

## Sound degradation as a distance cue in great tit (*Parus major*) song

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**Summary.** We report an experiment designed to test the ideas that: 1. male songbirds can use cues from the distortion of song by environmental factors (degradation) to estimate the distance of another singing male; 2. song degradation is assessed by reference to an internal standard. Great tits respond more strongly to undegraded than to degraded songs when both are played at the same amplitude and from the same position in the territory. This difference in response is shown only if the playback song is “familiar” to the test bird; familiar songs being those sung either by the test bird or neighbours of the test bird. We interpret these results as evidence that cues from song degradation can be used to estimate the distance of a singing conspecific and that degradation assessment is only possible if the bird has an internal representation of the song (because either it and/or a neighbour sings the song). We discuss the implications of these results for Morton’s (1982) ranging hypothesis, and for the distinction between learning and performance in bird song. Our results partially support the ranging hypothesis, but question the nature of “unrangeable” songs *sensu* Morton. The finding that birds can assess the degree of degradation of songs that they do not sing, supports the idea that birds learn more songs than they sing.

### Introduction

Birds generally respond more strongly to song playback at the centre of the territory than at the edge (review in Falls 1982). Part of this effect may arise through the ability of birds to discriminate between close and distant songs using cues from sound degradation (distortion by reverberation, irregular amplitude fluctuations and differential attenuation of high and low frequencies during transmission through the environment) (Wiley and Richards 1978, 1982; Richards and Wiley 1980). There is experimental evidence for distance estimation based on song degradation cues for 3 species:

Carolina wrens (*Thryothorus ludovicianus*) approach an undegraded song but they do not approach a degraded song of the same amplitude played from the same position in the territory (Richards 1981); great tits (*Parus major*) and western meadowlarks (*Sturnella neglecta*) respond more strongly to undegraded than to degraded song playback when amplitude and speaker position in the territory are held constant (McGregor et al. 1983 and McGregor and Falls, in press, respectively). Both the qualitative difference in response shown by Carolina wrens and the quantitative difference shown by great tits and western meadowlarks are consistent with the idea that undegraded songs are judged to come from within the territory boundary whereas degraded songs are not.

Morton (1982) has suggested a mechanism of degradation assessment; birds may compare the perceived songs with a remembered undegraded standard. He has further suggested that birds might develop an internal representation only of songs in their own repertoire. If this is true, discrimination between degraded and undegraded versions of a song type will be possible only if the song is in the repertoire. McGregor et al. (1983) reported evidence consistent with this view and in this paper we extend these results by investigating whether great tits can recognize degradation of songs with which they are familiar but which they do not sing (i.e. songs of neighbouring territory holders). If the birds are capable of recognizing degradation of songs not in their repertoire but in the repertoire of neighbours, this would suggest that birds memorise their neighbours’ songs, as has been implied by neighbour-stranger discrimination studies (Falls and D’Agincourt 1982).

### Materials and methods

The experiments were done in a roughly linear strip (2 km long) of pasture, hedgerows and parks in central Oxford from 28th March to 29th April 1983, between 0700 and 1030 hours (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 colour rings or by inspecting sonagrams of their songs (Falls et al. 1982). 36 birds were tested in the experiment. Four birds either failed to respond to one or more treatments, or the treatments had to be abandoned due to adverse weather conditions, these birds were excluded from the results. The data presented below are for 32 birds that responded to all four treatments.

The repertoires of all experimental and most other males in the study area 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 analysed on a Princeton Applied Research 4512 FFT analyser and a Kay 6061B sonograph using the narrow band, 80-8000Hz and FL-1 settings. Songs were categorized into song types on the basis of the overall appearance of sonagrams using the same criteria as McGregor and Krebs (1982).

Each bird was tested with two songs chosen from the repertoires of males > 500 m and < 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, whilst ensuring that all songs came from the same area. One song (the "familiar" song) was chosen because it could be classified as the same song type as a song in the repertoire of the test bird or contiguous neighbours of the test bird. Three categories of familiar songs were used (see Fig. 1 b: (1) song in test bird's repertoire but *not* in the repertoire of any contiguous neighbour ("Own"); (2) song in the repertoire of at least one contiguous neighbour but *not* in the repertoire of the test bird ("Neighbours"); (3) song in the repertoire of both the test bird and at least one contiguous neighbour ("Own + Neighbours"). Each individual was tested with only one of these categories.

The other song was chosen because it was a different song type from any in the repertoire of the test bird and was not in the repertoire of any male within 500 m of the test male – this we termed the "unfamiliar" song. The unfamiliar song was picked to have as few details as possible in common with any song in the repertoire of the test bird (Fig. 1 a).

Both familiar and unfamiliar songs were played to the test birds in "undegraded" and "degraded" form. 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 100 m. The song was broadcast through habitat of hawthorn scrub and open areas in the study area. The speaker-amplifier and microphone were placed 2 m and 2.5 m off the ground, respectively. Undegraded songs were made by re-recording the same songs with the speaker and microphone 5 m apart. Care was taken to record the same signal strength when making undegraded and degraded versions of the same song and during copying onto 10 s continuous tape loops (Cousino Audio-Vendor) by using the peak level meters of the recorders. The songs were filtered using a Kemo variable active high-pass filter set at 2 kHz. Thus the stimulus loops used in the experiments were 3rd generation copies.

We quantified the degree of degradation by comparing the distribution of amplitude peaks of undegraded and degraded songs (following Gish and Morton 1981). The amplitude-time traces were produced by a Cambridge 01033 pen recorder.

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 sited 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 sound pressure levels (SPLs) of all songs were measured with a Bruel and Kjaer 2219 sound level meter (slow response, A weighting) under standard conditions and the output settings on the amplifier were adjusted to give peak and average SPL readings that were as similar as possible for the undegraded and degraded songs comprising each stimulus pair.

The experiment was designed as a  $2 \times 2$  factorial with birds as blocks, the column treatments were undegraded and degraded song and the rows were familiar and unfamiliar songs. Each bird received the four treatments during one morning. Two birds were tested each morning. A treatment consisted of a 5 min pre-playback period during which the bird was silent and > 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 5 min post-playback observation. There was one hour between successive treatments on the same bird. The order of treatments was determined by a Latin square, subject to the constraints that the 2 birds tested on the same day had > 500 m separation between their nearest boundaries and that neighbouring birds were not tested on successive days.

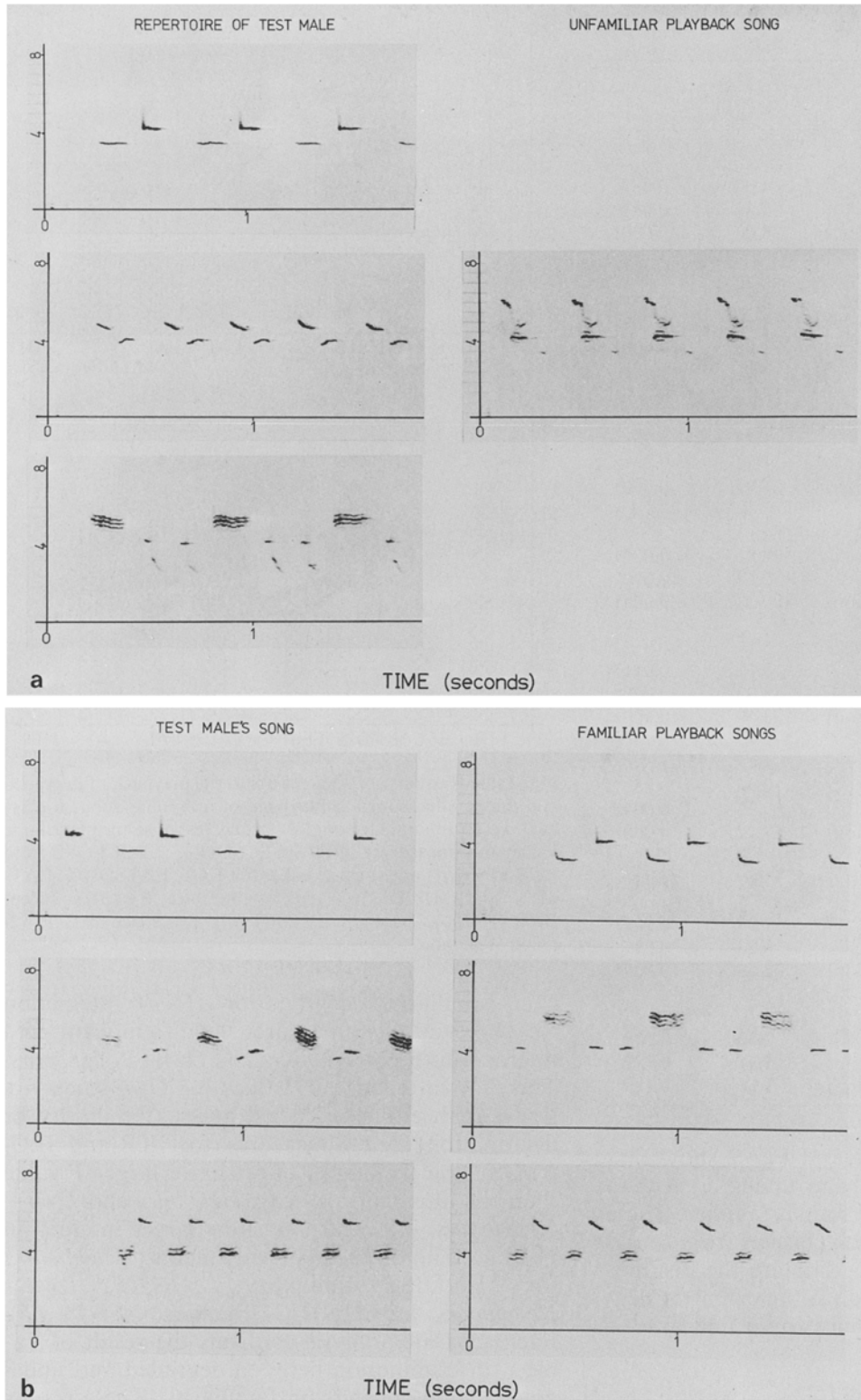
Two observers recorded the following measures of response during each treatment: total time responding (TTR) (a bird was taken to be responding if it was singing, calling or within 20 m of the loudspeaker, TTR = total time that one or more of these criteria were fulfilled); latency (LAT) (= time to first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

## Results

### *Familiarity, degradation and response strength*

Table 1 shows the results of a 2-way analysis of variance with blocks (birds) for the 32 individuals which responded to all four treatments on the same day. For 7 out of the 8 response measures (7/8) there is a significant interaction component (familiarity  $\times$  degradation), and in all these cases the interaction *F* value is bigger than either of the main treatment effects. This result supports the prediction that discrimination between degraded and undegraded songs depends on familiarity.

The mean response scores for degraded and undegraded songs are shown in Fig. 2. We would predict a stronger response to undegraded than degraded song because undegraded song simulates a singing intruding male inside the territory and such a male is likely to be a greater threat than one outside the territory. This prediction is supported for familiar songs. There is a significantly stronger response to undegraded song for all 8 measures of response. The prediction is not supported for unfamiliar songs. 5/8 measures are in the predicted direction but none approach significance; 3/8 measures are in the wrong direction, one of which (SECCLOSE) is significant.



**Fig. 1 a, b.** Sonograms of examples of the categories of playback song used in the experiment. **a** The *left-hand column* shows the 3 song types in the repertoire of the test male, the *right-hand column* shows the song picked to be different from these – the “unfamiliar” song. **b** The *left-hand column* shows the song which was used when choosing the playback song. This is a song from the repertoire of a test male (rows 1 and 3) or the song of a contiguous neighbour (row 2). The *right-hand column* shows “familiar” playback songs. There were 3 categories (see text for definitions): (1) = “Own + Neighbours”; see **a** row 1, column 1 for the song of the neighbour. (2) = “Neighbour”; the song of the *neighbour* of the test male is shown in the *left-hand column*, the repertoire of the test male used in this particular trial is shown in **a**, column 1. (3) “Own”

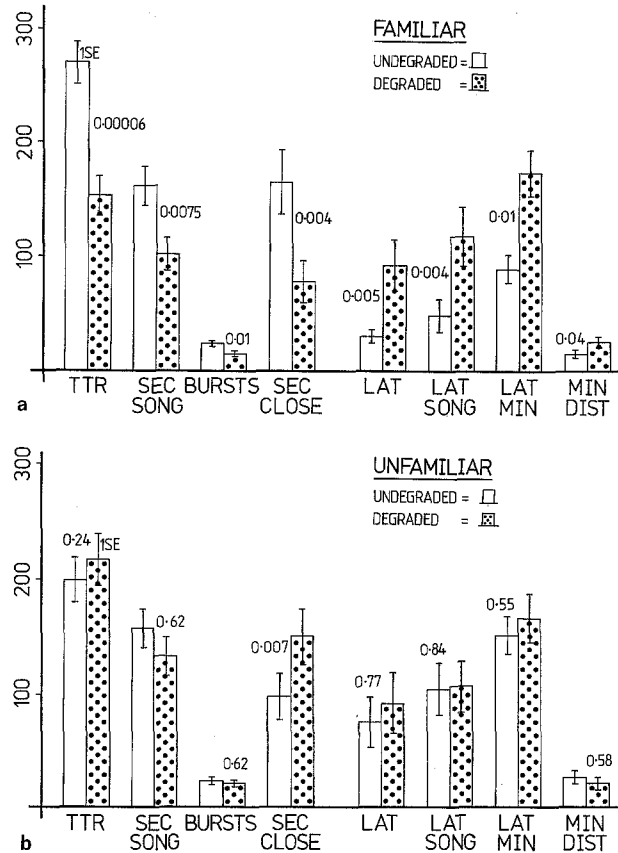
**Table 1.** Two-way analysis of variance of response to playback by 32 territorial male great tits

Source	F-ratio (1,31 <sub>df</sub> )	P
<i>a) Total time responding (TTR)</i>		
Song familiar/unfamiliar	4.67	0.039
Song undegraded/degraded	7.39	0.011
Interaction (familiarity × degradation)	78.08	≪0.0001
<i>b) Seconds of song (SECSONG)</i>		
Song familiar/unfamiliar	5.15	0.03
Song undegraded/degraded	3.01	0.093
Interaction (familiarity × degradation)	71.06	≪0.0001
<i>c) Seconds close to speaker (SECCLOSE)</i>		
Song familiar/unfamiliar	1.29	0.26
Song undegraded/degraded	1.24	0.28
Interaction (familiarity × degradation)	21.92	≪0.0001
<i>d) Number of song bursts (BURSTS)</i>		
Song familiar/unfamiliar	24.81	<0.0001
Song undegraded/degraded	32.47	<0.0001
Interaction (familiarity × degradation)	120.28	≪0.0001
<i>e) Latency (LAT)</i>		
Song familiar/unfamiliar	2.67	0.0113
Song undegraded/degraded	13.92	0.0008
Interaction (familiarity × degradation)	123.59	≪0.0001
<i>f) Latency to song (LATSONG)</i>		
Song familiar/unfamiliar	0.05	0.83
Song undegraded/degraded	9.32	0.0046
Interaction (familiarity × degradation)	67.22	≪0.0001
<i>g) Latency to closest approach (LATMIN)</i>		
Song familiar/unfamiliar	12.98	0.0011
Song undegraded/degraded	0.23	0.64
Interaction (familiarity × degradation)	52.59	<0.0001
<i>h) Closest approach (MINDIST)</i>		
Song familiar/unfamiliar	2.30	0.139
Song undegraded/degraded	1.91	0.177
Interaction (familiarity × degradation)	1.86	0.182

Taken together, Table 1 and Fig. 2 show that birds respond more strongly to undegraded than to degraded song only if the song is familiar. These results support the ideas that: (1) cues from sound degradation can be used to estimate the distance of a singing conspecific, and (2) the extent of degradation is judged by reference to an undegraded standard.

#### *Own versus neighbours' songs*

Three sorts of songs made up the familiar category: (1) *Own*, (2) *Neighbours*, (3) *Own + Neighbours* (see Methods for definitions). Table 2 shows the results of 2-way analyses of variance for each category of familiar song. 7/8 measures show a signifi-



**Fig. 2a, b.** Response of 32 great tits to the playback of degraded and undegraded songs. **a** Playback of a familiar song; **b** playback of an unfamiliar song. A strong response means a large value for measures: TTR, SECSONG, SECCLOSE and BURSTS (left) and a small value for LAT, LATSONG, LATMIN and MINDIST (right). Values are  $\bar{x} \pm 1SE$ s except BURSTS (number) and MINDIST (*m*).  $n = 32$  (see text),  $P = 2$ -tailed Wilcoxon

cant familiarity × degradation ( $f \times d$ ) interaction for *Own* and all 8 measures have significant  $f \times d$  interactions for *Neighbours* and *Own + Neighbours*. The  $f \times d$  interaction  $F$  values for *Own* songs are larger than either main treatment (familiarity or degradation) for 6/8 measures (for TTR and SECCLOSE the familiarity effect has a larger  $F$  value than the interaction). For *Neighbours* and *Own + Neighbours*, 7/8 measures show larger interaction  $F$  values than do the main treatments (*Neighbours*: for MINDIST familiarity  $F > f \times d F$ ; *Own + Neighbours*: for MINDIST familiarity  $F > f \times d F$ ). Each separate analysis confirms the result of Table 1, discrimination between degraded and undegraded song depends on familiarity. These results support the idea that either the birds' own songs or the songs of neighbours can be used as referents for estimating degradation.

Table 3 shows the mean response scores for the 3 familiarity categories. A 1-way analysis of variance of the data in Table 4 shows that only 2/8

**Table 2.** Two-way analyses of variance of the response to playback of three categories of familiar songs: (1) in test bird's repertoire but not in neighbours (*Own*),  $n=7$  (2) in repertoire of 1 or more neighbours of the test bird but not in test bird's (*Neighbours*),  $n=13$ ; (3) in repertoires of both test bird and 1 or more neighbours (*Own + Neighbours*),  $n=12$ . *Familiarity* song familiar/unfamiliar; *Degradation* song degraded/undegraded;  $F \times D$  familiarity  $\times$  degradation interaction. Values are  $F$ -ratios

Source	Familiarity category		
	<i>Own</i> (1,6 <sub>df</sub> )	<i>Neighbours</i> (1,12 <sub>df</sub> )	<i>Own + Neighbours</i> (1,11 <sub>df</sub> )
<i>TTR</i>			
Familiarity	20.43**	2.02	0.0
Degradation	0.59	3.16	13.46**
$F \times D$	8.08*	56.83****	24.57***
<i>SECSONG</i>			
Familiarity	1.53	0.08	7.55**
Degradation	0.04	2.29	0.02
$F \times D$	72.19****	4.85*	15.31**
<i>SECCLOSE</i>			
Familiarity	1.84	0.16	0.76
Degradation	0.21	5.16*	1.17
$F \times D$	1.75	52.09****	22.69***
<i>BURSTS</i>			
Familiarity	10.53*	10.53*	4.96*
Degradation	12.02*	14.13**	7.21*
$F \times D$	71.09***	38.22****	34.93***
<i>LAT</i>			
Familiarity	0.01	0.52	3.79
Degradation	0.86	5.78*	7.27*
$F \times D$	97.25****	26.75***	64.07****
<i>LATSONG</i>			
Familiarity	1.16	0.20	0.34
Degradation	0.38	6.25*	3.24
$F \times D$	19.05**	23.31***	27.56***
<i>LATMIN</i>			
Familiarity	2.54	5.15*	4.85*
Degradation	0.04	0.11	0.45
$F \times D$	8.72*	18.16**	23.90***
<i>MINDIST</i>			
Familiarity	6.64*	22.10***	17.88**
Degradation	1.31	15.39**	12.30**
$F \times D$	16.85**	20.80***	16.90**

\*  $P \leq 0.05$

\*\*\*  $P \leq 0.001$

\*\*  $P \leq 0.01$

\*\*\*\*  $P \leq 0.0001$

measures (SECSONG, BURSTS) show significant heterogeneity between the three familiarity categories, therefore there is no marked difference between categories in discrimination between degraded and undegraded songs. Another way of assessing the relative role of own and neighbours' songs in facilitating degradation estimation is to

compare the *difference* in response to familiar undegraded and familiar degraded songs for the categories *Own*, *Neighbour* and *Own + Neighbour* (McGregor et al. 1983). Assuming a larger difference in the predicted direction (undegraded > degraded) is an indication of the relative ease of degradation assessment, Table 4 suggests that *Own* songs are the most effective referent (for all 8 measures the largest difference in the predicted direction is for *Own* songs). However, in an earlier experiment, McGregor et al. (1983) found a weak tendency (which was not significant) for greater discrimination when played *Own + Neighbour* compared with *Own*. Therefore there is little evidence for category of familiar song having a marked effect on degradation discrimination.

#### *Response strength to degraded songs*

Morton (1982) has proposed that birds may disrupt the activities (e.g. foraging) of their neighbours by singing songs which neighbours do not sing. He argues that the neighbours will be unable to assess the distance ("range") of the singer (but see preceding section and Discussion) and will have to indulge in more costly activities such as search and flying rather than countersinging.

One way of looking at this idea is to compare the magnitude of response to familiar degraded with that to unfamiliar degraded songs. Morton's idea would predict a stronger response to unfamiliar degraded than to familiar degraded songs because the birds would be less able to range the unfamiliar song (see first section of results) and would have to spend more time and energy approaching and searching for the singer to determine its position in relation to the territory boundary. Table 5 shows that all 8 measures are in the direction predicted by Morton's hypothesis (response to familiar degraded < response to unfamiliar degraded); 2/8 measures (TTR, SECCLOSE) are significant and 2/8 (BURSTS, SECSONG) approach significance. Thus, males spend more time reacting and more time close to the speaker (there is also a tendency to sing more) when played a song which they were unable to range. These activities seem likely to disrupt the time and energy budgets of the responding males in the way Morton suggests. The extent of disruption can be estimated by the strength of response. The level of response to unfamiliar degraded is about the same as to familiar undegraded song (5/8 measures show no significant difference in response strength; for LAT, LATSONG and LATMIN there is a stronger response to undegraded familiar than to degraded unfamiliar (Wilcoxon matched pairs signed

**Table 3.** The responses of 32 birds to *Familiar* and *Unfamiliar* (UNFAM) songs for the 3 familiar categories: *Own*, *Neighbours* and *Own + Neighbours* (see Methods for definitions). Values are  $\bar{x} \pm 1$  SE seconds except BURSTS (*number*) and MINDIST (*m*). *P* value is 2-tailed for Wilcoxon matched-pairs signed-ranks test

Measure	Undegraded	Degraded	<i>P</i>
a) Familiar song is <i>Own</i> category ( <i>n</i> = 7)			
TTR			
<i>Own</i>	308.0 ± 28.1	134.1 ± 29.4	0.018
<i>Unfam</i>	172.3 ± 54.6	235.3 ± 28.2	0.24
SECSONG			
<i>Own</i>	221.1 ± 34.1	91.0 ± 27.3	0.028
<i>Unfam</i>	140.4 ± 41.9	153.9 ± 43.8	0.73
SECCLOSE			
<i>Own</i>	196.7 ± 55.7	33.7 ± 25.7	0.028
<i>Unfam</i>	97.6 ± 53.9	119.0 ± 52.9	0.47
Bursts			
<i>Own</i>	36.0 ± 5.8	12.9 ± 3.1	0.028
<i>Unfam</i>	21.3 ± 6.3	21.1 ± 5.6	0.061
LAT			
<i>Own</i>	25.5 ± 6.4	105.0 ± 35.3	0.018
<i>Unfam</i>	66.7 ± 23.6	61.3 ± 18.3	0.73
LATSONG			
<i>Own</i>	33.4 ± 8.3	150.6 ± 57.2	0.018
<i>Unfam</i>	106.1 ± 54.8	110.6 ± 53.1	0.99
LATMIN			
<i>Own</i>	76.9 ± 14.4	199.3 ± 39.5	0.018
<i>Unfam</i>	133.6 ± 22.1	147.9 ± 35.0	0.99
MINDIST			
<i>Own</i>	10.7 ± 2.8	26.4 ± 6.2	0.028
<i>Unfam</i>	28.6 ± 10.0	22.0 ± 5.8	0.88
b) Familiar song is <i>Neighbours</i> ( <i>Nei</i> ) category ( <i>n</i> = 13)			
TTR			
<i>Nei</i>	224.9 ± 27.9	132.1 ± 25.3	0.023
<i>Unfam</i>	188.1 ± 25.5	203.5 ± 40.8	0.59
SECSONG			
<i>Nei</i>	186.2 ± 26.4	98.8 ± 24.2	0.03
<i>Unfam</i>	159.4 ± 25.4	130.0 ± 29.1	0.31
SECCLOSE			
<i>Nei</i>	68.8 ± 33.7	57.0 ± 24.2	0.86
<i>Unfam</i>	55.5 ± 20.2	141.4 ± 41.5	0.085
BURSTS			
<i>Nei</i>	24.6 ± 3.5	14.5 ± 3.7	0.11
<i>Unfam</i>	23.2 ± 3.7	19.0 ± 4.2	0.45
LAT			
<i>Nei</i>	40.6 ± 13.3	87.9 ± 32.9	0.42
<i>Unfam</i>	97.9 ± 31.9	126.7 ± 46.3	0.99
LATSONG			
<i>Nei</i>	40.8 ± 13.3	96.2 ± 35.3	0.19
<i>Unfam</i>	139.2 ± 43.5	138.5 ± 45.9	0.88
LATMIN			
<i>Nei</i>	65.6 ± 15.8	183.1 ± 30.1	0.008
<i>Unfam</i>	161.8 ± 32.2	203.3 ± 43.6	0.65
MINDIST			
<i>Nei</i>	28.6 ± 6.1	30.6 ± 6.1	0.96
<i>Unfam</i>	36.7 ± 9.0	31.4 ± 10.6	0.58
c) Familiar song is <i>Own + Neighbours</i> ( <i>O + N</i> ) category ( <i>n</i> = 12)			
TTR			
<i>O + N</i>	300.1 ± 34.5	189.3 ± 34.2	0.01
<i>Unfam</i>	226.8 ± 35.0	221.8 ± 36.0	0.27

**Table 3** (continued).

Measure	Undegraded	Degraded	<i>P</i>
SECSONG			
<i>O + N</i>	103.3 ± 19.8	111.3 ± 21.8	0.86
<i>Unfam</i>	165.4 ± 30.1	121.5 ± 24.9	0.27
SECCLOSE			
<i>O + N</i>	253.1 ± 39.0	129.8 ± 32.4	0.023
<i>Unfam</i>	140.4 ± 34.6	178.8 ± 38.0	0.64
BURSTS			
<i>O + N</i>	16.5 ± 3.1	16.3 ± 3.2	0.88
<i>Unfam</i>	23.3 ± 3.9	20.8 ± 4.2	0.48
LAT			
<i>O + N</i>	20.9 ± 4.2	91.1 ± 44.7	0.083
<i>Unfam</i>	55.9 ± 15.7	62.8 ± 19.6	0.88
LATSONG			
<i>O + N</i>	66.8 ± 32.7	124.3 ± 47.7	0.091
<i>Unfam</i>	68.6 ± 17.3	105.1 ± 43.2	0.85
LATMIN			
<i>O + N</i>	122.4 ± 21.0	147.8 ± 38.1	0.48
<i>Unfam</i>	149.8 ± 25.8	133.7 ± 19.9	0.53
MINDIST			
<i>O + N</i>	5.3 ± 1.8	19.2 ± 8.4	0.029
<i>Unfam</i>	12.1 ± 4.5	9.3 ± 3.1	0.52

**Table 4.** The mean differences in scores of response to playback of undegraded and degraded familiar songs (i.e. familiar undegraded-familiar degraded). Familiar songs are divided into three categories *Own*; *Neighbours*; and *Own + Neighbours* (see text). *F*-ratio is for 1-way analysis of variance. Values are  $\bar{x} \pm 1$  SE seconds except BURSTS (= *number*) and MINDIST (= *m*)

Measure	<i>F</i> -ratio (2, 29 <sub>df</sub> )	Familiarity category		
		<i>Own</i> ( <i>n</i> = 7)	<i>Neighbours</i> ( <i>n</i> = 13)	<i>Own + Neighbours</i> ( <i>n</i> = 12)
TTR	1.16	174 ± 14.7	93 ± 39.0	111 ± 31.9
SECSONG*	4.75	130 ± 21.4	87 ± 35.8	-8 ± 23.9
SECCLOSE	3.21	163 ± 30.8	19 ± 38.1	123 ± 41.3
BURSTS*	5.04	23 ± 4.3	10 ± 5.0	0.2 ± 3.4
LAT	0.1	-79 ± 27.7	-53 ± 42.2	-70 ± 41.6
LATSONG	0.5	-117 ± 40.2	-55 ± 42.2	-57 ± 38.0
LATMIN	1.68	-122 ± 34.4	-117 ± 37.8	-24 ± 44.9
MINDIST	3.21	-15 ± 4.8	2 ± 7.8	-13 ± 8.2

\* *P* ≤ 0.025

**Table 5.** The mean response scores to familiar degraded and unfamiliar degraded songs by 32 males. Values are  $\bar{x} \pm 1$  SE s except BURSTS (= *number*) and MINDIST (= *m*). *P* values are 2-tailed, Wilcoxon matched-pairs signed-ranks test

Measure	<i>P</i>	Familiar degraded	Unfamiliar degraded
TTR	0.031	153.97 ± 17.80	217.31 ± 21.75
SECSONG	0.063	101.75 ± 13.74	132.03 ± 17.33
SECCLOSE	0.012	79.22 ± 17.65	130.53 ± 24.49
BURSTS	0.058	14.84 ± 1.98	20.13 ± 2.53
LAT	0.740	92.84 ± 22.13	88.44 ± 20.84
LATSONG	0.320	118.63 ± 25.51	103.47 ± 22.28
LATMIN	≈ 1.0	173.38 ± 20.38	165.06 ± 20.89
MINDIST	0.600	25.41 ± 4.13	21.03 ± 4.84

ranks test)). That is, an unfamiliar song in a degraded form elicits a response more comparable to a song that appears to come from inside the territory. Our results indicate that the extent of disruption is not particularly marked.

The question of whether songs that are sung by neighbours but not by the bird (familiar category (2) above) are unrangeable and therefore likely to cause interference as suggested by Morton is discussed below.

#### *Response strength and the degree of degradation*

We correlated the difference in response strength to undegraded v. degraded familiar songs with a measure of the degree of degradation of degraded songs relative to undegraded songs (Gish and Morton 1981). There was no significant correlation (Spearman rank correlation) between the 8 response measures and the degree of degradation. However, 6/8 correlations were in the predicted direction (i.e. positive correlations for measures such as TTR and negative correlations for LAT etc.). This result indicates that the variation in the degree of degradation between the different stimulus song types was small in relation to the other factors influencing response strength.

#### **Discussion**

The main results of our experiment are as follows: (a) great tits respond less strongly to degraded than to undegraded songs only if the songs are familiar to the birds, that is if they are sung by the birds themselves, or neighbours of the birds; (b) discrimination between degraded and undegraded songs seems to be enhanced when the bird possesses the song; (c) the response to degraded familiar songs is weaker than to degraded unfamiliar songs.

#### *Degradation, familiarity and distance estimation*

Our results confirm those of McGregor et al. (1983) in showing that great tits respond less strongly to degraded than to undegraded song if the song type played is familiar. This difference in response could result from two different processes: (a) 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 (Richards 1981); (b) the degraded song is a less effective stimulus because it lacks some species-specific releasing stimuli as a result of degradation. Richards (1981) and McGregor et al. (1983) argued in favour of the first process for Carolina wrens and great tits respectively. The results of this experiment make

the second explanation even less likely. The difference in response strength only occurs if the song is familiar, for the second explanation to hold we would have to suppose that familiar and unfamiliar songs differ in their propensity to lose species-specific releasers as a result of degradation. Two pieces of evidence allow us to discount this explanation. Firstly, there is no significant difference between familiar and unfamiliar songs in the degree of degradation (using Gish and Morton's (1981) index) of degraded versions relative to undegraded versions ( $P \approx 0.62$ , 2-tailed Mann-Whitney *U*-test). Secondly, the same song was used as a familiar song for one male and as an unfamiliar song for a different male in a number of instances.

The effect of familiarity with the stimulus on the difference in response to degraded and undegraded song is consistent with Morton's (1982) proposed mechanism for degradation assessment (comparison with an undegraded internal standard) and confirms an earlier result with great tits that suggested an effect of familiarity (McGregor et al. 1983). Morton suggested that a song in the repertoire of the test bird could be a possible internal standard against which degradation was judged, our results show that the songs of neighbours can also function in this way. Own song and neighbours' songs may be used in different ways when judging degradation. Own song will only be heard in an undegraded form and response strength may be gauged by the degree of overlap between own and perceived song. However, neighbours' songs will be heard at various distances, possibly allowing the bird to learn a relationship between degradation and distance (McGregor et al. 1983).

The effect of degradation and familiarity on distance estimation seems to be a general phenomenon. In birds, it has been shown in great tits (this paper, McGregor et al. 1983), western meadowlarks (McGregor and Falls, in press) and Carolina wrens (Richards 1981). Richards did not know the repertoires of his experimental birds, but it is likely that the playback song was familiar since it was a common song in the area and song sharing between neighbours is extensive in this species (Richards 1981, Morton 1982). In humans, it is known that two components of sound degradation are important for auditory distance perception: reverberation (von Békésy 1960, Mershon and King 1975) and frequency spectrum changes (Coleman 1968). There is also a suggestion that familiarity with the stimulus affects distance perception (Coleman 1962). An experiment analogous to those done on great tits and meadowlarks has confirmed that

degradation and stimulus familiarity are important in relative auditory distance estimation in humans (McGregor et al. 1984).

#### *Distance estimation and the adaptive value of song sharing*

We found that birds tended to react more strongly to unfamiliar degraded songs than they did to familiar degraded songs (Table 5). This result supports Morton's (1982) idea that songs which cannot be ranged (i.e., their distance estimated) will elicit a stronger response from a listener and may be used to disrupt the time and energy budgets of neighbours. Morton goes on to suggest that birds should learn some "unrangeable" songs when assembling their repertoires. The results of this experiment and those reported by McGregor et al. (1983) show that unrangeable songs would have to be songs that were not sung by either the intended listener or its neighbours. We conclude that it is unlikely that birds can disturb neighbours in the specific way that Morton suggests (singing songs which the neighbours do not sing), since we have shown great tits can range songs which are not in their own repertoire but which are sung by neighbours.

An alternative idea stresses the advantages to be gained by the singer from reducing the strength of response elicited from neighbours by singing songs which can be ranged, rather than the disadvantages to neighbours of unrangeable songs. As Table 5 indicates, a newly settling bird which sings song types familiar to its neighbours would elicit a weaker response than one singing unfamiliar songs. This advantage may result in new birds learning the songs of their neighbours.

#### *Learning and performance*

As McGregor et al. (1983) suggested, the ability of birds to assess degradation of songs they do not themselves sing is evidence for a distinction between learning and performance. Such a distinction is important in current theories of associative learning (Dickinson 1980). The methods we have used might be a useful way of investigating when birds are able to learn songs that they do not sing.

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