How Great Tits Use Song-Note and Whole-Song Features to Categorize their Songs

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Birds produce a wide variety of songs, but we know little about how they perceive this variation and use it to form categories that are important to them (e.g. own species versus different species, neighbors versus strangers, song type A versus song type B, etc.). Birds can categorize songs according to the classifications of song types developed by ornithologists (Shy et al. 1986, Falls et al. 1988), but we do not know how this is done. Weary (1990) examined the features birds use to categorize the separate components of their song and found that Great Tits (*Parus major*) categorize individual song notes primarily on the basis of frequency (relative to amplitude, duration, and the rapid, repetitive modulations in amplitude and frequency). However, Great Tit songs consist of more than a single note. The songs consist of repetitions of an identical phrase, with phrases consisting of groups of different notes (typically 1–3 notes per phrase; McGregor and Krebs 1982). My earlier study did not consider changes that occur over the course of the song.

In this experiment I used an operant procedure to determine how song features are used by Great Tits to categorize their songs. I played birds entire songs composed of repetitions of a single note (i.e. a one-note phrase). I modified these songs by changing either features of the repeated note or features of the whole song. In this way I could assess the importance of song-note features relative to features that must be evaluated over more than one note. The song-note features I varied were frequency and duration. The whole-song features were the number of notes in the song (song duration), and the progressive lengthening of the interval between notes during the song (song drift, see Lambrechts and Dhondt 1986). Weary (1990) found that frequency was the most important feature, and duration the least important, in the categorization of natural song notes. Thus, I used these features as a reference to judge the importance of whole-song features. I used song duration and drift as whole-song features because song duration could only be evaluated over the course of the entire song, and drift changed over the course of the song. Also, Lambrechts and Dhondt (1986) argued that song duration and drift are important indicators of male quality in Great Tits, and thus should be of special importance in this species. The actual values of the song and note features I used were determined on the basis

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of previous experimental work and on a detailed study of variance in a natural population.

Four male Great Tits served as subjects. The birds were captured from the wild several weeks before the experiment and were released after the tests. The experiment was performed after the normal breeding season, between the end of May and the beginning of November, 1987. Using an operant procedure, I trained the birds to discriminate between two songs. I rewarded subjects with food when they responded to one song (GO), but did not when they responded to the other (NO GO). They thus learned to respond selectively to GO. When a test song was played the subject could either respond, or not respond, and thus categorize the sound as "like GO" or "like NO GO." This technique has been used to study the categorization of natural sounds in birds (Shy et al. 1986; Dooling et al. 1987; Weary 1989, 1990).

The test cage for the experiment contained a perch attached to a microswitch (activated when the bird landed on it) and an electronic feeder that provided access to food (*Lucilia sencata* pupae). Two UHER 4000 tape recorders were used to play the training songs and three others were used to play the test songs. All songs were played through a NAGRA DH amplifier/loudspeaker located above the feeder. Amplitude was standardized to 76 dB at the perch. Experimental events were controlled and recorded by an ACORN IV computer.

Each bird was kept in the test cage until all training and test sessions were complete (usually about 6 weeks). Training and test sessions lasted 5–6 h during which time birds generally completed at least 1,000 trials. Birds could start a trial at any point by landing on the perch for 0.75 s. The bird had to remain on the perch for an additional 2 s while a song was played. The bird could then visit the feeder. If the bird visited the feeder following the GO stimulus, the feeder would open, providing the bird with a single pupa. Following any other set of events, the feeder remained closed. Visits to the feeder following the NO GO stimulus resulted in a 10-s "time-out" period during which the cage lights were extinguished.

I divided the experiment into training and test sessions. During the training period the two training songs (the GO and NO GO stimuli) were played in a random sequence with equal probability. Songs were also varied randomly with respect to tape recorder for any given session. Once a bird completed three successive sessions in which at least 80% of the visits to the feeder were in response to the GO stimulus, the reward rate was lowered from 100% to 50%. Once
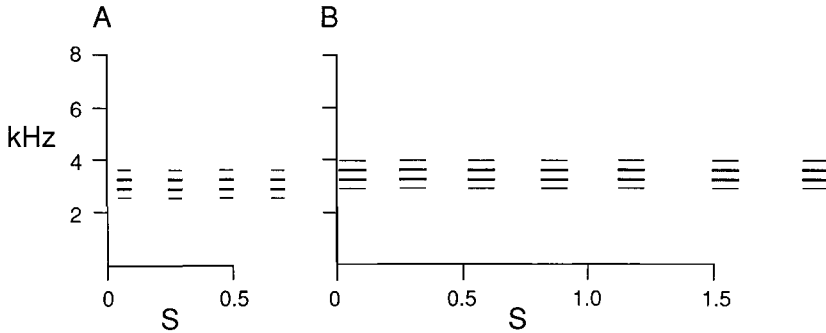
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Fig. 1.   A frequency by time illustration of the two songs used to train subjects in the experiment.

the same criterion was reached for the reduced reward rate, the bird proceeded to the test period where the reward rate remained reduced. Birds could be expected to learn to discriminate against test stimuli because responses to them were unrewarded, although the reduced reward rate for training stimuli slowed this learning. During test sessions the experimental conditions were identical to those in training sessions, with the exception that test stimuli were now played on 20% of the trials (in the other 80% of trials the training stimuli were played). Test songs were played randomly with respect to the training songs. Three tape recorders were used to present 3 different test songs during each session. In this way each test song of the entire sequence of 14 test songs was presented over 5 sessions (during the fifth session only 2 tape recorders were used). To control for differences between tape recorders, each song was played on each tape recorder, requiring a total of 15 test sessions. Test songs presented during each session were assigned in randomized blocks.

Songs were synthesized by computer (see Weary 1990) so that song parameters could be manipulated independently. These synthetic songs were typical of natural ones (and elicited territorial responses during playback trials, unpubl. data). The two training songs differed from one another in all 4 parameters. One training song (A; Fig. 1) was synthesized with four notes at 3.5 kHz and 50 ms in duration with all notes separated by 150 ms intervals (i.e. no drift). The other training song (B; Fig. 1) was synthesized with seven notes at 3.675 kHz and 87.5 ms in duration. The first two notes of this song were also separated by a 150 ms interval, with the interval between successive notes lengthened by 30 ms each (i.e. 180 ms, 210 ms, 240 ms, 270 ms, and 300 ms). For two of the subjects (the first and third), song A was used as the GO stimulus and B as the NO GO, while for the other two, B was the GO stimulus and A the NO GO.

Training songs were manipulated to form test songs. All combinations of the four parameters were synthesized resulting in 14 test songs (two levels in each of four parameters (i.e. 2^4) giving 16 combinations:

two training and 14 test songs), with separate stimulus tapes made from each song using tape loops. Drift in the shorter songs could never equal that in the longer because there were fewer intervals over which the expansion could occur (the longest inter-note interval was 210 ms for the short songs relative to 300 ms for the long songs). The values used for the note parameters reflect those found in natural song notes. The differences in frequency and duration between the training notes were designed so that the two features would be equally perceptible to the birds (see Weary 1990). This required a much larger difference in duration than in frequency, because birds are far more sensitive to small changes in the latter. The mean duration of songs recorded in the wild is 5.4 phrases ± 2.4 (±SD, based on the measurement of 298 song bouts recorded from 44 males; K. J. Norris and D. M. Weary unpubl. data), thus the values used here (4 and 7 phrase songs) were typical. The maximum drift observed in natural songs is a 30% increase of phrase length over the course of the song, while a 38% increase in phrase length occurred over just the first three phases of the songs used here. This high rate of drift was used so that it would be apparent over even the shorter test songs. These differences in song duration and drift were larger than the minimum differences that birds are able to perceive (see Dooling 1982 for data on just noticeable differences in temporal characters). The song stimuli were not designed to determine which features the birds could perceive, but rather which they use to categorize their songs.

I analyzed only responses to test stimuli. Birds could respond by either visiting the feeder (a GO response) or not visiting the feeder (a NO GO response). The stimulus and the bird's response to it were recorded for each trial. The proportion of GO responses was the number of GO responses for each stimulus divided by the total number of responses (GO + NO GOs). Thus, a high proportion of GO responses indicated that the subject categorized the test song as being similar to the GO training song. A low proportion indicated that the song was similar to the NO GO training song. Data were normalized by arcsine square-

root transformation as appropriate for proportional data (Sokal and Rohlf 1969). I analyzed the data with repeated measures analysis of variance (GLM procedure, SAS Version 6: SAS Institute Inc. 1986). The four acoustic features and differences between tape recorders were included as within-subject factors.

The Great Tits relied on note frequency and note duration to categorize the test songs. Song duration and drift, however, were of much less importance (Fig. 2). The most powerful of these effects on response was note frequency ($F = 23.17$; df = 1, 3; $P = 0.017$), although note duration was also very important ($F = 14.45$, df = 1, 3; $P = 0.032$). Neither the effect of song duration nor that of drift were statistically significant ($F = 6.50$; df = 1, 3; $P = 0.084$, and $F = 5.42$; df = 1, 3; $P = 0.102$ respectively). In fact, the subjects did not respond to drift as expected; they actually responded more to songs in which the level of drift was the same as in the NO GO training song. Interactions between the song features were not statistically significant.

The Great Tits could have used any of the four song features to categorize the test songs in this experiment, but they relied instead on the note features of frequency and duration. Thus, for the song categorization performed in this experiment, birds used features that could be evaluated over a single note rather than features that could be evaluated only over the course of several notes. There are at least two functional explanations for the difference in weighting between the song-note and whole-song features. One is that Great Tits may categorize songs very quickly and thus use only information contained in the first few notes. Because subjects were forced to remain on the perch while the song played, they did not benefit from making their decisions early in the song. In the wild, however, there may be advantages in these quick decisions. The fact that birds will occasionally approach a playback speaker before the first song has finished playing (unpubl. data) supports this idea.

A second explanation for the importance of the note features may be that a bird's measure of a parameter improves with the number of repetitions it hears or, in other words, with the feature's redundancy. The note features (which are heard several times in a song) would be measured with a degree of certainty as opposed to a low degree of certainty in those parameters that could be evaluated only over the course of the whole song. The importance of redundancy in communication is well known (e.g. see Cherry 1957).

Evidence from other studies also suggests that whole-song features are relatively unimportant in recognition. Western Meadowlarks (*Sturnella neglecta*) can match playback (i.e. respond with a song of the same type as that being played) using only the first half of the song (Falls et al. 1988). It is thus unlikely that whole-song features are important in categorization in this species as well. Species recognition experiments (reviewed by Becker 1982) show that note
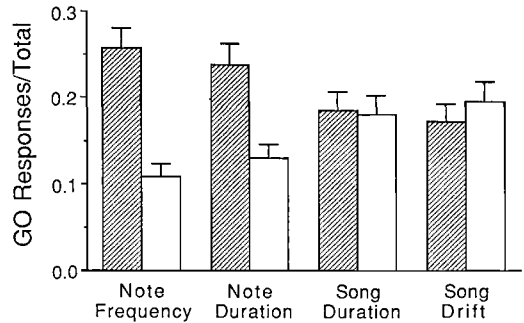

Fig. 2. The subjects' responses to test songs relative to the 4 song parameters. The hatched bars represent responses to test songs in which the value for the song parameter was the same as the GO training song; open bars are for responses in which the parameter was the same as the NO GO song. The response measure is the proportion of GO responses to the test stimuli. The heights of the wide bars represent the mean; the *T*-bars show 1 SE.

features ("element structure") are consistently important in species recognition, while song duration is unimportant in most studies of this type. Recent species-recognition experiments (Nelson 1988) have also shown that note frequency is weighted more highly than other song features. The effect of drift has never been examined, but the more general feature of changes in the intervals between notes has been evaluated and shown to be of little or no importance (see Becker 1982). The acoustic features of notes, and the perception of these features, are likely to be under strong stabilizing selection because of their importance in species recognition. They are thus weighted highly in other recognition tasks (like song categorization). Variation in whole-song features may still convey certain information, such as the motivational state (Weary et al. 1988) or quality (Lambrechts and Dhondt 1986) of the singer.

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Identification of Nest Predators by Photography, Dummy Eggs, and Adhesive Tape

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Predation of the eggs and nestlings of birds (nest predation) is thought to be the prime cause of nest failure in most species (Lack 1954, Nice 1957, Skutch 1966, Ricklefs 1969, Best 1978, Best and Stauffer 1980, Nilsson 1986), but the culprit is rarely recorded. Predation is rarely observed because acts of predation are distributed over a long period of time and occur quickly (Skutch 1966, Best 1974). The vast majority of these observations have been restricted to daylight hours and may also be unreliable because the presence of an observer may discourage or attract certain predators (Bart 1977, Lenington 1979, Westmoreland and Best 1985, Major 1990). Inference of predator identity from the presence of potential predators is neither conclusive nor relevant to the relative importance of different predators. Monitoring predator movements near nests (Moors 1978, Clarke 1988) and recording parental reaction to nearby predators (Clarke 1988, Maher 1988) refine the assessment, but the reliability of the latter may be complicated by similar reactions to nonpredators and by habituation to genuine predators (McNicholl 1973).

Traditionally, ornithologists have relied on signs left at nests to determine the identity of predators. Predation by mustelids (Flack and Lloyd 1978 cited in

Moors 1983) and snakes (Skutch 1966, Best 1978, Best and Stauffer 1980) is said to be "clean," with no signs left at the nest (but for mink, see McNicholl 1982) except sometimes a hole in its center (Best 1978). Damage to the nest and flattening of the nest surroundings is associated with large mammals such as cats and foxes (Best 1978, Best and Stauffer 1980, Westmoreland and Best 1985). Rats and mice are said to leave fragments of shell or nestling in or under the nest (Rowley 1965; Best 1978; Moors 1978, 1983). The literature is unclear on the signs left by predatory birds. Some authors reported that nests remain intact (Gottfried and Thompson 1978, Best and Stauffer 1980); others found nests torn to pieces (e.g. Skutch 1966). This may vary with the type of predator or the type of nest. Maher (1988) suspected that the domed nests of Brown-backed Honeyeaters (Ramsayornis modestus) were torn apart by corvids, whereas Westmoreland and Best (1985) believed that corvids removed eggs from the open nests of Mourning Doves (Zenaida macroura) and left the nest intact. Generalizations regarding signs at nests have been based on relatively few observations, although trials on animals held in captivity have increased sample size (Moors 1978). A further problem is that parents may remove nest materials from failed nests, which gives the appearance of nest damage by a predator (Skutch 1966, Marchant 1973). Parents might also remove their own eggs before nest desertion.

Predator identity is crucial for the management of

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