

THE REACTION OF GREAT TITS (*PARUS MAJOR*) TO PLAYBACK  
OF DEGRADED AND UNDEGRADED SONGS:  
THE EFFECT OF FAMILIARITY WITH  
THE STIMULUS SONG TYPE

PETER K. MCGREGOR, JOHN R. KREBS, AND LAURENE M. RATCLIFFE

*Edward Grey Institute, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom*

ABSTRACT.—We played degraded and undegraded song types to territorial Great Tits. Each bird was tested with degraded and undegraded renditions of a song type in its repertoire and of a song not in its repertoire. The birds responded less strongly to degraded than to undegraded songs, and the difference was significant only if the test song was of the same type as, or similar to, one in the bird's repertoire. These results are consistent with Richards' (1981) hypothesis that degradation cues are used to judge distance and Morton's (1982) idea that degradation may be judged by comparison with a standard consisting of the bird's own rendition of the song. We also found that birds are better able to discriminate between undegraded and degraded song types if their neighbors sing the song. The results are discussed in relation to hypotheses concerning song matching and neighbor-stranger discrimination. Received 1 November 1982, accepted 4 May 1983.

TERRITORIAL songbirds generally respond more strongly to song played near the middle of their territories than to song played at the edge or outside the territory [Great Tit (*Parus major*), Dhondt 1966; Gray Catbird (*Dumetella carolinensis*), Harcus 1973; White-throated Sparrow (*Zonotrichia albicollis*), Falls and Brooks 1975]. The most widely accepted interpretation of this result is that the responding bird hears both close and distant playback and recognizes that one is more distant than the other: the weaker response to a distant song stimulus is presumably because a singing male outside the territory boundary poses less of a threat to the territory holder. If birds distinguish between close and distant songs in this way, the question arises as to how the discrimination is made. Richards (1981) has suggested two possible cues: *amplitude* and *degradation* of the song. More distant songs will tend to be quieter and also more degraded (distorted by reverberations, differential attenuation of high and low frequencies, etc., during transmission through the environment). Richards showed that Carolina Wrens (*Thryothorus ludovicianus*) responded differently to degraded and undegraded songs of the same amplitude played from the same site inside the territory. The test birds' responses to degraded songs were the same as those to singing conspecifics outside the territory (song, but no approach), whereas undegraded songs elicited the same responses as singing conspecifics inside

the territory (silent approach). Richards concluded that territorial Carolina Wrens were using degradation cues to judge the distance between themselves and a singing rival. Degradation may be a more reliable indicator of distance than is amplitude, because amplitude does not change in a predictable way with distance (mainly because of irregular fluctuations due to gusts of wind, etc.; Richards and Wiley 1980), and because amplitude is under the control of the singer.

Morton (1982) extended Richards' hypothesis by suggesting that birds judge degradation of a song by comparing the stimulus with an undegraded "standard" consisting of a song from the responding bird's own repertoire. Krebs et al. (1981), Morton (1982), and Falls et al. (1982) used this idea to suggest that, when territorial neighbors countersing with the same song type (song matching), they exchange accurate information about their distance apart. This would be of advantage to both singers, as established neighbors are not thought to represent a threat to each other.

In this paper we describe an experiment in which we: (a) test whether Richards' result can be repeated with another species and (b) test Morton's hypothesis that the ability to discriminate between degraded and undegraded songs depends on the responding bird having the stimulus song in its repertoire. Our data also allowed us to test whether or not birds are bet-

ter able to distinguish between degraded and undegraded songs if the song is similar to one sung by their neighbors.

#### METHODS

The experiments were done in a roughly linear strip (2 km long) of pasture, hedgerows, and parks in central Oxford from 5 to 22 April 1982, between 0700 and 1030 G.M.T.

The territories of all experimental and most other males in the study area were plotted before the experiment started. Individuals could be recognized either by color rings or by inspecting sonograms of their songs (see Falls et al. 1982). Twenty birds were tested in the experiment, but some were later excluded from the analyses because they failed to respond to one or more treatments. We repeated these missing treatments some days later but decided to exclude the results from the analyses because of marked day-to-day variation in response levels. Twelve birds responded to all four treatments on one day, and a further four birds responded to a "pair" of treatments (see below).

Songs were recorded with a Sennheiser MKH 816T microphone and a Uher 4000 Monitor tape recorder. Each bird was visited several times to record its complete repertoire: both spontaneous songs and responses to a stimulus loop were recorded. Tapes were analyzed on a Princeton Applied Research 4512 FFT analyzer and a Kay 6061B Sonagraph with the narrow band, 80–8000 Hz, and FL-1 settings. We categorized songs into song types on the basis of the overall appearance of sonograms. We used the same criteria as McGregor and Krebs (1982), namely, the number of notes in a repeated unit, the pattern of frequency-amplitude change with time, and the time taken to repeat a unit. The duration, frequency range, and mean frequency of notes and the whole song, as well as presence of small elements that were sometimes missing, were also used, but these measures were given less weight. In addition to this classification, we found it necessary to quantify the similarity of songs *within* a song type for one analysis. We used an index of similarity developed by Falls et al. (1982)—index *I*. We also grouped different song types into classes of similar song types for another analysis. This grouping was based on the overall appearance of sonograms and the criteria listed above. The details of this method are explained in full in Results.

Each bird was tested with two songs chosen from the repertoires of males more than 500 m and less than 6 km away; these distances were chosen to make it unlikely that the test bird had heard the particular version of the song type before, while ensuring that all songs came from the same area. One song was chosen because it could be classified as the same song type as a song in the test bird's repertoire—the "in repertoire (IR)" song. The other was chosen because it was a different song type from any in the reper-

toire of the test bird—the "not in repertoire (NIR)" song. In the NIR category we tried to avoid using song types that were sung by males within two territories of the test bird; this was not possible in about 20% of cases.

Both IR and NIR songs were played to the test birds in "undegraded" and "degraded" form (Fig. 1). These two stimuli were produced from the same original song. To produce degraded songs we used the Uher and Sennheiser to re-record the stimulus song played on a Nagra III tape recorder through a Nagra DSM speaker-amplifier from a distance of 120 m. The song was broadcast through a habitat of hawthorn scrub and open areas. The speaker-amplifier was placed 3 m and the microphone 4 m off the ground. Undegraded songs were made by re-recording the same songs with the speaker and microphone 5 m apart and 4 m off the ground. Care was taken to record the same signal strength when making undegraded and degraded versions of the same song by using the peak-level meters of the recorders. All undegraded-degraded song-stimulus pairs differed by less than 1 dB (A) [except for one pair where the difference was 1.5 dB (A)] when measured under identical conditions with a Bruel and Kjaer 2219 sound-level meter (slow response). The songs were filtered using a Kemo variable active high-pass filter set at 2 kHz during copying onto 10-s continuous tape loops (Cousino-Audiovondor). Therefore, the stimulus loops used in the experiments were third generation copies. Figure 1 shows three examples of degraded and undegraded versions of stimulus songs. Note that our procedure for preparing loops reduces the background noise (by filtering) and therefore makes it less likely that this is a potential cue for birds to distinguish degraded and undegraded songs.

During the experiment, the loops were played on a Nagra III tape recorder through a Nagra DSM speaker-amplifier placed 2 m off the ground in a tree or bush and camouflaged with a brown cloth. The speaker was positioned about 25 m inside a known territory boundary facing into the territory. Observers were stationed 20 m from the speaker. To standardize the volume of playback, the same output settings were used on the tape recorder and amplifier for all tapes. The average sound pressure level at 1 m from the speaker was 94 dB (A), and the average difference between loops was about 1 dB (A) [maximum 1.5 dB (A)].

The experiment was designed as a  $2 \times 2$  factorial with birds as blocks, the column treatments as undegraded and degraded songs, and the rows as IR and NIR songs. Each bird received the four treatments during one morning. Two birds were tested each morning. A treatment consisted of a 5-min preplayback period during which the bird was silent and more than 20 m from the speaker (if the bird sang or approached, we extended the period until 5 min without song or approach had elapsed), 2 min of playback (in the pattern 4-s song, 6-s silence), and

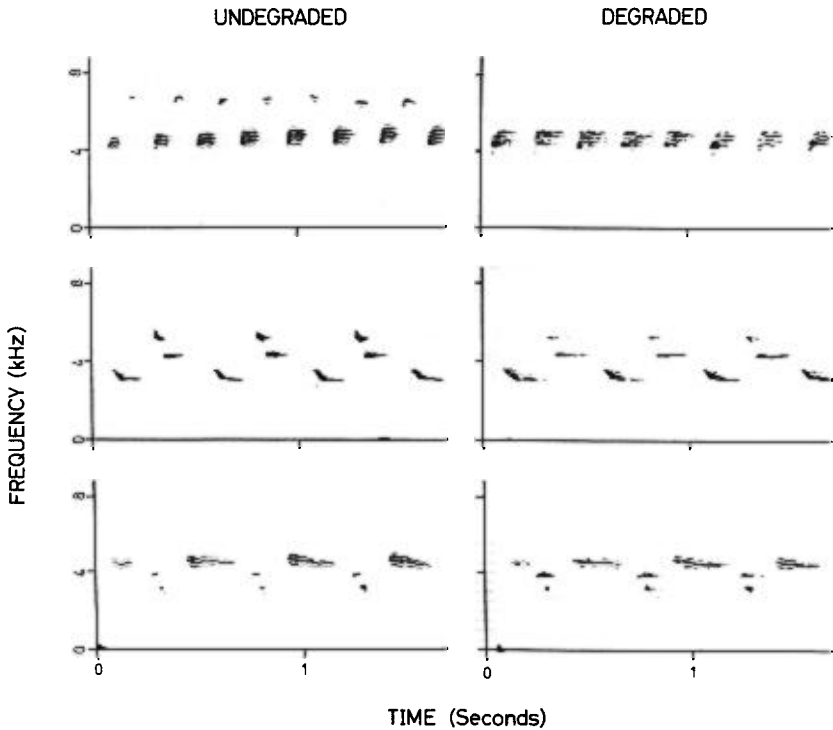


Fig. 1. Sonograms of undegraded and degraded forms of three of the song types used in the experiment.

5-min postplayback observation. There was 1 h between successive treatments on the same bird. The order of treatments was determined by a Latin square, subject to the constraints that the two birds tested on the same day had more than a 500-m separation between their nearest boundaries and that neighboring birds were not tested on successive days.

Two observers recorded the following measures of response during each treatment: total time responding (a bird was taken to be responding if it was singing, calling, or within 20 m of the loudspeaker; total time responding = total time that one or more of these criteria were fulfilled), latency (time to first song, call, or approach), closest approach, seconds of song, latency to song, number of song bursts (see Krebs 1976 for definition), latency to closest approach, and seconds within 20 m.

## RESULTS

### DEGRADATION AND RESPONSE STRENGTH

The results of a two-way analysis of variance with blocks (birds) for the 12 individuals that responded to all four treatments on the same day are shown in Table 1. For 4 out of the 8

response measures (4/8) there is a significant effect of degradation (considering both IR and NIR songs), and 3 other measures approach significance. Figure 2 is a representation of the mean response scores for the 12 birds analyzed in Table 1 plus 4 birds that responded to undegraded and degraded songs on the same day but not to the complete sequence. Two of these birds were in the IR category and two were in the NIR category, giving a sample size of 14 for both IR and NIR. We would predict that the stronger response should be given to undegraded song, because this simulates a singing intruder inside the territory. Our prediction seems to be borne out for both NIR and IR songs, i.e. a stronger response to undegraded than to degraded song 8/8 measures with IR songs (2/8,  $P < 0.05$ ); 7/8 measures with NIR songs (5/8,  $P < 0.05$ ).

### INFLUENCE OF HAVING THE TEST SONG IN THE REPERTOIRE

Both the ANOVA (Table 1) and the comparison of mean response scores (Fig. 2) reveal no

TABLE 1. Two-way analysis of variance of response to playback by 12 territorial male Great Tits (df = 1,11).

Measure	Source				<i>P</i> <sup>a</sup>
	Bird	Song not in repertoire (S)	Degradation (D)	S × D	
Total time responding (TTR)	119.58	0.86	14.92	0.03	<0.03
Seconds of song (SECSONG)	113.62	0.21	5.76	0.17	<0.04
Seconds close to speaker (SECCLOSE)	26.01	0.84	4.48	0.0	=0.058
Number of song bursts (BURSTS)	70.32	0.86	6.75	0.18	<0.03
Latency (LAT)	41.81	0.76	4.91	0.67	<0.05
Latency to song (LATSONG)	42.87	1.30	3.80	0.32	=0.077
Latency to closest approach (LATMIN)	66.29	0.15	0.05	1.03	>0.5
Closest approach (MINDIST)	22.40	0.55	4.48	2.51	=0.058

<sup>a</sup> *P* value refers to the *F*-ratio in "Degradation" column.

effect of the playback song being in the test bird's repertoire (S × D interaction in Table 1). This appears to be evidence against Morton's hypothesis (1982), but, as we show in the next section, the data can be analyzed in more detail and shown to be more consistent with Morton's hypothesis than appears at first.

#### SIMILARITY TO OWN SONG AND EFFECT OF DEGRADATION

In the analyses in Table 1 and Fig. 2, we considered the songs to be either "not in repertoire" or "in repertoire," but in retrospect we found (a) that some NIR songs were rather similar to songs in the test bird's own repertoire and (b) that there was variation in the similarity of IR songs to the bird's own rendition of the song type. We therefore reanalyzed the data to take into account these two kinds of variation.

*Similarity of NIR songs and the effect of degradation: between-song-type effect.*—During the experiments we formed the impression that some birds replied to playback of NIR songs with a song that sounded quite similar to the playback song (in all cases these songs had been recorded during the pre-experiment recording of repertoires; they were not new songs). The following method was used to assign values to the similarity between the NIR song and the songs in the repertoire of the test bird for each of the 14 birds used in subsequent analyses. Each author independently compared the playback song with each song in the repertoire of the test bird by visual inspection of the sonograms

and scored similarity as 0 (no similarity to any song in the repertoire), 0.5 (some similarity to one or more songs), or 1 (very similar to one or more songs). The final value for each bird was the sum of the authors' scores. The criteria for assigning similarity scores were those used by McGregor and Krebs (1982) (see Methods). In this instance, however, we were using the criteria to combine distinct song types into groups of similar types. The 14 males were then assigned to one of two categories on the basis of their score: NIR song similar to song in repertoire (score > 1.5, *n* = 7) or not similar (score < 1.5, *n* = 7). We compared the difference for each bird between response to undegraded and response to degraded songs for these two groups. The values in Table 2 are the means of these differences. This method of analysis was chosen to control for individual variation in absolute response level.

Table 2 shows that 3/8 measures show a significant effect of degradation when the NIR song type is similar to one in the test bird's repertoire, and one other measure approaches significance. No measures show an effect when the NIR song is dissimilar. Therefore, one possible reason for our failure to find a difference between responses to IR and NIR songs with respect to the effect of degradation (Table 1, Fig. 2) is that some NIR songs, although of different types, were sufficiently similar to one in the test bird's repertoire to allow discrimination of degraded and undegraded songs.

*Similarity of IR songs and the effect of degradation: within-song-type effect.*—We carried out an analogous analysis of IR songs to that described

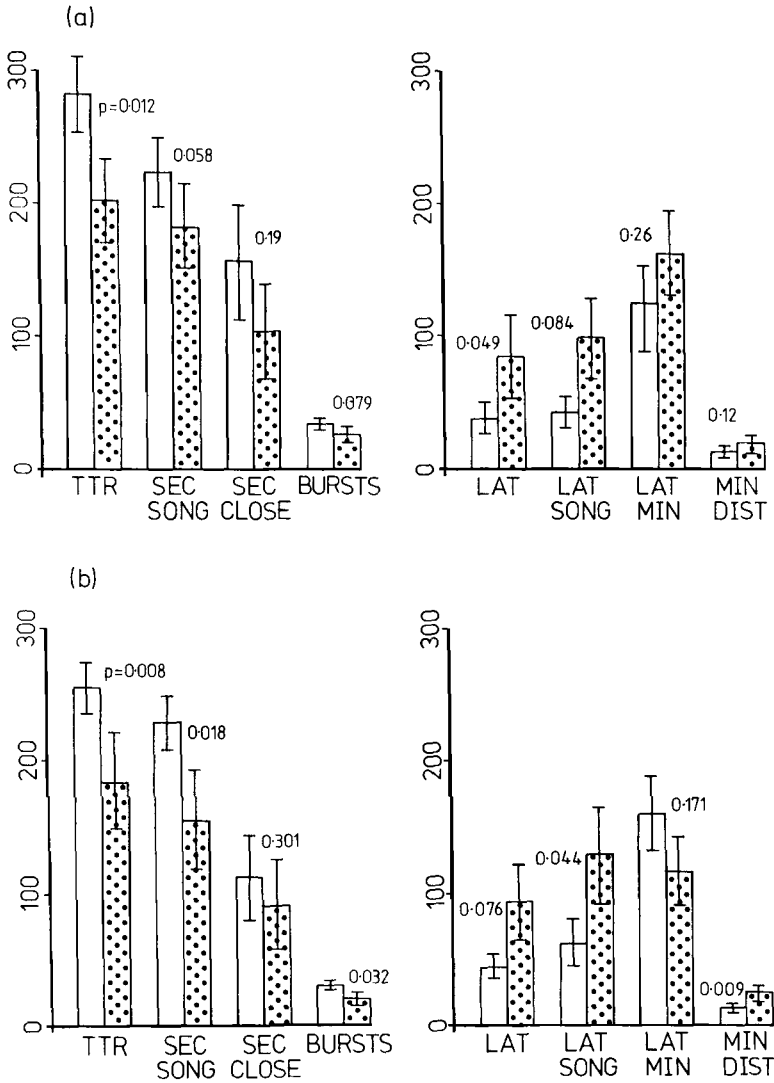


Fig. 2. Response is stronger to playback of undegraded (open histograms) than to degraded (dotted) song for both (a) IR and (b) NIR songs. A strong response means a large value for TTR, SECSONG, SECCLOSE, and BURSTS (left of figure) and a small value for LAT, LATSONG, LATMIN, and MINDIST (right of figure). Values are  $\bar{x} \pm 1$  SE,  $n = 14$  (see text);  $P =$  one-tailed Wilcoxon; all measures are in seconds except BURSTS (number) and MINDIST (meters). See Table 1 for definition of acronyms.

in the last section for NIR songs. Instead of dividing IR songs into "similar" and "dissimilar" by inspection of sonograms, however, we used the difference index  $I$  described by Falls et al. (1982) for comparing similarity within a song type. We then calculated correlations between the value of  $I$  and the difference in response (undegraded-degraded). If similarity to

the bird's own song is important in judging degradation, then we would predict a negative correlation between index  $I$  and difference in response, i.e. the more similar the song, the larger the difference in response to degraded and undegraded song. We found that 7/8 measures were negatively correlated, but none of these correlations was significant. Thus, there

TABLE 2. Differences in response to undegraded versus degraded NIR song when the playback is similar or dissimilar to NIR (see text). Values are  $\bar{x} \pm 1$  SE of (response to undegraded) - (response to degraded). We predict larger values in the left-hand column irrespective of sign ( $P$  = one-tailed Wilcoxon matched-pairs signed-ranks test *within* columns).

Measure	Mean difference in response			
	Playback similar ( $n = 7$ )	$P$	Playback dissimilar ( $n = 7$ )	$P$
TTR (s)	87.9 $\pm$ 36.8	0.043	53.3 $\pm$ 38.0	0.276
SECSONG (s)	78.4 $\pm$ 34.5	0.047	67.7 $\pm$ 44.3	0.276
SECCLOSE (s)	7.4 $\pm$ 22.0	0.341	39.9 $\pm$ 87.7	0.381
BURSTS ( $n$ )	8.6 $\pm$ 4.8	0.062	10.3 $\pm$ 5.9	0.129
LAT (s)	-65.0 $\pm$ 52.2	0.221	-32.9 $\pm$ 34.1	0.276
LATSONG (s)	-40.7 $\pm$ 66.8	0.347	-95.7 $\pm$ 56.3	0.091
LATMIN (s)	10.5 $\pm$ 36.8	0.33	-22.3 $\pm$ 55.1	0.9
MINDIST (m)	-18.0 $\pm$ 5.9	0.042	-5.3 $\pm$ 4.67	0.347

is only a suggestion that the degree of similarity to the bird's own song *within* a song type has an effect on judging degradation of IR songs.

*Combining IR and "similar" NIR songs.*—The results in the previous two sections suggest that exact similarity between the playback song and the bird's own rendition is not necessary for discriminating degraded and undegraded songs but that approximate similarity may be important. We therefore recombined our original data into two groups: songs in repertoire (IR) or songs similar to songs in repertoire (the "similar" NIR songs) and songs dissimilar to anything in the test bird's repertoire (the remaining NIR songs). In Table 3 it is shown that there is a significant difference in response to degraded and undegraded songs in the first category for 3/8 measures and that two other measures approach significance, while there are no significant differences in the second category. We conclude that the test birds can discrimi-

nate only if the playback song is of the same type as, or similar to, one in their repertoire. This is consistent with Morton's hypothesis (1982).

THE EFFECT OF NEIGHBORS' SONGS

As mentioned earlier (see Methods), in some cases the playback songs were of the same type as one produced by the test birds' neighbors (defined as birds less than two territories away). In order to test whether or not familiarity with a song type through experience of a neighbor's rendition influenced the ability to discriminate between degraded and undegraded song stimuli, we compared the difference in response (undegraded minus degraded) between test birds with neighbors possessing the playback song type and those without such neighbors. There is a greater difference in response when neighbors possess the playback song type than when they don't for 6/8 measures (3/8 signif-

TABLE 3. Differences in responses to degraded and undegraded renditions of songs in relation to their "similarity" (IR + similar NIR) to songs in their own repertoire. Values are  $\bar{x} \pm 1$  SE of difference in response (undegraded - degraded);  $P$  = two-tailed Wilcoxon *within* columns.

Measure	Similar ( $n = 21$ )		Dissimilar ( $n = 7$ )	
		$P$		$P$
TTR (s)	82.1 $\pm$ 21.7	0.005	53.3 $\pm$ 38.0	0.270
SECSONG (s)	53.4 $\pm$ 21.0	0.021	67.7 $\pm$ 44.3	0.210
SECCLOSE (s)	31.3 $\pm$ 32.1	0.251	39.9 $\pm$ 87.7	0.730
BURSTS ( $n$ )	7.2 $\pm$ 3.1	0.039	10.3 $\pm$ 5.9	0.132
LAT (s)	-52.6 $\pm$ 28.9	0.062	-32.9 $\pm$ 34.1	0.270
LATSONG (s)	19.4 $\pm$ 28.6	0.290	-95.7 $\pm$ 56.5	0.091
LATMIN (s)	10.5 $\pm$ 36.8	0.713	-22.3 $\pm$ 55.1	0.942
MINDIST (m)	-9.8 $\pm$ 4.7	0.059	-5.3 $\pm$ 4.7	0.354

icant) for IR songs (Table 4). This effect is less clear for NIR songs: 5/8 measures are in the predicted direction, but the only significant effect goes in the wrong direction (MINDIST).

#### THE EFFECT OF NEIGHBORS' AND OWN SONGS

The above results suggest that the similarity of test songs to IR songs and the familiarity of test birds with neighbors' songs both affect the ability to discriminate between degraded and undegraded songs. Some idea of the relative importance of these two factors, having the song in repertoire and neighbors having the song, can be obtained by comparing the difference in response to degraded and undegraded song between NIR songs that are in the neighbors' repertoires (familiarity with neighbors effect) and IR songs that are not in neighbors' repertoires (own song effect). The familiarity with neighbors effect for each measure of response is shown in Table 4, column 1, row 2 ( $n = 4$ ), and the bird's own song effect is shown in Table 4, column 2, row 1 ( $n = 8$ ). When the song is NIR, in neighbors' repertoire, 6/8 measures indicate a greater (but not significant) difference in response than when the song is IR, not in neighbors' repertoire; therefore, there is a hint that familiarity with neighbors' songs plays a greater role in assessing degradation than having the song in the bird's own repertoire. Further work on this is needed, however.

#### DISCUSSION

The main results of our experiment are as follows: (a) Great Tits respond less strongly to degraded than to undegraded songs; (b) the effect of degradation is apparent only when the playback song is of the same type, or of a similar type, to one in the bird's repertoire; and (c) discrimination between degraded and undegraded songs seems to be enhanced when neighbors of the test bird have the playback song type in their repertoires.

*Degradation and distance estimation.*—Our results show that Great Tits respond less strongly to degraded than to undegraded songs. This effect could be the result of two different processes: (a) as proposed by Richards (1981), the bird uses degradation cues to estimate the distance between itself and the stimulus song, and degraded songs are treated as though they are from a distant singer; or (b) the degraded song

TABLE 4. Discrimination of song degradation as a function of whether or not a neighbor has the playback song type. Values are  $\bar{x} \pm 1$  SE of (response to undegraded) - (response to degraded). Predicted result is a larger value in left-hand column irrespective of sign ( $P$  values are one-tailed Mann-Whitney  $U$ -test between right and left columns).

Measure	Neighbors have song <sup>a</sup>	Neighbors do not have song <sup>b</sup>	$P$
TTR (s)			
IR	90.3 $\pm$ 39.8	70.3 $\pm$ 40.2	0.431
NIR	36.0 $\pm$ 60.8	84.4 $\pm$ 28.0	0.111
SECSONG (s)			
IR	24.3 $\pm$ 37.9	53.4 $\pm$ 38.3	0.281
NIR	81.8 $\pm$ 69.5	69.6 $\pm$ 28.8	0.441
SECCLOSE (s)			
IR	121.2 $\pm$ 89.6	3.1 $\pm$ 45.1	0.099
NIR	55.0 $\pm$ 138.9	11.1 $\pm$ 34.9	0.440
BURSTS ( $n$ )			
IR	3.3 $\pm$ 5.8	9.0 $\pm$ 5.8	0.221
NIR	14.0 $\pm$ 8.0	7.8 $\pm$ 4.2	0.221
LAT (s)			
IR	-108.3 $\pm$ 59.9	-2.4 $\pm$ 38.1	0.014
NIR	-8.8 $\pm$ 46.0	-65.0 $\pm$ 38.3	0.221
LATSONG (s)			
IR	-120.0 $\pm$ 58.8	-9.9 $\pm$ 34.2	0.023
NIR	-118.8 $\pm$ 96.1	-48.0 $\pm$ 47.9	0.341
LATMIN (s)			
IR	-149.5 $\pm$ 53.0	43.8 $\pm$ 49.3	0.012
NIR	-61.0 $\pm$ 94.6	85.6 $\pm$ 38.9	0.110
MINDIST (m)			
IR	-10.8 $\pm$ 13.3	-1.9 $\pm$ 5.4	0.078
NIR	-1.0 $\pm$ 5.7	-15.9 $\pm$ 4.6	0.033

<sup>a</sup> IR,  $n = 6$ ; NIR,  $n = 4$ .

<sup>b</sup> IR,  $n = 8$ ; NIR,  $n = 10$ .

is a less effective stimulus, because, as a result of distortion, it lacks some of the species-specific releasing stimuli. Richards (1981) argued in favor of the first process, because, in his study species, the response of territorial males to song from within and outside of the territory differs qualitatively (song within the territory elicits silent approach; song outside produces counter-singing and no approach). The difference he observed in response to degraded and undegraded song was qualitatively different in the direction predicted if degraded song is judged to be from outside the territory boundary. In the Great Tit the difference in response to song from inside versus outside of the territory is probably quantitative rather than qualitative (Falls et al. 1982); therefore, we cannot use

quality of response to discount a lack of species-specific releasers as an explanation of our results. The strongest argument against this process as an explanation is that the similarity between stimulus song type and the bird's own song, and perhaps neighbors' songs, influences the magnitude of the difference in response to degraded and undegraded songs. This seems to rule out the possibility that all degraded songs are ineffective stimuli because they lack some species-specific releasers. An *ad hoc* modification of this idea could be that familiarity influences sensitivity to species-specific properties of the song. This idea seems less parsimonious than taking our results as evidence in favor of Richards' hypothesis that degradation cues are used to estimate distance.

We conclude that our results show that Great Tits can use degradation cues to estimate the distance of a song stimulus, as suggested by Richards (1981) for Carolina Wrens.

*Discrimination and familiarity.*—Our results show that Great Tits apparently do not have to possess a song type in their repertoire to distinguish between degraded and undegraded forms of the song (Table 1 and Fig. 2) but that some similarity to a song in the repertoire is important (Table 3). This is consistent with Morton's idea (1982) that the bird's own songs may be used as a standard against which to judge degradation. Experiments with human subjects have also shown that familiarity with a sound is necessary in order to judge how far away it is (Coleman 1962).

Our results suggest that very precise similarity to the bird's own song is not essential. This argues against the suggestion of Falls et al. (1982) and Morton (1982) that song matching between neighbors that is based on precise similarity is a method of communicating information about distance. The possibility still remains, however, that with a greater range of similarities (including playback of the bird's own song) and a larger sample size, some more subtle effects of similarity may be revealed. Further, we may have inadvertently included some distance cues in unfiltered background noise, or we may have produced an exaggerated degradation effect by our choice of distances for rerecording stimuli; both factors may permit the birds to recognize the degree of degradation with less reliance on similarity to an undegraded standard than would normally be the case.

A bird's response also appears to be influenced by the degree of similarity between the stimulus song and the songs of its neighbors. This result raises some interesting possibilities. First, the bird's own song and neighbors' songs may be used in different ways when judging degradation. The bird's own song will only be heard in an undegraded form and response strength may be gauged by the degree of overlap between its own and perceived song. Furthermore, in using its own song as a standard, a bird would have to compare perception of the songs of other birds with feedback from its own song: this is analogous to the template hypothesis of song learning (Marler 1975), but with the translation occurring in the reverse direction. In contrast, neighbors' songs will be heard at various distances, possibly allowing the bird to learn a relationship between degradation and distance. Second, the possibility of neighbors' renditions of a song acting as a standard against which degradation is judged suggests that birds have learned characteristics of other songs in addition to the songs they sing. Falls et al. (1982) and Falls and D'Agincourt (1982) have suggested the same idea in order to explain the ability of a number of species to distinguish neighbors from strangers. The idea is also consistent with the finding that Swamp Sparrows (*Melospiza georgiana*) appear to learn many more songs than they eventually sing (Marler and Peters 1981).

Although it was not the aim of this experiment to examine procedural aspects of playback experiments, it is worth noting that our results imply that the quality of response to playback may be affected by the distance from which stimulus song was recorded.

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#### ERRATA

There is an error in the caption of Fig. 4 of Ainley (1980. *Auk* 97: 837-853). The words "summer" and "winter" should be switched so that the last phrase of the caption reads "... ; and Guadalupe Island, winter (D) and summer (E)."

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Contrary to the statement in the review of "Capture-recapture and removal methods for sampling closed populations" (1983. *Auk* 100: 793), that volume is not a primer for "Statistical inference from band recovery data—a handbook." Rather, it is a primer for "Statistical inference from capture data on closed animal populations (Otis et al. 1978. *Wildl. Monogr.* No. 62). In addition, the volume reviewed is available to biologists free of charge from David R. Anderson, Utah Cooperative Wildlife Research Unit, Utah State University, UMC 52, Logan, Utah 84322.