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# Effects of Social Interaction on the Development of Starling Song and the Perception of These Effects by Conspecifics

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To examine the effects of contact with a conspecific in the absence of species-typical song models, the authors raised starlings in male–male pairs in acoustic isolation. The songs of these birds differed significantly from those of either individual isolates or wild adults and resembled in some respects the songs of starlings tutored by live conspecifics. Operant conditioning techniques were used to demonstrate that these differences among songs were perceptually salient to conspecifics. The results indicated that (a) wild-caught adult starlings are capable of forming open-ended categories for isolate and wild song, (b) starlings perceive the songs of isolated pairs as more "isolatelike" than "wildlike," and (c) starlings can distinguish the songs of isolated pairs from those of individual isolates. Both experiments point to the importance of social factors in avian song development.

The study of avian song learning began with the observation that oscine songbirds learn their songs by imitating those of adult conspecifics (see Kroodsma & Baylis, 1982, for a review). The importance of song models for vocal development was inferred from two sets of observations: first, that young birds copy the fine details of songs to which they are exposed and, second, that young birds raised in isolation, without access to song models, typically develop abnormal songs (Konishi & Nottebohm, 1969; Marler, Mundinger, Waser, & Lutjen, 1972; Nottebohm, 1972; Thorpe, 1961). In many species, exposure to tape recordings of conspecific song is sufficient for normal vocal development (Marler & Peters, 1987, 1988; Thorpe, 1958).

These initial observations, and an early reliance on tape-recorded stimuli in song-learning studies, highlighted the importance of auditory experience in song development. Sensitive periods, mechanisms of attention, and learning predispositions were defined with reference to auditory stimulation (Marler, 1987). Correspondingly, the outcomes of song-learning studies were typically assessed through analyses of song structure and only rarely in terms of the song's function in communication.

As song learning came to be studied in the field or in more complex social environments, it was shown that social interaction can exert a powerful influence on the learning process. Social context can affect the selection of song models to be imitated (Baptista & Morton, 1981; Baptista & Petrinovich, 1984; Beecher, Campbell, & Stoddard, 1994; DeWolfe, Baptista, & Petrinovich, 1989; Marler et al., 1972; Payne, 1981), the timing of song acquisition (Baptista & Petrinovich, 1984, 1986; Kroodsma & Pickert, 1984; Petrinovich, 1988; Petrinovich & Baptista, 1987), and perhaps the timing of motor development (DeWolfe & Baptista, 1995). Social cues influence the process of attrition or selection in a repertoire of previously acquired songs (DeWolfe et al., 1989; Dietrich, 1980; Kroodsma, 1974; Marler & Nelson, 1993; Nelson, 1992). In addition, many birds learn more from live tutors than from tape recordings (Chaiken, Böhner, & Marler, 1993; Marler & Waser, 1977), and others refuse to copy tape-recorded song (Thielcke, 1970). Social modeling may also play a role in both the acquisition and appropriate use of avian vocalizations (Pepperberg, 1985, 1993).

Social factors are now recognized as important variables in avian song learning, but the roles of social and auditory stimulation are not yet clear. Initially, social factors were considered to exert their effects by directing the young bird's attention to the song model to be copied or by inducing a state of arousal conducive to learning (Marler, 1987). More recently, Nelson and Marler (Marler & Nelson, 1992; Nelson & Marler, 1994) have deemphasized the role of imitation, proposing that song learning may be largely a process of selection among a set of preencoded song elements, with auditory or social stimuli playing a significant role in the selective process.

The possibility of a more direct role for social factors in song learning comes from work on cowbirds (*Molothrus ater*). Female cowbirds can shape a male's singing behavior and the structure of his song through a process of social reinforcement even in the absence of song models (King & West, 1983). However, it has been possible to consider

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cowbirds as a special case. As brood parasites, which hatch into the nests of other species, they do not appear to require exposure to conspecific song models in order to develop normal songs (West & King, 1980). Demonstrations of such model-independent effects in other species would therefore be of special interest.

The purpose of the present research was to assess the contribution to song learning of social and acoustic contact with a conspecific in the absence of adult song models. To this end, young male starlings were raised in pairs without an adult tutor. We reasoned that if social interaction affected song learning only indirectly by modulating the bird's use of the song model, the songs of isolated pairs would resemble those of individual isolates. On the other hand, if social interaction had direct effects independent of the song model, the songs of isolated pairs would show some species-typical features not present in individual isolates. We include vocal exchanges between untutored birds as one aspect of social interaction.

We expected to find some effect of group rearing. Several studies have found that the songs of birds reared in group isolation appear more normal than those of isolates (Marler, 1970; Marler, Kreith, & Tamura, 1962; Thielcke, 1970; Thorpe, 1958; Volman & Khanna, 1995), although there are some exceptions (Kroodsma, 1977; Marler, 1967). Interpretation of the early studies is hampered by variations in the experimental conditions. Birds were housed either together or in adjacent cages, and female birds or heterospecific male birds were in some cases present and in other cases absent. With the notable exception of Volman and Khanna's (1995) study, the effects of group rearing remained something of a footnote in the birdsong literature, and there has been little exploration of the implications.

In the present research, we assessed the effects of group rearing in two ways. First, we quantified differences in song structure and repertoire size between the songs of birds raised as isolated pairs and the songs of individually isolated, tape-tutored, live-tutored, and wild-caught starlings from a previous study. Then we used an operant conditioning procedure to test whether starlings can perceive differences among the songs of some of these groups. Different methods of assessing the normality of singing behavior can yield surprisingly different results (see, e.g., Freeberg, King, & West, 1995; West, King, & Freeberg, 1996). Because songs are social signals, the functional significance of such differences between songs depends on how or whether they are perceived by conspecifics. Wild-caught starlings were first required to discriminate between wild and individual-isolate songs, presumably the most extreme contrast between groups. Playback experiments in the field have established that isolate song is ineffective or significantly less effective than normal song in intra- and intersexual communication (Searcy & Marler, 1987; Searcy, Marler, & Peters, 1985; Thielcke, 1970; see also Williams, Kilander, & Sotanski, 1993, on the lower reproductive success of untutored male zebra finches). The conspecific responses that were observed in these cases were similar to but significantly weaker than the normal response to wild conspecific song. This leaves open the question whether the birds perceive isolate and wild song as belonging to distinct categories. The use of an operant procedure to address this question of discriminability allows us access to a wide array of behavioral measures designed explicitly to test hypotheses about stimulus differences and higher level perceptual representations such as natural categories (Herrnstein, Loveland, & Cable, 1976). After establishing the ability of starlings to discriminate between isolate and normal songs, we went on to ask into which of these putative categories they placed the songs of the isolated pairs.

European starlings were a natural choice for combining tutoring and operant techniques to study social effects on song learning. Starlings have shown themselves to be sensitive to social stimulation in previous tutoring studies (Chaiken et al., 1993; Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995; West, Stroud, & King, 1983). Quantitative techniques that successfully distinguish among treatment groups have been developed for the analysis of starling song (Chaiken et al., 1993). At the same time, starlings have been used extensively in psychoacoustic studies (Braaten & Hulse, 1991, 1993; Cynx, 1995; Cynx, Hulse, & Polyzois, 1986; Dooling, Brown, Klump, & Okanoya, 1992; Dooling, Kazuo, Downing, & Hulse, 1986; Hulse, 1995; Hulse, Cynx, & Humpal, 1984; Klump & Maier, 1990; Klump & Okanoya, 1991; Loesche, Stoddard, Higgins, & Beecher, 1991). Thus, starlings provide a link between two research traditions that we believe can be mutually illuminating.

## Experiment 1: Vocal Development in Isolated Pairs of Starlings

### *Method*

#### *Subjects*

Starling nestlings 6 to 8 days old were collected from nest boxes in Millbrook, New York. The nestlings were reared by hand until they could feed themselves, at approximately 36 days after hatching. Sex was ascertained by chromosomal sexing (Avian Genetic Sexing Laboratory, Bartlett, TN) from feather samples at about 19 days, and 8 male birds were used in the experiment. At 21 to 23 days of age, the birds were housed in pairs in sound-attenuated chambers and were kept on a light schedule corresponding to the natural photoperiod for their hatching site.

#### *Recordings*

Singing was monitored frequently with tape recordings (Marantz PMD 221). At 6 months and at 9 months of age, the birds were separated for a week or less and were recorded individually. At least 90 min of singing was obtained for each bird at each of these sample periods. The songs sampled at 9 months were used in the analysis. By the time the birds had reached this age, their songs had crystallized and their bills were turning yellow, an indication that their circulating levels of testosterone were rising and they were coming into breeding condition (Gwinner 1975; Witschi & Miller 1938).

#### *Analysis of Songs*

Analog recordings of the songs were digitized at a sampling rate of 22.6 kHz at 16-bit resolution on a Gateway 2000 486/33 computer (North Sioux City, SD) equipped with DT2821 analog-to-digital board (Data Translation, Marlboro, MA) and were displayed spectrographically on computer screen using SIGNAL sound analysis software (Engineering Design, Belmont, MA).

Starling song can be described as a succession of motifs, that is, fixed combinations of acoustic elements lasting about 0.5 to 1.0 s (Chaiken et al., 1993). (Note that Eens, Pinxten, and Verheyen, 1989, used a different terminology: Our *motifs* are equivalent to their *songs*, and our *songs* to their *song bouts*.) To determine repertoire size (i.e., the number of motif types in the repertoire), we examined the first 800 motifs recorded from each bird. Each time a new motif type was encountered, a hard copy was printed. Subsequent motifs displayed on the computer screen were compared with the hard copies until a complete library was compiled for each bird. To determine the number of motifs shared by two birds, we compared the libraries for each bird and identified shared songs by eye. Agreement between two observers was calculated for 25% of the sample and was over 98%.

We also analyzed songs with respect to two features of starling song syntax: three-part structure and distribution of breaks. Three-part structure refers to the division of wild starling songs into three sections: The first section consists of low whistles and introductory notes, the second of a rapid succession of click motifs, and the third of a series of high whistles. Low whistles have been defined as narrow-band simple tones, some parts of which fall below 5 kHz, with a minimum duration of 250 ms or greater. Introductory notes are highly variable in phonology, and no commonly defining features have been specified. Click motifs consist of a series of clicks, with maximum energy below 4 kHz, delivered at a rate of approximately 16/s. High whistles include relatively narrow-band tones that remain above 6 kHz for at least 250 ms (Chaiken et al., 1993; for additional descriptions of starling song syntax, see Adret-Hausberger & Jenkins, 1988; Eens et al., 1989). For the analysis of three-part structure, we sampled the first 35 songs from each bird with a duration of more than 15 s and calculated the percentage of these songs that displayed the three sections in sequence. For the purposes of this analysis, low whistles with a duration of less than 250 ms and clicks delivered at a rate of less than 16/s were accepted as defining the first and second sections of the song.

The distribution of breaks refers to the duration of intermotif intervals throughout the song and is a measure of temporal organization. In wild starling song, there are usually pauses between the first few motifs; as the song progresses, motifs follow each other in increasingly rapid succession. Using a cursor on the computer screen, we measured the distribution of breaks by counting the number of breaks greater than 0.5 s in the first and the last 7.5 s of the song. (For the shortest songs of 15 s in duration, this is equivalent to counting the number of breaks in the first and in the second half of the song.) We then calculated a difference score for each song by subtracting the number of breaks at the end from the number at the beginning.

These measurements were taken for the purpose of comparing the songs produced by the isolated pairs with those produced by starlings reared under different conditions and described in an earlier experiment (Chaiken et al., 1993). The measures used here were selected because they were the most effective in differentiating the songs of individually isolated starlings from those of wild-caught birds in the earlier experiment and because we were confident that these measures would be comparable across experiments. For both these reasons, we do not report frequency measures, although the songs of isolated pairs did show the species-typical significant increase in frequency from the beginning to the end of the song.

### Comparisons With Published Data on Starling Song Development

The measures of song repertoire and syntax were compared with those reported in a previous study (Chaiken et al., 1993) of starlings reared under the following conditions: (a) tutored with live wild-caught male starlings for 12 weeks (live-tutored group), (b) tutored with tape recordings of wild and wild-caught adult male starlings for 2 hr daily for 12 weeks (tape-tutored group), (c) housed alone in sound-attenuated chambers (isolate group), and (d) collected from the field in at least their 2nd year (wild-caught group). All of the birds, except those in the wild-caught group, were hand-reared and were 9 months old at the time of recording. Tape-tutored and live-tutored birds were tutored from the age of 36 to 97 days old at the time of tutoring.

### Statistical Analysis

We compared the song measures for the isolated pairs with those reported for isolated, tape-tutored, live-tutored, and wild-caught starlings using a Kruskal–Wallis nonparametric analysis of variance (ANOVA) followed by two-tailed Mann–Whitney $U$ tests. Values were averaged for the two members of each pair because they could not be considered independent.

## Results

### Repertoire Size

The mean (± $SD$) repertoire size for the isolated-pair birds was 33.38 ± 11.10 (see Table 1 for individual values). Figure 1 displays the mean repertoire size for isolated-pair birds in relation to those reported by Chaiken et al. (1993) for individually isolated, tape-tutored, live-tutored, and wild-caught birds. Repertoire sizes vary significantly among these five groups (Kruskal–Wallis, $p < .001$). Post hoc Mann–Whitney $U$ tests indicate that the mean repertoire size of the isolated-pair birds was significantly smaller than that of the wild-caught birds and significantly larger than those of both isolated and tape-tutored birds ($p < .05$).

### Motif Sharing

Paired birds that had been housed together shared an average of 75% ± 18% of the motifs in their repertoires (see Table 1 and Figure 2).

### Development of Motif Categories

All of the isolated pairs developed the four species-typical categories of motifs: low whistles, introductory notes,

Table 1
*Repertoire Sizes and Motif Sharing Among Isolated Pairs of Starlings*

| Bird | No. motif types in repertoire | % shared with cage mate |
|---|---|---|
| 1 | 29 | 48 |
| 2 | 28 | 50 |
| 3 | 39 | 90 |
| 4 | 40 | 88 |
| 5 | 52 | 67 |
| 6 | 39 | 90 |
| 7 | 21 | 81 |
| 8 | 19 | 89 |

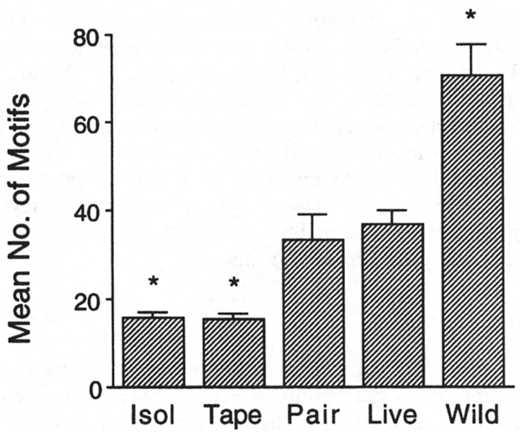

*Figure 1.* Mean repertoire sizes for isolated pairs of starlings compared with repertoire sizes reported in Chaiken et al. (1993) for individually isolated (Isol), tape-tutored (Tape), live-tutored (Live), and wild-caught (Wild) starlings. Asterisks indicate significant difference ($p < .05$) from isolated pairs in a post hoc Mann–Whitney *U* test.

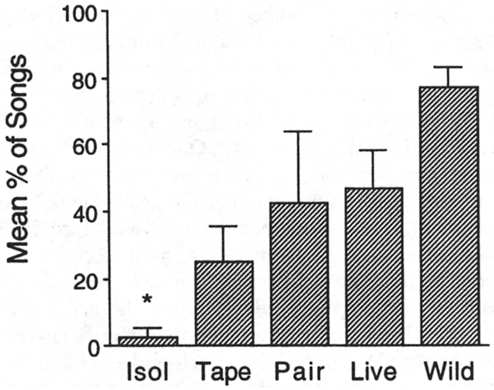

*Figure 3.* Mean percentages of songs that display the species-typical three-part song structure. Percentages for isolated pairs of starlings compared with percentages reported in Chaiken et al. (1993) for individually isolated (Isol), tape-tutored (Tape), live-tutored (Live), and wild-caught (Wild) starlings. Asterisk indicates significant difference ($p < .05$) from isolated pairs in a post hoc Mann–Whitney *U* test.

clicks, and high notes. The phonology of these motifs was normal, by the criteria described earlier, with the following exceptions: For 3 birds, the durations of the low whistles were never as great as 250 ms; for 2 birds, the rate of click production was never as high as 16/s.

### Three-Part Song Structure

The mean percentage of songs showing the species-typical three-part structure was 42.4 ± 37.35. Figure 3 displays this value in relation to data for the four other groups described earlier. The percentages vary significantly among the groups (Kruskal–Wallis test, $p < .002$). Post hoc Mann–Whitney *U* tests indicate that compared with the songs from the individual isolates, a significantly greater percentage of the songs from the isolated pairs displayed the three-part organization ($p < .05$); but there was no significant difference in the percentage of songs showing three-part organization between the isolated pairs and any of the other

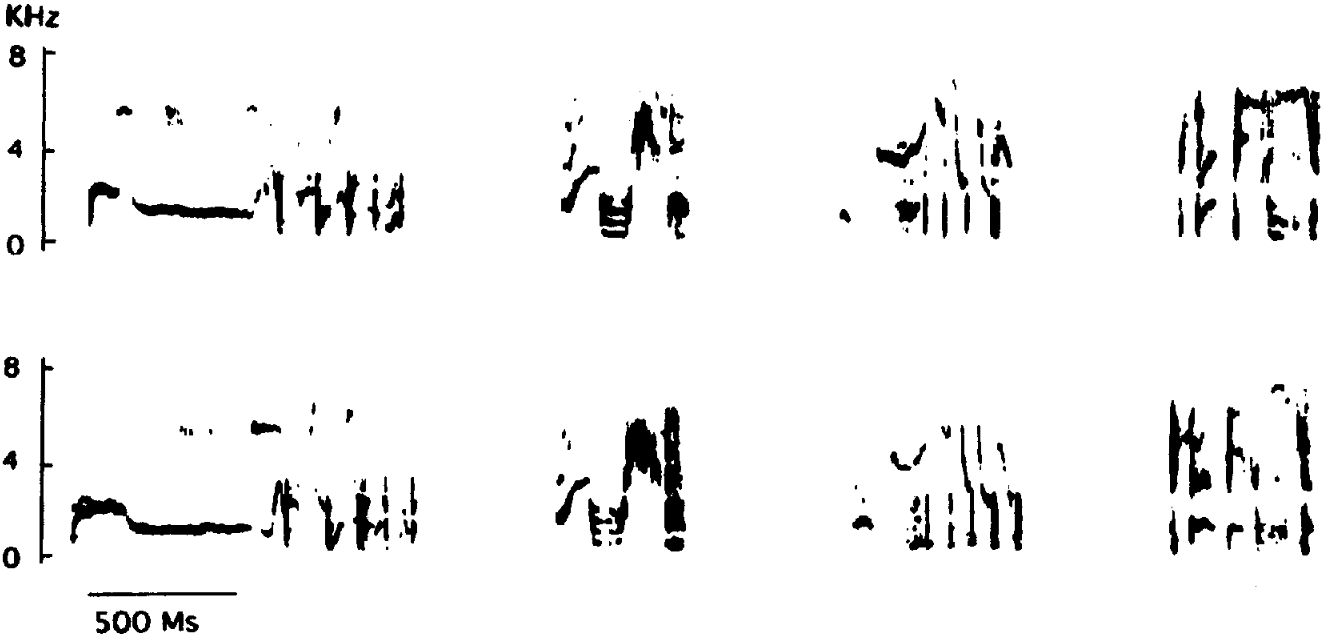

*Figure 2.* Sound spectrograms of motifs shared by isolated pairs of starlings. Each column shows matching motifs by the two members of each pair. The examples show one motif from each species-typical category: (from left to right) low whistles, introductory notes, clicks, and high notes.

groups. As with repertoire size, the values for isolated pairs most nearly resemble those for the live-tutored group.

### *Distribution of Breaks*

The songs of the isolated pairs displayed the species-typical distribution of breaks greater than 0.5 s within a given song (1.81 ± 0.55 breaks in the first 7.5 s compared with 0.84 ± 0.44 in the last 7.5 s). The mean difference between the number of breaks at the beginning and at the end of the songs was 0.88 ± 0.73. Figure 4 shows this difference score for isolated pairs in relation to difference scores calculated from data reported for individually isolated, tape-tutored, live-tutored, and wild-caught birds. The scores differed significantly among the five groups (Kruskal–Wallis test, $p < .007$). Post hoc Mann–Whitney $U$ tests indicate that the scores for the isolated pairs did not differ significantly from those of the other groups ($p > .05$). The difference scores for isolated pairs were intermediate between those for the live-tutored and tape-tutored groups.

## *Discussion*

Our analysis indicates that raising starlings in isolated pairs has significant effects on song development. By all of our measures, the songs of the isolated pairs were more "normal" than those of the individual isolates (taking the songs of wild-caught adults as the standard) and most nearly resembled those of the live-tutored birds. As compared with the individual isolates, the isolated pairs had significantly larger repertoires, and a significantly larger proportion of their songs displayed the species-typical three-part organization.

The songs of isolated pairs were intermediate between those of individual isolates and wild-caught birds, with significantly smaller repertoire sizes than the latter group. The wild-caught starlings were included to provide a benchmark for species-typical song. They differed from the other groups in that they were of unknown age but were at least in their 2nd year, whereas the laboratory-reared birds were recorded when their song first crystallized at 9 months. Yearling starlings in the field have smaller repertoire sizes than older birds (Eens, Pinxten, & Verheyen, 1992), roughly equivalent to laboratory-reared yearlings tutored by wild adults (the live-tutored group). For this reason, it is most telling to compare the isolated pairs with the birds in the three other groups that were of the same age and also reared under laboratory conditions.

The significant differences between the songs of isolated pairs and those of individual isolates imply that exposure to a conspecific companion has significant effects on song development, independent of the presence of a species-typical song model. The finding that the isolated pairs have significantly larger repertoire sizes than birds tutored with tape recordings suggests that these effects are not due solely to auditory stimulation but also to some aspect of the social contact or vocal interaction with the companion.

Our judgments about the species typicality of the isolated-pair songs depend, of course, on the variables we chose to measure. For this reason, we sought converging evidence for the effects of social contact in a series of operant conditioning tasks. The first task required wild-caught starlings to discriminate between the songs of individual isolates and wild-caught starlings. We then asked into which of these two putative categories the birds would assign the isolated-pair songs. The assignment of the isolated-pair songs into either the wild-caught or individual-isolate category can be used to infer the relative importance of our song measures in determining species typicality. The third task required the birds to discriminate between the songs of individual isolates and isolated pairs. Discriminative differences among all three classes of song would demonstrate that the effects we describe on the basis of our acoustic analysis could have functional significance for the birds.

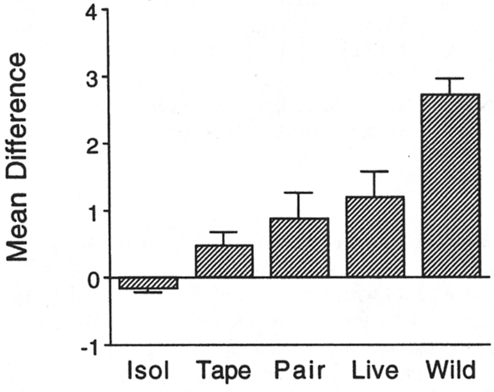

*Figure 4.* Mean differences between the number of breaks greater than 500 ms in the first and in the last 7.5 s of the song. Difference scores for isolated pairs of starlings compared with scores for individually isolated (Isol), tape-tutored (Tape), live-tutored (Live), and wild-caught (Wild) starlings (calculated from data reported in Chaiken et al., 1993).

## Experiment 2: Discrimination of Wild-Caught, Individual-Isolate, and Isolated-Pair Song Classes by Starlings

## *Method*

### *Subjects*

Five male European starlings that had been captured in the wild as adults were used in this experiment. Three of the birds had previous experience in the experimental apparatus but were naive to procedures involving stimuli other than short synthetic tones, both pure and complex (MacDougall-Shackleton & Hulse, 1996). The remaining 2 birds were wild caught in Baltimore, Maryland, and were naive to all experimental procedures. All of the birds were housed in individual cages in a mixed-sex aviary containing approximately 50 other European starlings. Fluorescent fixtures lit the aviary with an on/off schedule in synchrony with the natural photoperiod in Baltimore. Throughout the course of training and testing, all of the birds were maintained on a diet of Purina Start and Grow (Purina, St. Louis, MO) at 85% of their ad libitum weights. The birds had access to water at all times and to grit while in their home cages. While the birds were in the test apparatus, a coarsely ground mixture of Start and Grow, Doggie Burgers (Giant Foods

Inc., Washington, DC), chopped carrots, and hard-boiled eggs (with the shells) reinforced instrumental responding.

## *Apparatus*

All of the experimental sessions were conducted inside a sound-attenuating test chamber (Industrial Acoustics, Model AC-3, New York, NY). The chamber measured 80 × 60 × 60 cm (width × height × depth). We transported the birds from the aviary to the testing apparatus in a stainless steel weld-wire cage measuring 30 × 28 × 20 cm that attached to a response panel mounted inside the test chamber. The response panel was suspended from the ceiling of the test chamber and formed one end of the test cage. The birds gained access to the response panel once a sliding door on the transport cage was removed at the start of each session. The panel contained three horizontally aligned, translucent response keys. The keys were 2 cm in diameter and were spaced 6 cm apart, center to center. Food hoppers (Gerbrands, Model G5610, Cambridge, MA) delivered food to a 6.0 × 4.5-cm opening below each of the right and left response keys. Two 10-W incandescent lamps, located behind a translucent screen mounted on the back wall of the test chamber, provided indirect illumination of the test chamber. A monitor (Bose, Model 101, Framingham, MA) was located above and behind the response panel and was shielded from the view of the bird by a 5 × 20-cm rectangular 3-mm thick aluminum plate. A 386 PC equipped with a parallel digital interface board (Keithley Metrabyte, Model PIO-12, Tauton, MA) and a digital-to-analog (D/A) board (Data Translation, Model DT 2812-A, Marlboro, MA) for D/A signal conversion controlled the stimulus presentation, response contingencies, and data collection.

## *Stimuli*

We constructed the stimuli by sampling from recorded songs of European starlings raised in individual isolation, from starlings caught in the wild (see Chaiken et al., 1993), and from the isolated-pair starlings in Experiment 1. In all, 94 separate exemplars were made for use in this experiment. We took a total of 32 different samples from 8 different wild-caught starlings, a total of 30 samples from 5 different individual-isolate starlings, and a total of 32 samples from 8 different isolated-pair starlings (see Table 2). Each exemplar was 15 ± 0.5-s long. Because a 15-s sample never captured an entire song, we controlled for sampling position within a song by taking equal numbers of stimuli from the beginning, middle, and ends of songs. Samples for each bird were taken from more than one recording session (i.e., recorded on different days). All the analog master recordings used as the source for the stimuli were made on Marantz PMD 221 or 222 cassette recorders. Some recordings in each group (isolated pair, wild, or individual isolate) were made in anechoic chambers. No group was characterized by a unique set of recording conditions. Figure 5 shows examples of wild-caught, individual-isolate, and isolated-pair exemplars used in the experiment. Measurements of some of the acoustic properties of the exemplars are given in Table 3.

Table 2
*Sources of Stimuli Used in Experiment 2*

| Group | No. of singers | No. of songs per singer |
|---|---|---|
| Wild | 8 | 4 |
| Individual isolate | 5 | 6 |
| Paired isolate | 8 | 4 |

All of the birds began the experiment by making discriminations among a baseline stimulus set that contained 12 exemplars from songs of wild-caught starlings and 12 exemplars from songs of individual-isolate starlings. Following proficient discrimination of the baseline stimulus set exemplars, we used subsequent presentation of two sets of novel test stimuli to rule out the use of either shared phonetics or singer identity as a basis for this baseline discrimination.

The first set of test, or probe, stimuli, was novel with respect to the song from which the stimuli were sampled but not with respect to the bird that sang them. That is, the same wild-caught and individual-isolate starlings whose songs were sampled for the baseline stimulus set were again sampled for the first probe stimulus set, but the actual songs sampled for the baseline and first probe stimulus sets were different. We refer to the exemplars in the first probe stimulus set as novel song probes. We used 21 novel song probes: 12 from the songs of wild-caught starlings and 9 from the songs of individual-isolate starlings.

The second set of probe stimuli was novel with respect to both singer and song. For this second set, we sampled songs of wild-caught and individual-isolate starlings that our test birds had never heard before. We refer to the exemplars in the second stimulus set as novel singer probes. We used 12 novel singer probes: 6 from the songs of wild-caught starlings and 6 from the songs of individual-isolate starlings.

A third set of probe stimuli was used to examine the perception of songs from the isolated-pair starlings. We refer to the exemplars in this third set as isolated-pair song probes. We used 32 isolated-pair song probes: All were sampled from the songs of isolated-pair starlings raised in Experiment 1.

All of the samples were digitized at a rate of 22050 Hz with 8-bit resolution to hard disk from a magnetic tape analog master using a personal computer (Apple Macintosh Quadra 650, Cupertino, CA) with a digital signal processing board (Digidesign Audiomedia II, Menlo Park, CA) running Sound Designer II Version 2.8 software. We equated each sample for maximum loudness, high pass filtered each one at 100 Hz to remove background noise, and then converted it from 22050 Hz to 20000 Hz using the Sound Designer software. We used Soundview Version 1.10 (Peabody Computer Music Department, Baltimore, MD) to convert the samples to a PC binary format and then transferred the sound files to the hard disk of the computer controlling the experiment.

Analog signals from the controlling computer were amplified (Crown Model D-75, Elkhart, IN) and then sent to the speaker in the test chamber. Before testing, we set the maximum sound level within the test chamber at 70 ± 2 dB (A) sound pressure level by placing a microphone, connected to a sound level meter (Rion Model NA-20, Tokyo, Japan), at a position inside the test chamber that approximated that of the bird's head during experimentation.

## *Procedure*

*Shaping.* All of the birds were trained to eat from the food hoppers and then, over several sessions, to associate key pecks on the response panel with food reward. For the initial portion of this training, access to food was not associated with any response. However, access was preceded by a flashing light on the center key for 2 s, immediately after which either the right or left key flashed ($p = .5$) for 3 s, then the birds were allowed 10-s access to the food hopper below that key. This sequence repeated for the entire session. Once a bird showed a reliable weight gain during a single session, access to the hoppers became contingent upon appropriate key pecks in the next session. The birds quickly learned to peck at a flashing center key to gain a 3-s access to either one of the hoppers ($p = .5$). We then arranged the response contingencies so that a

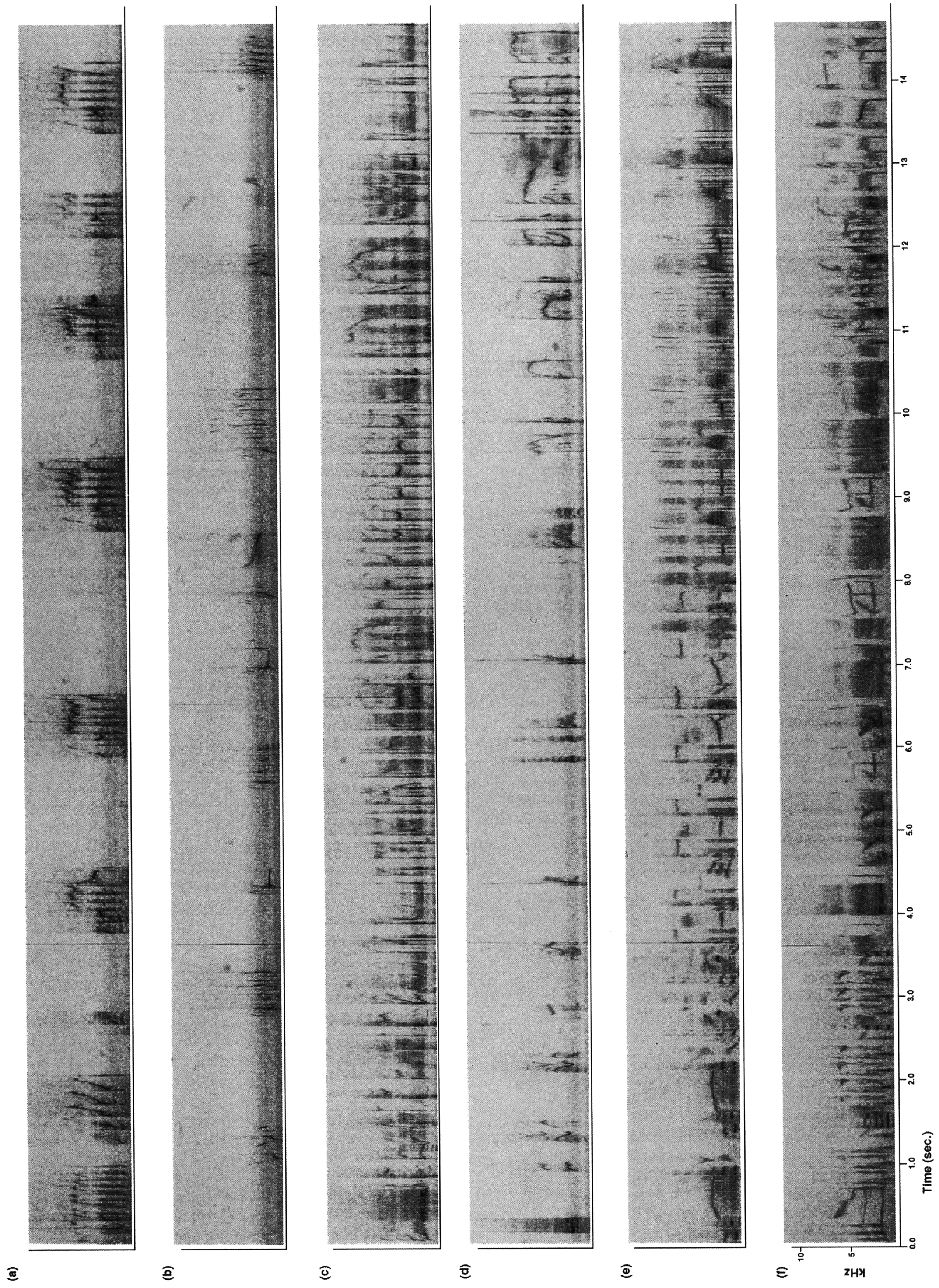

*Figure 5.* Sound spectrograms displaying 6 of the 94 exemplars used in Experiment 2: (a) and (b) are from the songs of 2 individually isolated European starlings, (c) and (d) are from the songs of 2 isolated-pair starlings, and (e) and (f) are from the songs of 2 wild-caught starlings. The vertical line at approximately 3.6 is a photographic artifact.

Table 3

*Acoustic Parameters of Stimuli Used in Experiment 2, Recorded From Individual Isolates, Isolated Pairs, and Wild-Caught Starlings*

| Acoustic parameter | Isolate | | Pair | | Wild | | |
|---|---|---|---|---|---|---|---|
| | *M* | *SD* | *M* | *SD* | *M* | *SD* | $F(2, 95)^a$ |
| Duration (s) | 15.13 | 0.32 | 14.97 | 0.33 | 15.10 | 0.35 | 2.24 |
| Average intensity (Db) | −69.40 | 2.03 | −69.36 | 3.03 | −69.84 | 2.47 | 0.35 |
| Peak frequency (Hz) | 1383 | 723 | $2013^c$ | 339 | 1548 | 728 | $8.89^b$ |
| Maximum frequency (Hz) | $6697^c$ | 1424 | 7944 | 694 | 7837 | 920 | $14.06^b$ |

[a] *F* ratios for one-variable analysis of variance. [b] $p < .001$. [c] Significant difference from both other groups; Scheffé's post hoc tests, $p < .05$. Maximum frequency was measured from the spectrographic display on SIGNAL Version 2.23 sound analysis software (Engineering Design, Belmont, MA), with a cutoff amplitude of −20 Db relative to the maximum amplitude of the motif. The remaining measures were calculated using Canary Version 1.2.1 software (Cornell Laboratory of Ornithology, Ithaca, NY).

peck to the flashing center key stopped the key flashing and started either the left or the right key flashing ($p = .5$). Another peck to the newly flashing key then allowed for a 3-s access to the hopper below. Once the birds again showed reliable performance, this time by completing over 100 trials in a session, we replaced the key light stimuli with acoustic stimuli and training for the baseline discrimination began. From this point in the experiment, the key lights were no longer used.

*Baseline discrimination training.* We used a two-alternative choice task to train the starlings in a baseline discrimination-transfer procedure (see Hulse, 1995, for a general review of this type of procedure). For this specific experiment, the birds discriminated between individual-isolate and wild exemplars from the baseline stimulus set by responding to either the left or the right key on the response panel following the presentation of a given exemplar. For example, the birds were trained to peck left when they heard an exemplar from the wild group and to peck right when they heard an exemplar from the individual-isolate group.

A peck to the center key initiated a trial by starting the playback of a randomly selected wild or individual-isolate exemplar. A response period immediately followed playback. A correct response (e.g., a right key peck following a wild exemplar) resulted in access to the food hopper for 3 s. Incorrect responses resulted in a 5-s time-out during which the house lights were extinguished and the hopper remained inaccessible. The assignment of individual-isolate and wild response categories to the right and left keys was counterbalanced across birds.

The starlings were free to base the discrimination between wild and individual-isolate exemplars on any of the acoustic cues within each exemplar. To temper any bias to respond to acoustic cues early in the stimulus event, we gradually increased the interval between stimulus onset and the point at which responses triggered reinforcement from 0 to 14 s over the course of several of the earliest sessions. During the introduction of this observation period, the birds were exposed to only four exemplars from the baseline stimulus set (two individual isolate and two wild). For the first session, birds were allowed to respond immediately following stimulus onset. Over the following two sessions, the observation period was gradually lengthened to 14 s. Responding within the observation period caused the abortion of that trial and was punished with a time-out. The trial then reset and another one of the four stimuli was played. A full 14-s observation period and the abort criterion were in effect for all of the fourth session. For the fifth session, the abort criterion was removed to increase stimulus exposure.

The intertrial interval between all trials was 3 s. In the event that a bird failed to respond within 5 s following the completed presentation of a given exemplar, the trial ended, and the computer waited for a center key peck to begin the next trial. In addition to causing a 10-s time-out, incorrect responses to baseline stimulus set exemplars initiated a correction trial sequence in which the exemplar with incorrect responses was repeated on the subsequent trial. Correction trials continued until the bird responded correctly or no response was made.

We recorded the number of correct responses for both wild and individual-isolate exemplars across sessions, and as soon as an individual bird had maintained mean performance above 85% correct for three consecutive sessions, 4 new exemplars from the baseline stimulus set (2 wild and 2 individual isolate) were added to the pool of exemplars being discriminated. Once the starlings again attained the performance criterion, we added 4 more exemplars from the baseline stimulus set to the group of those being discriminated. This continued until any of the 24 exemplars from the entire baseline set could be presented within a single experimental session. For a given baseline training session, 50% of all trials involved the presentation of 1 of the 4 most recently added exemplars ($p = .125$) chosen at random, whereas the other 50% of the trials were equally divided among presentations of the already accurately discriminated exemplars, again chosen at random. After all of the baseline stimuli had been introduced in this manner, the presentation probabilities of all the stimuli were equated, and performance was allowed to reach asymptote. Again, we set an arbitrary performance criterion at 85% correct. Once performance had been maintained above this criterion for at least 3 days, we decreased the rate of reinforcement for correct responses to 80% (in 5% decrements) over the course of four sessions. When performance was again at asymptote, the first of three partial transfers to probe stimuli began.

Partial transfer sessions were identical to baseline sessions in every way, except that on 10% of the trials the bird was presented with an exemplar from one of the three probe stimulus sets. We refer to these 10% of the total trials as probe trials, and we refer to sessions in which they were used as probe sessions. After reaching criterion on the baseline stimulus set, the birds began the novel song probe sessions during which novel song probe stimuli were presented on the probe trials. Once a bird had made at least 20 responses to each of the novel song probe exemplars (this took several sessions), the novel song probe sessions were discontinued. Following a few sessions with just the baseline stimulus set to ensure that performance was still above criterion, the birds began the novel singer probe sessions during which the novel singer probe stimuli were presented on the probe trials. After at least 20 responses to each of the novel singer probe exemplars (again over multiple sessions), the novel singer probe sessions were discontinued. After a few sessions with just the baseline stimulus set, the birds began the isolated-pair probe sessions during which the isolated-pair song probe stimuli were presented along with four novel song probes (two wild and two individual-isolate) that served as controls. Again after at least 20 responses to each of the probe stimuli, the probe trials were discontinued.

All probe stimuli in a given session were randomly selected for presentation with equal probability. For all probe trials, both left and right key responses to a probe stimulus were rewarded 80% of the time. Correction trials did not occur following incorrect responses to probe stimuli.

Following the results of the isolated-pair probe sessions, a final condition became necessary to test whether the birds were capable of discriminating between the isolated-pair and individual-isolate exemplars. For this final condition, the birds were required to make discriminations between the individual-isolate and isolated-pair exemplars used in the previous conditions. Reinforcement contingencies for the final condition were identical to those used for the terminal baseline stimulus set discrimination except that the wild song exemplars were simply replaced by those from the isolated-pair probe set.

All experimental sessions lasted approximately 1.5 hr and occurred once daily at the same time for each bird. We conducted test sessions Monday through Saturday. On Sundays no testing was conducted, and the birds were fed 20 g of food.

*Statistical analysis.* We recorded a single key peck (either right or left) for each bird on every trial. The total numbers of all key pecks to a given exemplar were summed across trials, then across sessions, and then averaged across birds. These performance data could be easily expressed as either a mean percentage correct score or as the likelihood of a given response to a particular stimulus type. We used chi-square to assess performance within each stimulus set with respect to chance. Performance with the different stimulus sets was assessed with a one-way repeated measures ANOVA. *F* values reported in the text are for arcsine transformed percentage correct scores, which corrected for deviations from normality (Zar, 1984). ANOVAs were also done on untransformed percentage correct scores with similar results. For ease of interpretation, the figures and tables show untransformed percentage correct scores.

Data from correction trials were not included in any of the analyses. In some cases, the starlings simply did not respond with a key peck following stimulus presentation, even after initiating the trial. These nonresponses to a given stimulus type were not included in the calculation of performance scores. However, we examined the tendency for birds to withhold responses to some probe stimuli during early probe sessions.

## *Results*

All of the birds rapidly acquired the discrimination between the wild and individual-isolate songs in the baseline stimulus set (see Figure 6). Asymptotic performance over the 10 sessions before the first probe session was significantly above chance, $\chi^2(9, N = 5{,}353) = 2{,}255.45, p < .01$. Table 4 presents the overall mean percentage correct scores for the wild and individual-isolate exemplars in the baseline stimulus set.

The starlings showed no significant change in performance on trials with either the novel song probes, $F(1, 9) = .4449, p > .5$, or the novel singer probes, $F(1, 9) = 7.21, p > .05$, as compared with their performance on trials with the baseline stimuli during the same sessions. The results for probe sessions involving the novel song probes and novel singer probes are presented in Table 4. Table 5 shows the response data by bird for the novel song probes and the novel singer probes, as well as the mean number of responses to each of the different probe types (averaged across birds). Both the novel song probes and the novel singer probes were correctly classified at a level significantly above chance: $\chi^2(4, N = 648) = 234.135, p < .01$ for novel song probes; $\chi^2(4, N = 345) = 83.72, p < .01$ for novel singer probes.

There was a significant bias for all birds to classify the isolated-pair song probes as if they were the songs of individual-isolate starlings as opposed to those of wild-caught starlings, $\chi^2(31, N = 4{,}128) = 1{,}021.25, p < .01$. The wild-caught and individual-isolate exemplars presented as controls during the isolated-pair probe sessions were classified correctly. That is, the percentage correct scores for the wild and individual-isolate controls differed significantly

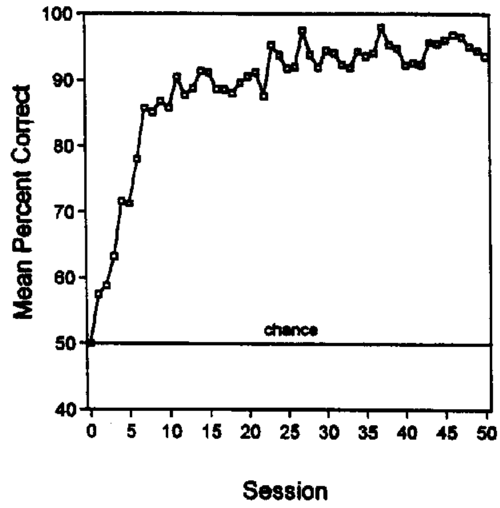

*Figure 6.* Acquisition data for the discrimination between the baseline stimuli. Each data point is a mean of the percentage correct scores for all birds for a given session.

Table 4
*Mean Percentage Correct for Exemplars of Each Stimulus Type by Experimental Condition*

| Condition | *M* | *SE* |
|---|---|---|
| Wild vs. individual isolate | | |
| Wild | 95.76 | 1.31 |
| Individual isolate | 94.41 | 1.85 |
| Novel song probe sessions | | |
| Baseline stimuli | 93.97[a] | 0.98 |
| Probe stimuli | 92.97 | 1.68 |
| Novel singer probe sessions | | |
| Baseline stimuli | 94.45[a] | 1.48 |
| Probe stimuli | 80.30 | 5.87 |
| Pair vs. individual isolate | | |
| Isolated pair | 86.32 | 4.69 |
| Individual isolate | 94.45 | 2.82 |

*Note.* All means were significantly different from chance ($p < .001$, chi-square).
[a] Combined performance on all wild and individual isolate baseline stimulus exemplars.

Table 5
*Number of Correct and Incorrect Responses for Novel Song and Novel Singer Probe Stimuli for Each Bird*

| Bird | Song probe responses |  | Singer probe responses |  |
|---|---|---|---|---|
|  | Correct | Incorrect | Correct | Incorrect |
| A63 | 124 | 11 | 52 | 6 |
| A66 | 115 | 11 | 29 | 23 |
| A03 | 94 | 3 | 44 | 12 |
| A16 | 152 | 4 | 63 | 11 |
| 287 | 97 | 14 | 97 | 8 |

from chance in the direction that we would expect: $\chi^2(1, N = 218) = 23.60, p < .01$ for wild-caught controls; $\chi^2(1, N = 217) = 92.39, p < .01$ for individual-isolate controls. Figure 7 shows the results for the isolated-pair probe sessions. One bird showed a significant bias to classify two of the isolated-pair probes as if they were wild songs ($p < .0005$ in both cases, sign test). Although the last result is compelling in that it may point to important acoustic features that help to distinguish wild-caught songs from individual-isolate songs, a proper mathematical analysis of these particular data is beyond the scope of this article.

In the final condition, all of the birds quickly learned to discriminate between the individual-isolate and the isolated-pair song probes with an accuracy significantly above chance, $\chi^2(4, N = 1{,}884) = 539.61, p < .01$. Three of the 5 birds were responding with above 85% accuracy by the end of the first session and continued responding at or above 85% correct for several sessions until the experiment was terminated. The remaining 2 birds required 3 and 11 sessions, respectively, to reach the 85% criterion. The results of the final experimental condition are shown in Table 4.

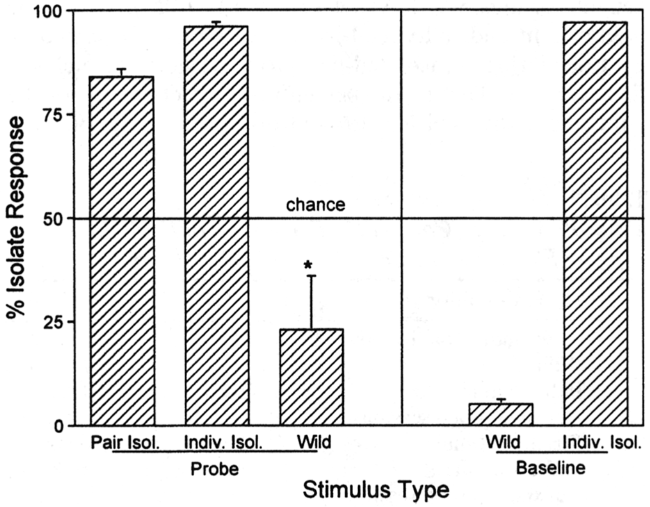

*Figure 7.* Results of the isolated-pair probe sessions. Data are shown as the percentage of pecks to the isolate key following the presentation of one of five stimulus exemplar types: isolated-pair (Pair Isol.) probe, individual-isolate (Indiv. Isol.) control, wild control, wild baseline, or individual-isolate baseline. Asterisks indicate significant difference between responses to wild control and individual-isolate control stimuli.

On some of the probe trials, birds simply did not respond. There was a trend for the percentage of no responses to probe stimuli to decrease as the birds gained experience with the probe stimuli. This tendency to withhold responses indicates that the starlings were capable of perceiving differences between the probe stimuli and the baseline stimuli, even though they were simultaneously classifying probe stimuli according to the categories established by the baseline stimulus set. The no-response data are presented in Figure 8.

## *Discussion*

All 5 starlings were capable of discriminating between exemplars from wild and individual-isolate songs. Moreover, the results of the novel song and singer probe sessions show that the acoustic cues relied on to maintain performance on the wild versus individual-isolate discrimination are specific to neither an individual song nor an individual singer. There was a small but nonsignificant decrease in accuracy for the novel singer probes, suggesting that during the earlier phases of testing some efficiency in this task may have be gained by using individual recognition. However, the capacity for individual recognition remains to be shown directly in starlings, and the birds had no difficulty relying on more general cues when the task dictated they do so. This experiment was not designed to test explicitly the notion of a natural category in its strict sense (Herrnstein, 1979, 1990), but the rapid acquisition of the baseline stimuli and strong generalization to the novel probe stimuli are consistent with such an interpretation.

Categorization and discrimination are, of course, two different tasks. Song sparrows are capable of using within-

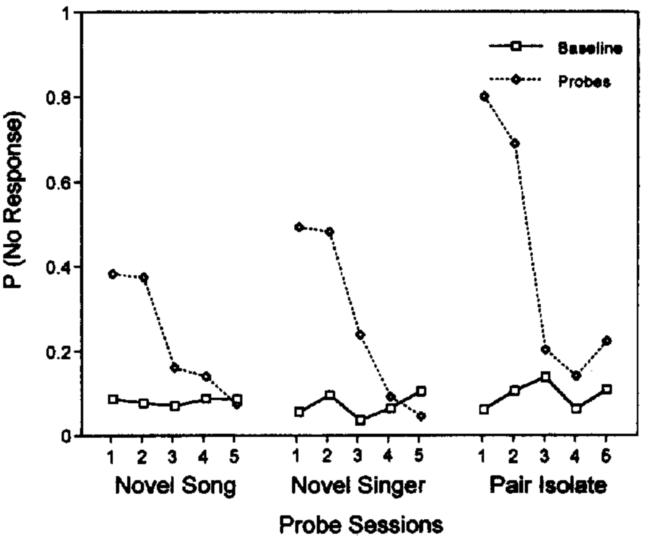

*Figure 8.* Probability (P) that a bird made no response following the presentation of either a baseline or a probe stimulus exemplar during the first five sessions of each probe type: novel song probes, novel singer probes, and isolated-pair probes.

song-type variation to make discriminations in one task and of classifying those same variable song types in a single category in a second task (Stoddard, Beecher, Loesche, & Campbell, 1992). The starlings in the present experiment had no problem discriminating between isolated-pair and individual-isolate songs, but they assigned nearly all of the isolated-pair probe stimuli to the individual-isolate key when they were required to categorize them as either individual-isolate or wild. This result suggests that the starlings perceived the songs of the isolated-pair birds as more isolatelike than wildlike while still perceiving them as different from isolate song. Recall from Experiment 1 that the songs of isolated pairs were intermediate between those of individual isolates and those of wild-caught birds and differed significantly in some respects from each. If one assumes that the birds in Experiment 2 used the same rules to classify the isolated-pair songs as they used to correctly classify the novel exemplars of both wild-caught and individual-isolate songs, then one is led to the conclusion that repertoire size and temporal organization play a large part in the determination of species typicality.

In some cases, different subjects may use a variety of different cues to solve similar discriminations (see Loesche, Beecher, & Stoddard, 1992). The precise cues used to make the discriminations in Experiment 2 remain to be shown explicitly. We have shown that wild-caught, individual-isolate, and isolated-pair songs are discriminably different from one another and that exemplars of at least two of these song classes are capable of defining open-ended stimulus categories that differ at a level of organization above the individual. Therefore, the capability of the birds to discriminate between individual-isolate and isolated-pair songs provides convergent evidence for the significance of the effects of social interaction on the development of species-typical song.

## General Discussion

Our analysis of repertoire size and song structure in the songs of isolated pairs of starlings suggests that interaction with a conspecific is surprisingly effective in stimulating the development of species-typical song, even in the absence of species-typical song models. By all our measures, the songs of the isolated pairs were significantly different from those of individual isolates and most nearly resembled the songs of birds tutored by wild-caught adults. The operant experiments proved an interesting complement to the more traditional acoustic analysis of songs. The results suggest that the effects on song of social stimulation can be perceived by conspecifics and are therefore of potential functional significance in communication.

All of the starlings that participated in the operant experiment were capable of discriminating among the songs of conspecifics raised in individual isolation, in isolated pairs, or in the wild. Moreover, the results of the probe sessions with both novel songs and novel singers provide at least initial evidence for the formation of open-ended natural categories (Herrnstein, 1979, 1990).

### *Perceptual Basis of Discrimination*

The results of the operant experiments were predictable from the analysis of repertoire size and song structure. First, the reported differences between the songs of individually isolated and wild starlings suggest that our birds should be able to discriminate between exemplars of these classes. Second, the songs of the isolated pairs more nearly resembled individual-isolate than wild songs in repertoire size and distribution of breaks. Thus, it is not surprising that the songs of isolated pairs were classified with the songs of individual isolates when the birds were given only two choices (i.e., wild or individual isolate). Third, the songs of isolated pairs were significantly different from those of individual isolates in repertoire size and proportion of songs showing three-part structure, which is consistent with the starlings' ability to discriminate between exemplars of isolated-pair and individual-isolate song.

Although our song measures were consistent with the starlings' performance in the operant tasks, we cannot assume that these measures reflect the actual cues used by the starlings in classifying songs because we have not identified the conditions under which systematic discrimination errors occur. We can surmise, however, that the birds were using some combination of the features we measured or perhaps different features, because no single feature was sufficient to account for all of the results. An additional analysis of some of the acoustic properties of the stimuli used in Experiment 2 does not suggest any simple cues the birds might have used to solve the discriminations; for instance, if they had relied on either of the measures that varied significantly among groups, they would have classified isolated-pair exemplars as wild rather than as individual isolate (see Table 3). The question of what cues the birds actually used will require further analysis and playback of altered stimuli. Current work is under way investigating the perceptual importance of repertoire size and other possible cues.

### *Possible Mechanisms for Effects of Untutored Conspecifics on Song Development*

Our results raise interesting questions about the mechanism by which interaction with an untutored conspecific can exert an effect on song development. Consider first the question of repertoire size. What could account for the development of repertoire sizes in isolated pairs that were more than twice those of individual isolates and, even more impressive, equivalent to those of live-tutored birds of the same age? Two possibilities are that the birds imitated each other or that each bird simply stimulated the other to improvise a greater number of motifs. Both are probably correct. We suspect that imitation was key, because members of a pair shared an average of 75% of the motifs in their repertoires. Members of a pair resembled each other from the earliest recordings, so it was not possible to separate the contributions of each bird, but it seems plausible that each member improvised some motifs and copied the remainder from its partner.

Young songbirds of other species appear to be willing to copy the songs of untutored peers when no other song models are available. Zebra finches are similar to starlings in that siblings housed together without a tutor share from 50% to 78% of their song syllables (Volman & Khanna, 1995). Zebra finches also copy the songs of untutored adults (Williams et al., 1993). Young chaffinches (Thorpe, 1958), white-crowned sparrows (Marler, 1970), and canaries (Waser & Marler, 1977) share songs when isolated in a group without adult tutors, although copying was minimal among Oregon juncos (Marler et al., 1962).

Starlings tend to improvise roughly 15 motifs regardless of whether they are isolated, tutored with tapes, or exposed to live tutors, and repertoire sizes above this number can be accounted for by imitations (Chaiken et al., 1993). In the present study, if each member of an untutored pair contributed roughly 15 motifs and imitated 15 from its partner, it would account for the mean repertoire size of 33 motifs. However, because the birds shared only an average of 75% of the motifs in their repertoires, they would need to have improvised an average of 20 motifs to account for their average repertoire sizes. This suggests that isolated pairs improvise more motifs than do individual isolates.

Although imitation appears to account in large part for the development of large repertoire sizes in starlings, in previous experiments simple exposure to tape-recorded song was not sufficient to promote much imitation or to increase repertoire sizes over individual-isolate levels (Chaiken et al., 1993). Thus, in the isolated pairs, the stimulation provided by a companion appears to have promoted imitation, which in turn resulted in the development of larger repertoire sizes.

Isolated pairs may have copied aspects of each other's song structure as well as imitating individual motifs. The measures for distribution of breaks and the percentage of songs showing a three-part organization were highly correlated between members of a pair (Spearman's rho averaged .80 in each case). However, this does not explain how two birds with no experience of species-typical song could develop aspects of species-typical syntax that are not present in the songs of individual isolates. We suspect that the development of syntactic features may not require exposure to a song model but may still require some more general form of social or acoustic stimulation. This would be consistent with Böhner and Todt's (1996) finding that starlings develop these same syntactic features when exposed to heterospecific song in the presence of a human with whom they had interacted. We concur with these authors' suggestion that the auditory stimuli contributing to song development may fall along a continuum from highly specific to relatively nonspecific, and we suggest that the principle may apply to nonvocal social stimuli as well.

One simple mechanism to explain the effects of contact with a conspecific could be that the presence of a companion stimulates a bird to spend more time singing than is typical of individual isolates, so that species-typical features of song emerge as a result of practice. This does not seem likely, however, because individual-isolate birds do not appear to have lower singing rates than live-tutored birds (unpublished data). We envision a more complex scenario in which each bird stimulates the other to produce a greater number of motif types and syntactic variants than it would have produced in isolation and also to imitate more than it would from tape recordings. Given this enlarged pool of song variants, the birds have an increased opportunity to express their song preferences by retaining, imitating, or socially reinforcing those variants displaying a more species-typical structure (see King & West, 1983; West & King, 1988).

### *Implications for Interpretation of Isolation Studies*

Whatever the basis for the social effect on song development, our results suggest that untutored starlings know more about song organization than we would have suspected on the basis of individual isolation experiments. Our results point to a need to reconsider the interpretation of isolation studies, particularly in the light of work by Nelson and Marler (1994) and Böhner and Todt (1996) discussed earlier. The vocalizations of individual isolates can no longer be assumed to provide a straightforward readout of innate specifications for song. Certain specifications or predispositions may be expressed only under specific or general conditions of social or acoustic stimulation.

### *Role of Peers in Normal Song Learning*

Although our results suggest that social interaction can go further than we expected in steering song development along a normal track, we do not mean to imply that adult song models play no more than a minor part in the normal song-learning process. Most or all songbirds do end up singing songs that match those of adults to which they are exposed. But as Volman and Khanna (1995) point out, interactions with peers as well as with adults may play a role in song learning in the field. Young starlings, for example, initially have more contact with age mates than with adults, because they join juvenile flocks about a week after fledging (Feare, 1984). Interactions between young birds during this period might well have implications for subsequent vocal development.

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