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Song Features Birds Use to Identify Individuals

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The ability of birds to discriminate between individuals on the basis of song has been widely demonstrated (Falls 1982). Despite its prevalence, little is known about how the birds perform this discrimination. Only two relevant experiments have been performed (Brooks and Falls 1975, Nelson 1989), both of which examined only variation within a single song type. The ability of birds to discriminate between the songs of neighbors and strangers in playback experiments decreases as the repertoire size of the species increases (Falls 1982). This suggests that a repertoire of song types is less recognizable than a single song.

Male Great Tits (*Parus major*) have an average rep-

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ertoire size of approximately three songs (McGregor et al. 1981). Neighbor-stranger discrimination in this species has been demonstrated in a variety of contexts (e.g. Krebs 1971, McGregor and Avery 1986); therefore, their songs must have individually distinctive features that allow discrimination. Three processes could be involved: (1) repertoires might contain song types that are peculiar to an individual, a distinctive combination of song types, or a distinctive sequencing of their delivery; (2) each song type might have individually distinctive variation, as in species with a single song; or (3) all the songs in a repertoire might share a distinctive common quality, as in human voice. We attempted to determine how Great Tit songs were used in individual identification, and which specific acoustic features were involved.

We recorded 44 male Great Tits in Wytham Woods, Oxford, during 1986 (n = 27) and 1987 (n = 27, 10 of which were recorded in 1986). Individuals were color-banded, and each was recorded several times, both during the dawn chorus and later in the day. Great Tit song occurs in bouts (i.e. they sing many repetitions of the same song type before switching to the next). Each song consists of several repetitions of an identical phrase. Each phrase consists of a group of notes (one to three notes per phrase in this population). Recordings were made with Sennheiser MKH 815T microphones and Uher 4000 tape recorders, and analyzed using a Princeton Applied Research 4512 FFT spectrum analyzer. Five variables were extracted from each of the 298 song bouts recorded. These variables were mean *song duration* (number of phrases in a song); *duration of the first phrase* in the song (measured on the screen of the spectrum analyzer using a millimeter scale); *song drift* (duration of the first phrase minus that of the last phrase; see Lambrechts and Dhondt 1986); and *maximum* and *minimum frequency* in the song (mean frequency in kHz of the highest and lowest notes). Mean song duration was measured over all repetitions of a song type recorded in a bout. Other variables were measured from only one song in the bout (where possible the song used was longer than seven phrases). Song types were classified according to McGregor and Krebs (1982).

We found that repertoires often contain song types that were peculiar to an individual. Of the 33 song types produced by this population, 16 were *signature songs* (i.e. unique to an individual). Five other song types were sung by fewer than five individuals in the population, which conferred some distinctiveness. The birds also sang distinctive sets of song types (i.e. the songs composing their repertoire). Within each year of our study, every bird sang a different set, and across years only two males shared a repertoire.

Some song types were very common in the population. We wanted to determine whether individuals in a group in which more than one bird sings the same song or songs tend to sing these in an individually distinctive manner. To perform the most rigorous test of this question, the variance due to features that could obscure differences between individuals was statistically removed. Thus differences between years (recorded in 1986 or 1987), time of day (recorded during the dawn chorus or later), and the song type were removed from the data using a general linear model. Residual variance was then used to test for differences between individuals. All tests reported here were based on residual variance once other factors in the analysis had been accounted for. Individuals produced their song types in distinctive ways in terms of song duration (F = 4.83, df = 43, 217, $P <$ 0.0001), phrase duration (F = 2.81, df = 43, 217, $P <$ 0.0001), drift (F = 2.00, df = 43, 217, $P < 0.001$), maximum frequency (F = 4.51, df = 43, 217, $P < 0.0001$), and minimum frequency (F = 3.94, df = 43, 217, $P <$ 0.0001). By using any one of these variables, at least some of the individuals in this population could be discriminated.

Our analyses also revealed differences between years, periods of the day, and song type. Song duration was greater in 1986 than in 1987 (F = 12.10, df = 1, 296, $P < 0.001$), probably because playback was occasionally used to elicit song in 1986, whereas only spontaneous song was recorded in 1987. The minimum frequency of songs in 1986 was also slightly lower than in 1987 (F = 6.76, df = 1, 296, $P < 0.01$), but there was no significant difference between years in phrase duration (F = 0.14, df = 1, 296, NS), drift (F = 1.61, df = 1, 296, NS), or maximum frequency (F = 0.74, df = 1, 296, NS). The maximum frequency of songs sung at dawn was higher than those sung later in the day (F = 10.86, df = 1, 295, $P < 0.01$). Other song features showed no consistent difference with time of day: song duration (F = 0.00, df = 1, 295, NS), phrase duration (F = 0.05, df = 1, 295, NS), drift (F = 0.00, df = 1, 295, NS), and minimum frequency (F = 1.98, df = 1, 295, NS). Song features differed sharply between the different song types: song duration (F = 2.64, df = 35, 260, $P < 0.0001$), phrase duration (F = 9.06, df = 35, 260, $P < 0.0001$), drift (F = 1.88, df = 35, 260, $P < 0.01$), maximum frequency (F = 17.46, df = 35, 260, $P < 0.0001$), and minimum frequency (F = 15.40, df = 35, 260, $P < 0.0001$). For Great Tits to identify individuals by song, they must also block out the "noise" resulting from factors outlined above. The most important of these factors is the difference between song types.

To determine if listeners that did not recognize song types could still identify individuals on the basis of these song features, we tested whether all the songs in an individual's repertoire share a distinctive quality. We calculated a mean for each of the five song variables across the song types in an individual's repertoire. The variance due to year and time of day effects was removed statistically, and the residual variance was then used to test for differences between individuals. These differences were significant for song duration (F = 1.79, df = 43, 143, $P < 0.02$), drift (F =

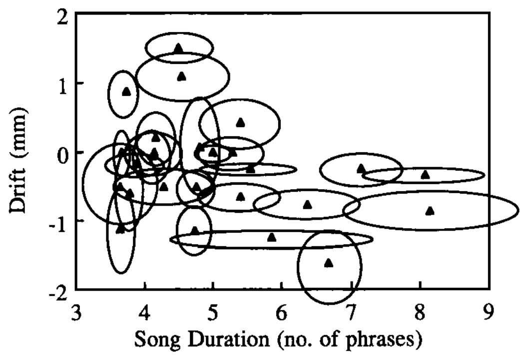

Fig. 1. Each ellipse represents the mean ± SE across the song types in a Great Tit's repertoire. The extent to which the ellipses are separate is thus a measure of the individual distinctiveness of the repertoires. Data are for 1986, but pattern is similar for 1987.

1.67, df = 43, 143, $P < 0.02$), and maximum frequency ($F = 1.59$, df = 43, 143, $P < 0.03$), but not for phrase duration or minimum frequency ($F = 1.03$, df = 43, 143, NS, and $F = 1.20$, df = 43, 143, NS, respectively). These analyses of variance results do not necessarily show that all individuals can be discriminated. The extent to which each bird's repertoire was distinct from every other was tested in terms of song duration and drift, the two most powerful univariate discriminators (Fig. 1). A discriminant analysis based on the three significant song features assigned 69.9% of the songs to the correct individuals in 1986, and 80.4% in 1987. Thus most individuals could be statistically discriminated upon the basis of "voice" quality.

Similar results were found by Falls (unpubl. data) in songs from 19 males recorded in the Oxford University Parks in 1981. He showed that deviations in frequency from the mean of a song type were correlated across the different song types that an individual sang (i.e. individuals sang consistently high or consistently low versions of their song types [$r = 0.56$, $P < 0.01$]). Falls found no relationship with phrase length.

We believe that Great Tits have adequate information within their songs to recognize individuals. This information is in the form of signature songs, distinctive repertoires, distinctive ways of singing each song type within their repertoire, and a common "voice" quality to all song types in their repertoire. Which features birds actually use remains unknown. Discrimination on the basis of signature songs or distinctive repertoires has never been shown, although there is some evidence to suggest that discrimination on the basis of common songs is more difficult (McGregor and Avery 1986). In Great Tits and other species, discrimination can take place on the basis of only a single song (Falls 1982). Perhaps birds are cueing into the distinctive ways individuals sing each song within their repertoire or into the shared features of all the songs an individual sings. In laboratory experiments males can recognize individuals on the basis of songs that they have not previously heard (Weary 1988), which demonstrates that birds can recognize the distinctive qualities of an individual's voice.

Two of our results are of particular importance. First, we demonstrated which acoustic features are suitable for individual recognition. Second, we have shown that all the songs in a bird's repertoire share distinctive qualities. This finding disputes the idea that individual recognition is somehow more difficult in species with repertoires, and is contrary to the notion that repertoires function to obscure individual identity, such as in the Beau Geste hypothesis (Krebs 1977).

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