

## Song perception in the song sparrow: birds classify by song type but not by singer

MICHAEL D. BEECHER, S. ELIZABETH CAMPBELL & JOHN M. BURT  
*Animal Behavior Program, NI-25, University of Washington, Seattle, WA 98195, U.S.A.*

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**Abstract.** Recent theories have identified song repertoires and song sharing among neighbours as potential obstacles to individual recognition. These obstacles can be at least partially overcome if the differing song types of an individual have common 'voice' or 'signature' traits, for these would allow a listener to discriminate between different singers' renditions of the same song type and generalize between the different song types of the same singer. Two perceptual experiments were carried out in the laboratory using operant conditioning methods, to compare the relative effects of song sharing and vocal signature traits on song discrimination. Song sparrows were first trained to classify the songs of several singers and then tested on unfamiliar song types of the same singers and unfamiliar shared songs of neighbours of the singers. Subjects failed to generalize from the familiar to unfamiliar song types of a singer, suggesting that 'voice' traits in song sparrows are non-existent or trivial at best. Subjects did, on the other hand, confuse the shared song types of different singers. These findings suggest that learning to discriminate between the shared song types of neighbours in the field may be no simple task, and that the songs of newcomers might be confused with those of residents, at least for a time.

Several recent theories suggest that birds may confuse the songs of new neighbours with those of old neighbours (Payne 1981, 1982; Craig & Jenkins 1982; Falls 1982). These theories propose two potential causes of such identity confusions. (1) Song sharing: in many songbird species, neighbours have similar song types. In some cases, there is evidence that this sharing is a result of the younger birds having learned these types from their older neighbours (e.g. Beecher et al. 1994). (2) Song repertoires: in most songbird species, an individual sings several (sometimes many) different song types. The differences between song types in an individual's repertoire generally appear to be about as large as are the differences between the different song types of different singers. Several reasons have been offered as to why song repertoires should interfere with individual recognition (Kroodsma 1976; Krebs & Kroodsma 1980; Falls 1982). We mention here only the least debatable of these, that it should take longer to learn all the song types of an individual if he has many types. Although neighbour confusion might seem unlikely given the several playback experiments showing that birds discriminate between the songs of different neighbours, all these studies

have been of long-term neighbours (Falls & Brooks 1975; McGregor & Avery 1986; Brindley 1991; Godard 1991; Stoddard et al. 1991). The various theories above, on the other hand, refer to the recognition of new neighbours. Finally, two comparative studies have shown poorer neighbour-stranger discrimination in species with larger song repertoires (Falls & d'Agincourt 1981; Searcy et al. 1981).

All of these theories make an assumption of equivalence between the bird's perception of the songs and the investigator's classification of the songs. While it is likely that the human classification of bird songs is at least partly correct, the perceptual equivalence assumption could be misleading. In particular, if a bird's song types contain 'signature' characteristics or 'voice' quality (Beecher 1989), then (1) the different song types of an individual might be readily perceived as sung by the same individual and (2) two singers' versions of a shared song type might be readily perceived as sung by two different individuals. Weary et al. (1990) argue that in the great tit, *Parus major*, individual singers have a 'voice' quality common to all the song types in their repertoire. Their conclusion is based on an analysis of sonagrams, and thus it remains to be shown

that birds actually perceive and use this information in discriminating among individuals.

The present experiment was designed to address two questions about song perception in song sparrows, *Melospiza melodia*. First, do the songs within an individual's repertoire share vocal signature features which would facilitate individual recognition? Second, are the shared songs of neighbours as similar perceptually to birds as they sound (or appear in spectrograms) to human observers? The experiment was designed to oppose the potential effects of 'voice quality' and song type sharing and so to assess their relative importance. Under normal circumstances, vocal signature traits, if they exist, would facilitate neighbour recognition, whereas song sharing would impede it. To address these questions, we used the laboratory operant-conditioning procedure we developed to study bird perception of songs and calls (Beecher et al. 1989; Beecher & Stoddard 1990; Loesche et al. 1991, 1992). In this procedure the bird is trained to classify songs for food reward. These operant conditioning procedures have been used by a number of investigators in recent years to address questions concerning the perception of bird song and calls (e.g. Dooling 1986; Shy et al. 1986; Brown et al. 1988; Weary 1989, 1990, 1991; Cynx et al. 1990). In our own research on the function and mechanisms of song, we use the operant-conditioning procedure to complement more traditional field approaches for investigating song, such as playback experiments. The central advantage of this laboratory procedure is that it allows us to examine questions concerning song perception in the absence of confounding social factors. The question of whether vocal signature traits facilitate learning a neighbour's songs simply cannot be addressed at all in the field, where the birds will typically have learned all the songs of their neighbours before the experimenter arrives on the scene. In the laboratory, on the other hand, by using songs and singers that the subject has never heard before, we can teach the bird songs of several singers and then observe how he classifies new songs of the same singers.

## METHODS

### Subjects

The subjects were seven song sparrows, six males and one female. Five of the subjects were used in experiment 1 and six in experiment 2. All

birds were captured in the field as adults (all six males sang normal species song). The female (bird GS) was captured with her mate (bird LB). The birds were taken from a site 10 km from the site where we recorded the songs used in this experiment, and so were unfamiliar with these songs when they began the experiment. During the experiment, birds were maintained at approximately 90% of their free-feeding weight in the laboratory, but within the normal weight range we measure in the field.

### Song Stimuli

We used 57 song sparrow songs in experiment 1 and 19 in experiment 2. The songs were originally recorded in the field with a Sennheiser RF condenser microphone MKH-816U and a Sony or Marantz cassette-recorder. Stimuli were bandpass filtered and digitized with 12 bits resolution at 30 ksamples/s into files on computer disk. Stimuli were then re-scaled to equate for loudness, and edited in the time domain to eliminate noise.

### Apparatus

The entire training procedure was executed by computer. An enclosed coaxial full-range speaker located within a sound-attenuating chamber played digitized songs through a 12-bit D/A converter at 30 ksamples/s. A seven-pole elliptic lowpass filter with a 10 kHz corner frequency eliminated signal aliasing. A four-pole Butterworth highpass filter set at a corner frequency of 1.5 kHz reduced environmental noise from the field recordings to eliminate extraneous identification cues. The animal was trained in his home cage within the sound-proof chamber. A panel containing two piezo-electric peck keys (Stoddard 1988) and a solenoid-activated feeder was inserted in the cage door opening. A peck on the green key at the appropriate time began a trial (produced a song), a peck on the red key at the appropriate time delivered millet seed from the feeder.

### Basic Behavioural Procedure

The bird triggered the computer to play a song (initiated a trial) with a peck on the green ('observing') key. When the song (2–3 s in length) was completed, the red ('response') key was illuminated. The bird could then either peck the

**Table I.** Basic design of experiment 1 showing three songs from each of the various classes

Classification of standards and predicted for probes	Standards, a priori classification	Match probes, as predicted by match hypothesis	Voice probes, as predicted by voice hypothesis
GO	1A	7A	1G
	2B	8B	2H
	3C	9C	3I
NOGO	4D	10D	4J
	5E	11E	5K
	6F	12F	6L

Singers are designated by numerals, song types by letters (e.g. song '1A' is type A sung by singer 1). The subject is trained on the standards, six to 10 distinct song types, each from a different singer. The probe songs are introduced in the test phase. By hypothesis, the subject should classify the six probe songs shown in the top half of the table as GOs because his previous training has placed that singer (for voice probes) or that type (for match probes) in the GO class. Similarly, the probe songs in the bottom half of the table should be classified as NOGOs.

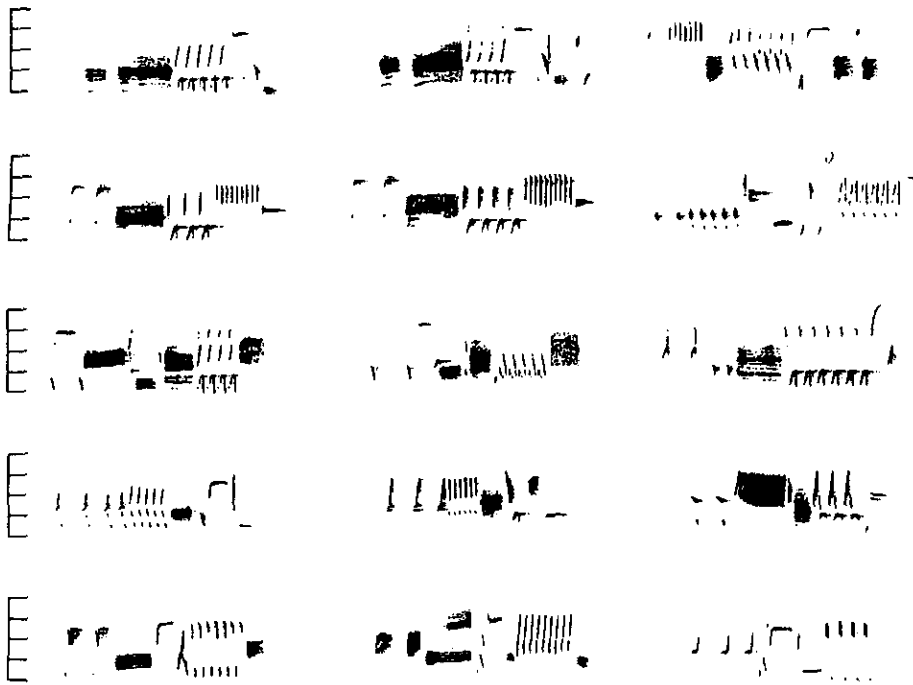
response key (GO response) or not (NOGO response). The stimulus song belonged to one of three classes. If it belonged to the GO class and the bird pecked within 1.5 s of the end of the song (correct response), it was immediately rewarded with seed. The bird could then initiate a new trial with a peck on the observing key. If the presented song belonged to the NOGO set and the bird did not peck (correct response), there was no reward, but the bird was immediately able to initiate a new trial. Errors (a peck following a NOGO song, or failure to peck following a GO song) resulted in a time-out (chamber lights went out for 5–10 s). At the end of the time-out the chamber lights came back on and the bird could initiate a new trial. Finally, if the song was a 'probe' (test) song, responses (pecks or waits) were without effect: they were neither rewarded with food nor punished with a time-out. Probe or test songs get their names from the fact that they were presented at much lower frequency than the GO and NOGO 'standards', and only in later test sessions, after the bird had been trained to discriminate between all of the standard stimulus songs. For all songs, the bird was required to wait through the entire song before responding: a peck during the song produced a time-out.

### Design of Experiment 1

We describe first the general logic of the experiment. The subject was trained to classify six to 10

songs into the two arbitrary classes, GO and NOGO. Each of these songs (the standards) was from a different singer and each was a distinctly different type. Once the bird had learned to classify these songs to a criterion of at least 85% correct, the experiment entered the 'test' phase. During the test phase, an additional 20–24 test or 'probe' songs were introduced. These songs were presented inter-mixed with the standards, but much less frequently (about two times per probe song per session, versus 12–18 presentations of each standard). A probe song was one of two types: (1) a 'voice probe', a different song type from a singer of one of the standards, or (2) a 'match probe', a song type resembling one of the standards but from a different singer. If singers have vocal signature traits common to all their song types, the subject should classify a voice probe in the same class as the singer's standard song. If songs we have classified as similar ('same type') are perceived by the subject as similar, the bird should classify a match probe in the same class as the standard song it matches. The logic of the experiment is summarized in the schema of Table I. To take an illustration from Table I, voice probes 1G, 2H and 3I should, on average, be classified as more GO-like (receive more pecks) than voice probes 4J, 5K and 6L.

The GO–NOGO procedure has a limitation when there are more than two standard songs (i.e. more song exemplars than response classes): if the bird classifies a test stimulus as, say, a GO, this



**Figure 1.** A sample of the songs used in experiment 1. Although different subjects had particular song exemplars as either standards or probes, the figure is set up as if the songs in the centre row are standards. Then the song immediately to the left of a song in the centre row is a match probe (different singer, same or similar song type) and the song immediately to the right is a voice probe (same singer, different song type). The match probes were chosen to span a range of similarity from the close similarity of the top two matches to the general similarity of the bottom two matches. Analysing filter bandwidth 117 Hz.

implies that the subject perceives it as similar to some standard song (or songs) in the GO response class, but the method does not identify which particular song (or songs) it sounds like. To minimize this problem, and at the same time avoid pseudoreplication (Kroodsma 1989), we used 20–24 test songs. Our hypothesis predicts into which of the two classes the bird should place each one of these songs. Because other factors besides voice or type similarity affect how a bird classifies a particular probe song, our dependent variable was an average taken across the 20–24 probe songs.

A sample of the songs used in experiment 1 is shown in Fig. 1. The layout of Fig. 1 is the same as the schema of Table I. Thus if a song in the central row were a standard, the match probe (same or similar song type, different singer) is shown immediately to its left, and the voice probe (same singer, different song type) immediately to its right. Figure 1 also illustrates the range of

matches we selected for our match probes. The top two songs in the left row are clearly the same type, while the bottom two are merely similar; we would regard the middle song as an intermediate match. We emphasize that we were not interested in inventing 'objective' criteria of song similarity; ultimately these criteria will have to be derived from a series of perceptual experiments such as the present one. Instead, our goal was to choose match probes spanning the fairly wide range of similarity we see among neighbours in the field. In fact, only about a third of the match probes would have been suitable for use in our playback experiments on song-type matching (Stoddard et al. 1992a).

Experiment 1 consisted of two sub-experiments. Experiment 1a investigated song confusions as a result of 'voice' (different song-type but same singer), and experiment 1b investigated song confusions as a result of 'matching' (different singer but same or similar song type). Two of the

Table II. Design of experiment 2

Classification of standards and predicted for probes	Standards, a priori classification	Probes, predicted by voice hypothesis	Probes, predicted by match hypothesis
GO	1A	1E	
	1B	1F	
	1C		2C
	1D		2D
NOGO	2G	2L	
	2H	2M	
	2J		1J
	2K		1K

The two singers are designated by numerals 1 and 2, song types by letters (e.g. song '1A' is type A sung by singer 1). The birds are trained on eight distinct types, four from each bird (the standards). The probe songs are introduced in the test phase. By the voice hypothesis, the subject should classify probe songs 1E and 1F as GOs and 2L and 2M as NOGOs because the previous songs he has learned from singer 1 and singer 2 have all been in the GO class and NOGO class, respectively. By the match hypothesis, songs 2C and 2D should be classified as GOs and 1J and 1K as NOGOs because they match song types previously learned as GOs and NOGOs, respectively (the voice hypothesis makes the opposite prediction).

subjects went through experiment 1a first, and three experiment 1b first; we detected no order differences and do not refer to this factor further. In each of experiments 1a and 1b, we used a set of 30 different songs (three songs were common to both sets, so there were 57 songs total). All birds received different permutations of the stimuli (e.g. a song that was a GO standard for one bird was a NOGO standard for a second bird and a probe for a third bird). The only exception to this generalization were birds GS and LB, which received identical regimes throughout. This was done because GS was the single female subject, and we wanted to avoid confounding the sex difference with procedural differences. We detected no systematic difference between GS and the other birds, however, and do not comment on this factor further.

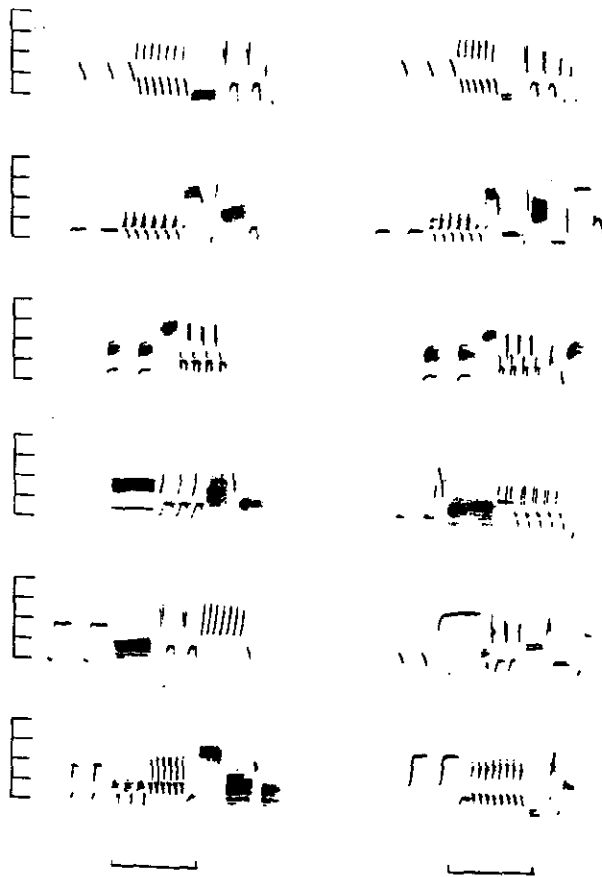
Test sessions began when subjects had reached a criterion of at least 85% correct on the standard songs for 3 consecutive days. In the test sessions, the GO and NOGO standards were presented 12–18 times per song per session, and responses were reinforced (food or time-out) as before. Probe songs were presented about two times per song per session, and responses to them were without effect. About 20–25 test sessions were run, yielding about 40–50 total trials per probe song. For all the data, we compared the first and second halves of the test sessions, and detected no

systematic bias that could be attributed to learning the probe songs; hence we do not comment on this factor further.

### Design of Experiment 2

Experiment 2 addressed the same question as experiment 1, but attempted to place the problem in a fully realistic context, by using song types from the repertoires of two neighbours that shared about half their song types (typical for neighbours in our population, Beecher et al. 1994). It is, in a sense, a 'stimulation' of the problem that would be faced by a neighbour of these two birds. If this hypothetical neighbour had learned some of the songs of these two singers ('familiar' songs), would this learning facilitate his classifying unfamiliar songs of these birds (i.e. a voice effect)? Or, for songs shared by the two singers, would the listener confuse an unfamiliar song of singer 1 with the familiar, similar (matching) type of singer 2 (i.e. a match effect)? Note that in this experiment, the match effect is put in opposition to the voice effect, since a shared song of singer 1 should be classified as another song of singer 1 if the voice effect predominates, and as a song of singer 2 if the match effect predominates.

Table II shows the exact design of this experiment. The two singers (hereafter, 1 and 2) whose songs were used were neighbours in 1987 and



**Figure 2.** A sample of the songs used in experiment 2. Singer 1 on the left, singer 2 on the right. The top three pairs of songs are shared song types (matches). The bottom three song pairs (six song types) are unshared. Analysing filter bandwidth 117 Hz.

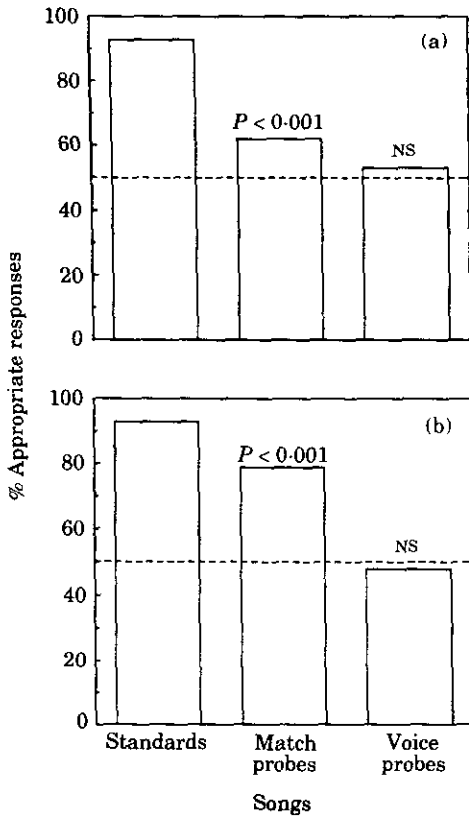
1988. We used nine songs of singer 1 and 10 songs of singer 2. Each of our six subjects was trained on four song types from singer 1 and four song types from singer 2, chosen such that none of these songs matched. When the bird reached the 85% criterion, test sessions began. As in experiment 1, probe songs were introduced such that each was presented about twice in a session versus about 12–18 presentations of the standards. Eight probe songs were used, four from each singer. For each singer, two of the four probe songs were matches to the standards of the other singer, and two of the four were non-matches. Figure 2 shows six songs each from the two singers; the top three are obvious matches, the bottom three are not. Although we used only two singers for our stimulus songs, each of the six subjects received a different selection and arrangement of songs. We

varied (1) which singer was in the GO class, and which in the NOGO class; (2) which songs were standards and which were probes; and (3), to some extent, the actual selection of songs, since for each subject we took only eight each of singer 1's nine types and singer 2's 10 types.

All other aspects of the procedure were as in experiment 1. We used six subjects, four from experiment 1 and two new birds. All were males except subject GS (again matched with LB). We found no differences between subjects that did versus those that did not participate in both experiments.

## RESULTS

The results of the two experiments are presented in parallel form in Fig. 3. The dependent variable



**Figure 3.** Mean percentage appropriate responses for (a) experiment 1 ( $N=5$  birds) and (b) experiment 2 ( $N=6$  birds). Appropriate responses: either pecks or waits, depending on the classification (standards) or the hypothesis (probes). For the standards, pecks were appropriate for GO songs, waits for NOGO songs. For the probes, pecks or waits were appropriate depending on the relation of the probe to its associated standard, for example, a wait was appropriate for a voice probe if the other song(s) of that singer was (were) NOGO standard(s). Chance level as indicated was 50%.

is the percentage of songs classified as per the a priori classification (standards) or as per hypothesis (probes). For example, if the subject pecked on 30% of the trials to voice probe 5K (Table I), this would be 70% 'appropriate' responses, since singer 5's standard song was a NOGO. If the subject pecked on 30% of the trials to match probe 8B (singer 8, Table I), this would be 30% appropriate responses, since the shared type B (of singer 2) was one of the NOGO standards. We averaged this measure across all songs in a probe category

(match or voice) for each subject, and then across all subjects in the experiment ( $N=5$  in experiment 1,  $N=6$  in experiment 2). In experiment 2, to avoid double counting, we classified matching songs in the match category only, although technically they could be classified in the voice category too. We tested the percentage of appropriate responses against the null hypothesis of 50% appropriate.

In experiment 1, match probes were classified appropriately on 62% of the trials (range=58–67%), significantly different from chance ( $t=6.66$ ,  $P<0.001$ ). Voice probes were classified as per hypothesis on 53% of the trials (range=48–59%), not significantly different from chance ( $t=1.46$ ,  $0.10>P>0.15$ ). Parallel results were obtained in experiment 2: match probes were classified as per hypothesis on 79% of the trials (range=67–95%,  $t=6.59$ ,  $P<0.001$ ), voice probes on 48% (range=37–65%), actually below the 50% chance level. The larger match effect in experiment 2 compared with experiment 1 is undoubtedly the result of the fact that all the matches in experiment 2 were close, compared with only about a third of them in experiment 1.

## DISCUSSION

In neither experiment did birds generalize from the one or several song types of a singer they had learned to unfamiliar songs of that singer. The negative evidence is actually stronger in experiment 2 than in experiment 1, despite the fact that in experiment 2 more songs of a singer had been learned (four versus one) when the test songs were introduced. We thus conclude that the different song types of a song sparrow do not have perceptually salient signature characteristics or an individually distinctive voice quality. Although detailed measurements of song sparrow songs might well turn up signature characteristics in the songs, much as has been found in great tits (Weary et al. 1990), it is absolutely necessary to gather evidence from perceptual experiments before concluding that birds actually discriminate between songs on the basis of such signature characteristics (Beecher & Stoddard 1990).

Weary & Krebs (1992) have recently carried out a perceptual study much like ours and report a voice effect in great tits. The generality of the results must be questioned, however, since their

conclusion is based on only two test songs and two standards from each of only two singers, and all subjects received the same permutation of these songs. That is, the voice effect may not extend beyond this one permutation of the songs of these two singers; indeed, with so few songs used, the entire result could be because of the similarity of a single test song to a single standard song of one of the singers.

In general, we would argue that conclusions as to whether the different songs in a repertoire have common voice characteristics requires replication across a number of songs of a number of singers, with these songs arranged in different permutations for different subjects. Otherwise there is the danger of pseudoreplication (Kroodsma 1989). This was our rationale for using 30 songs from 10 singers in experiment 1a and 19 songs from two singers in experiment 2, with each subject receiving a different permutation of the various songs. Moreover, some attempt should be made to scale a potential voice effect against a meaningful standard, as we have done in the comparison with the similar songs of different singers (and especially the shared songs of neighbours): a small voice effect is theoretically trivial if it is swamped by confusions between the similar songs of different singers.

Our finding that the songs in a song sparrow's repertoire lack vocal signature characteristics supports the hypothesis that song repertoires could impede a bird's learning to recognize all the songs of a neighbour (Falls 1982). Again, we repeat our opinion that the several field experiments showing discrimination between song types of neighbours (including ours on song sparrows, Stoddard et al. 1991) limit but do not refute this hypothesis, since all of these studies to date have been carried out on established neighbours that have had some time to learn one another's songs. The hypothesis is limited further by another perceptual experiment of ours (Stoddard et al. 1992b). Using the same GO-NOGO procedure, we trained two song sparrows to classify 64 pairs of songs (all distinct song types). Final performance was better than 90% correct despite the fact that each song type was heard just once or twice in a session at this point. When variations on the training songs were substituted for the originals, performance was virtually unaffected. Moreover, there was no evidence that later songs took longer to learn than earlier songs. Although we believe this study

refutes the notion that song sparrows cannot memorize all the song types of their neighbours, the fact remains that it may well take a song sparrow in the field longer to learn all his neighbour's song types than the comparable task would take an individual of a non-repertoire (or smaller-repertoire) species.

Although we obtained no evidence for a voice effect, we had clear evidence that the similar songs of different birds are confused. In experiment 1 the effect was modest (62% versus a chance level of 50% and 93% correct classification on the standards), and in experiment 2 it was substantial (79%). The difference between the two experiments reflects the wide range in song type similarity in experiment 1 and the close song type matches of experiment 2. We believe that the match effect of experiment 2 provides the better answer to the question posed in the Introduction: are the shared songs of neighbours confused? The degree of song similarity of experiment 2 is precisely the sort that we see in our population and that has led us to ask whether new territory owners might not, at least for a time, get some 'cover' by singing the songs of established neighbours. We have found that young birds learn the songs of several adjacent neighbours and ultimately settle next to or amongst these neighbours. Furthermore, these young birds preferentially learn the songs shared by their tutor-neighbours (Beecher et al. 1994). Thus, for example, a young bird with our singers 1 and 2 of experiment 2 (Fig. 2) as tutors, would learn the shared songs of these two birds (e.g. the top three song types in Fig. 2) rather than the non-shared songs (e.g. the bottom six song types in Fig. 2). One clear advantage of this strategy is that should our hypothetical young bird set up a small 'insertion' territory next to or between these two older birds, then when he sings one of these shared song types, singer 1 could mistake him for singer 2, while singer 2 could mistake him for singer 1. It is possible that the substantial confusion of shared song types, and the lack of vocal signature traits, could lead an established resident to confuse the songs of a new bird with those of other established birds, at least when the songs are heard at a distance, and at least for a period of time. A few weeks might be sufficient to provide the young bird with a significant competitive advantage during a critical period, the initial stages of territory establishment.



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