Habituation and Song Repertoires in the Great Tit

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Summary. This paper is concerned with the idea that the song repertoires of passerine birds are an evolutionary adaptation to reduce habituation in listeners. In an experiment involving 16 territorial males I played either a single song or a repertoire of songs for 15 two-min trials through a single loudspeaker near the edge of the territory. In a second experiment with 10 birds I played the songs through one of two loudspeakers in different parts of the territory, alternating between loudspeakers on successive trials. The birds tended to habituate more rapidly to single song playback than to repertoires. In the second experiment the overall level of habituation was lower and the difference between the two treatments was less marked.

Two features of song repertoire organisation are consistent with the habituation hypothesis (1) the avoidance of low recurrence intervals in switches between song types, and (2) the fact that within repertoire variability is as great or greater than between repertoire variability.

The main problem with the habituation hypothesis is that habituation by listeners does not seem to be adaptive, so it is not clear why they should habituate. I suggest a hypothesis. Intruders may assess the density of birds in an area by listening to songs, so that habituation may be a mechanism by which this density assessment is achieved. Repertoires could be a mechanism by which resident birds cheat, through increasing the apparent density of singing birds.

Introduction

About three quarters of all song birds have song repertoires (Hartshorne, 1973). Each individual male has a variety of forms of the species-specific reproductive song. The average number of song types in a repertoire varies considerably between species, although straightforward interspecific comparison is difficult because of varying complexity of individual song or phrase types (Kroodsma,
1975). Hartshorne (1973) has attempted to classify repertoires into several grades of complexity, ranging from ‘discontinuous singers’ with small repertoires to ‘continuous singers’ with large varied repertoires. Species in the former group usually have between two and twenty song types (e.g. Chaffinch Fringilla coelebs, Western Meadowlark Sturnella neglecta, Song Sparrow Melospiza melodia, Great Tit Parus major). They tend to repeat each song type a number of times—a ‘bout’—before switching to a bout of a new song type, and within a bout usually each song burst is followed by a silence several times the length of the song itself. At the other extreme are species with repertoires of more than 100 song types, which usually do not repeat each song several times in succession, and move rapidly from one song to the next with hardly a pause (e.g. Robin Erithacus rubecula, Blackbird Turdus merula). The Great Tit has a very small repertoire (mean 2.8 songs, usual range 2–7, Gompertz, 1961; pers. obs.) and it is a typical discontinuous singer. The songs consist of a short repeated phrase of about three notes (Fig. 1) and a singing male repeats one song type many times before switching to a bout of another song. A bout of one type usually lasts for 30–300 s, and it is made up of short (3-s) bursts of song interspersed with longer pauses. Sometimes a bird forages during the pauses, but more often it sits on its song perch and looks around. The different song types in a repertoire are used in the same context and at the same time of year. Neighbouring males usually share some song types (Fig. 5) and matched countermasking between neighbours is quite common (Gompertz, 1961; Krebs, in prep.). The seasonal peak of singing in the Great Tit is correlated with the emergence of territorial behaviour, rather than with the

![Fig. 1](image-url)