



Vocal neighbour–mate discrimination in female great tits despite high song similarity

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Discrimination between conspecifics is important in mediating social interactions between several individuals in a network environment. In great tits, *Parus major*, females readily distinguish between the songs of their mate and those of a stranger. The high degree of song sharing among neighbouring males, however, raises the question of whether females are also able to perceive differences between songs shared by their mate and a neighbour. The great tit is a socially monogamous, hole-nesting species with biparental care. Pair bond maintenance and coordination of the pair's reproductive efforts are important, and the female's ability to recognize her mate's song should therefore be adaptive. In a neighbour–mate discrimination playback experiment, we presented 13 incubating great tit females situated inside nestboxes with a song of their mate and the same song type from a neighbour. Each female was tested in two trials with the opposite order of stimulus presentation. Eleven females responded to the song of their mate in both trials, while two females responded to those of their mate in one trial and a neighbour in the other. Thus, great tit females are able to perceive subtle individual differences between their mate's song and a neighbour's rendition of the same song type despite being inside nestboxes, which are known to alter the received song structure and intensity. We suggest that this female discrimination ability inside nest holes is mediated by a high perceptual sensitivity towards small variations in song structure that should be adaptive to this hole-nesting bird species.

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The ability to discriminate between conspecific individuals forms the foundation of many social and reproductive behaviours in a wide variety of taxa (Colgan 1983; Sherman et al. 1997) and is frequently mediated by the use of signals of various modalities (Krebs & Davies 1993; Bradbury & Vehrencamp 1998). This ability is adaptive because it enables animals to direct appropriate responses to specific individuals during social interactions in different contexts (Colgan 1983; Sherman et al. 1997;

Bradbury & Vehrencamp 1998). Recognition based on acoustic signals is important when cues of other modalities are limiting, particularly in long-range communication (Krebs & Davies 1993; Johnstone 1997; Wehner 1997). It is thus especially appropriate when communication occurs in large networks of individuals that exchange social information. In songbirds, vocally mediated discrimination between individuals is well documented, although most studies have focused predominantly on males as potential receivers of conspecific song (Falls 1982; Ratcliffe & Otter 1996; Stoddard 1996). Discrimination between neighbours and strangers, for instance, has been considered to be of primary importance in territory defence, hence emphasizing the advantages of neighbour recognition from the perspective of male territory holders, even in birds where song is multipurpose and serves both territory defence and mating functions (Falls 1982; Lambrechts & Dhondt 1995; Stoddard 1996). For females,

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too, it should be highly adaptive to be able to discriminate males by their song in various contexts when visual cues are absent.

For a breeding pair to reproduce successfully, both members must coordinate their efforts effectively, a task that should be easier if they can recognize one another (Marler & Hamilton 1966; Falls 1982; Lambrechts et al. 1993). In the great tit, *Parus major*, females spend a considerable amount of time inside natural nest holes or nestboxes over the entire breeding season. During the period of incubation, the male often sings quietly outside the nest cavity to call out the female, using the same types of song as in territorial contexts (Hinde 1952; Slagsvold et al. 1994). As soon as the female emerges, both sexes usually produce calls, forage together, or simply follow each other until the female returns to the nest (Kluijver 1950; Hinde 1952). This male calling-out behaviour can be observed at dawn during the fertile period of the female (Hinde 1952; Mace 1986, 1987a, b) as well as throughout the day during incubation (Lind et al. 1996) and may, together with the subsequent joint activities, serve to strengthen the pair bond (Kluijver 1950) in addition to reducing predation risk for the female (Mundinger 1970; Miller 1979; Johnson & Kermott 1991; Slagsvold et al. 1994). Thus, the ability to recognize mates by song in the absence of visual or other cues may be essential in facilitating the coordination of the reproductive behaviour of nesting great tit pairs.

Lind et al. (1996) were the first to conduct a field experiment with female great tits, in which incubating females were presented with playbacks of their mate's song versus those of a stranger. All females responded exclusively to their mate's song by leaving the nestbox, indicating vocal mate recognition. Although belonging to similar song types, most of the song pairs that were presented to each female differed substantially in their fine spectral and temporal composition. Among male great tits on neighbouring territories, however, high rates of song type sharing are common, resulting in song type renditions with similar frequency and temporal patterns (Krebs et al. 1981; McGregor & Krebs 1982; Björklund et al. 1989). Consequently, female great tits are likely to experience a different, and potentially more difficult, recognition problem when vocally discriminating between mates and neighbours than when discriminating between mates and strangers. A recent transmission study with great tit song in the field (Blumenrath et al. 2004) and a study involving artificial sounds re-recorded inside nestboxes in an anechoic chamber (unpublished data) have revealed that the acoustic conditions inside nestboxes, compared to conditions outside, affect the pattern of signal degradation in a complicated and rather unpredictable manner. Hence, sound degradation inside both natural and artificial nest cavities potentially compounds the recognition problem faced by females of discriminating between their mate and territorial neighbours based on the perception of similar shared songs.

In the present study, our goal was to investigate the responsiveness of female great tits to subtle interindividual variation in the spectral and temporal composition of male song. We asked whether incubating females are able to

discriminate between the song of their mate and a very similar rendition of the same song type recorded from a neighbour. Because the experiment was carried out in the middle of the incubation period when female great tits were no longer fertile and would not be expected to receive any benefit from extrapair copulations, we predicted that females would leave the nestbox only in response to the song of their social mate. The same responses to a neighbour's song would reflect the female's inability to discriminate between her mate and a neighbour.

METHODS

We conducted the experiments at Strødam Biological Field Station, Hillerød, Denmark from 10 to 19 May 2001 and 15 to 22 May 2004 between 0900 and 1900 hours. The experimental subjects were 13 paired, female great tits (females 1–13), which were identified by their ring combinations (only in 2001; females 1–9) and the nestbox in which they were breeding (both years; females 10–13). During nest building, we followed great tit pairs to map territories and to record the song repertoire of the respective males as well as their closest neighbours. We also checked the nest-building status and the number of eggs laid for all nestboxes in the area every day. This procedure allowed us to identify the beginning of each female's incubation period, which on average lasts about 2 weeks (Kluijver 1950; Hinde 1952; personal observations). All females were tested in the middle of their incubation period and in only 1 of the 2 years.

Songs were recorded from a distance of 5–10 m during periods of low background noise, with a Sennheiser MKH816T directional microphone and a HNB Portable DAT recorder (PDR 1000). Spectrograms were displayed and analysed on a Kay DSP Sona Graph model 5500 (DC–8000 Hz, 128 points fast Fourier transform, narrow bandwidth and flat input shaping). We chose two representative renditions of the same song type (in the following also referred to as 'song') as playback stimuli for each female: one from her mate and one from a neighbour whose song post locations inside his territory, and thus his singing, were well within the female's hearing range (Langemann et al. 1998; Langemann & Klump 2005). In one case, the neighbour's song was also used as a 'mate' song for the neighbour's female (see Kroodsma 1989, 2001 and McGregor et al. 1992 on reciprocal playback designs). Across the remaining 11 females, however, the chosen song types differed. Visual inspection of the frequency and time domain sound representations displayed in spectrograms assured us that the songs presented to a female were renditions of the same song type as defined by McGregor & Krebs (1982). Because great tit song categories are very broad (Falls et al. 1982; Weary et al. 1990), we used an additional criterion for selecting the song renditions constituting the stimulus pair: we chose the two song type renditions that had the highest possible similarity in the frequency and time domains over each separate note as well as over the entire phrase (a phrase usually consists of two to three notes and is the largest repeated unit in great tit song; see also McGregor & Krebs

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