines, if they are sexually dimorphic, could also underlie the females' preference for males singing Field Center songs. Previous studies have shown that females and males of several songbird species respond to different aspects of conspecific song: to the syllable phonology (males) or temporal structure (females) of song sparrow, *Melospiza melodia*, and swamp sparrow, *Melospiza georgiana*, song (Searcy et al. 1981, 1982), and to the initial notes (females) or final trill (males) of red-winged blackbird, *Agelaius phoeniceus*, song (Searcy & Brenowitz 1988). Brown-headed cowbird, *Molothrus ater*, females have a genetically determined predisposition for responding to certain song characteristics, but males from different subspecies can alter their songs to match different females' preferences (King & West 1983; West & King 1988). Auditory responses in female zebra finches' song system differ from those of males (Williams 1985), and some song discriminations are acquired at different rates in male and female zebra finches (Cynx & Nottebohm 1992). Such differences between the sexes in preference for song characteristics could explain our results, as males would be biased towards (and females away from) untutored song.

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