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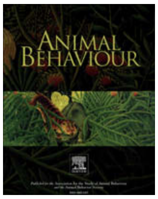

Repertoire size and composition in great tits: a flexibility test using playbacks

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In many bird species, song repertoire characteristics play an important role in intersexual competition and intrasexual attraction. Studies on the importance of having a large repertoire typically assume the available song types as a fixed trait. However, repertoire composition may be flexible. We explored the effects of playbacks on the composition and use of the song type repertoire in great tits, *Parus major*. Playbacks simulate a nearby competitor male, vocally advertising territoriality. We compared the effects of novel song types with two control groups, one in which we played back one of the song types from the repertoire of the focal individual, and one without playback. The repertoire size for individual great tits of actively used song types remained more or less constant, but playbacks led to a significant turnover in repertoire composition over a relatively short period (about a week). The repertoire assessment across three experimental phases led to significantly larger accumulated repertoires compared to the more traditional short-term assessment method. The appearance of new song types was especially prominent among birds treated with a novel song type, suggesting the process is socially mediated. None of the 'new' song types were accurate copies of the novel unfamiliar song types played back. We discuss the potential origin of these 'new' song types and the impact of repertoire plasticity on signal value for sexual selection.

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Many bird species sing a variety of songs making up a repertoire of distinct song types. Vocal repertoires can also comprise a set of different song notes or syllables producing a set of variable songs. Such song repertoires can play an important role in mate attraction and territorial defence (Searcy & Andersson 1986; Collins 2004). Many studies on repertoires have focused on size, although composition and rate of use could also be important. Moreover, repertoire composition may be flexible and being able to make changes in the repertoire throughout life may permit birds to adjust to changing environmental conditions, such as new neighbours or acoustic characteristics of the local habitat (McGregor & Krebs 1989; Nordby et al. 2001; Slabbekoorn & den Boer-Visser 2006; Nicholson et al. 2007).

Individual repertoire composition and its potential for modification will depend on when songs can be memorized in life. In most songbirds learning of song features is largely restricted to one or more sensitive periods for song memorization (Hultsch & Todt 2004). Based on the timing of these sensitive periods, species can be broadly divided into two groups: one for which song learning is age limited (closed-ended learners, e.g. Marler 1970; Jones et al. 1996) and one for which learning can continue throughout life (open-ended learners, e.g. Kiefer et al. 2006; Nicholson et al. 2007). Closed-ended learners have been studied in detail, whereas only a few species have been shown to be open-ended learners. Some examples of open-ended learners are canaries, *Serinus canaria* (Nottebohm & Nottebohm 1978), European starlings, *Sturnus vulgaris* (Eens et al. 1992) and nightingales, *Luscinia megarhynchos* (Todt & Geberzahn 2003). However, anecdotal evidence and field observations suggest that a long-lasting ability to pick up new songs is more common than previously thought (e.g. Laskey 1944; Derrickson 1987; McGregor & Krebs 1989; Kroodsma 2004).

Individual repertoire composition and potential for modification will also depend on from whom birds learn their songs. Songbirds do not copy all that they hear; several studies have shown that there is a predisposition to copy vocalizations from conspecifics (Thorpe 1958; Marler 1976), or even to copy vocalizations from their own subspecies in favour of those of a related subspecies (Nelson 2000a). Furthermore, among conspecifics there is a variety of individuals from whom it is possible to learn. Depending on when the sensitive phases for song learning occur and the kind of interactions, social parents, neighbours in the natal territory, birds encountered during dispersal or neighbours in the breeding territory may serve as tutors (see e.g. Baptista & Petrinovich 1984; Bell et al. 1998; Freeberg 1999; Liu & Kroodsma 2006; Bertin et al. 2007).

Great tits, *Parus major*, are an ideal species for repertoire-related studies, given their moderate but variable repertoire size of clearly

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distinct stereotypically produced song types (Gompertz 1961; McGregor & Krebs 1982; Lambrechts 1996). The repertoire sung by individual males consists of two to six, up to nine, song types, and although males within a locality share song types, there is considerable variation in repertoire composition between males (McGregor et al. 1981; McGregor & Krebs 1982, 1989; Slabbekoorn & Peet 2003). A large song type repertoire in great tits is important in territorial defence as shown by speaker replacement experiments (Krebs et al. 1978), and song type sharing among males is a critical factor for male success during vocal interactions (Krebs et al. 1981; Falls et al. 1982; McGregor et al. 1992). A repertoire can also affect male attractiveness as larger repertoires seem also more effective in triggering great tit females to show copulation solicitation displays (Baker et al. 1986).

The repertoire size of adult great tits appears rather stable across years, but changes in song type composition have been reported (McGregor & Krebs 1989). Some song types may be dropped while others are incorporated into the repertoire, leading to a turnover in repertoire composition. In McGregor & Krebs's (1989) study, new song types added to the repertoire of adult males were similar to those of newly arrived neighbours. This led the authors to suggest that males directly copied these song types from these new neighbours when adult, potentially after having heard them for the very first time. However, an alternative explanation for this learning of song types anew is recalling them from memory. Early in life, young birds could have heard and memorized a wide variety of song types, which may all be sung at some point, but only some of which may be culled from this original repertoire during vocal interactions at a later stage in life. This phenomenon has been labelled 'selective attrition' (Marler & Peters 1982; Marler & Nelson 1993; Nelson 2000b). Song types that have dropped out of a repertoire in this way, or song types that were memorized but were never even sung, might be retained in memory as 'silent song types' and then be (re)activated when triggered by external stimulation (Hough et al. 2000; Geberzahn et al. 2002; Geberzahn & Hultsch 2003).

Our objective in this study was to test the flexibility of the song type repertoire of adult territorial great tits and to test experimentally whether they would copy novel, unfamiliar song types when adult. We explored the effects of playbacks of novel song types on the repertoire composition and use of individual great tits (treatment Novel). The effect of playing back novel song types was compared with the effect of two control sets: one in which we played back a song type from the repertoire of the focal individual (treatment Own), and one without any playbacks (Control). With the novel song type we intended to simulate a new neighbour, and the two controls allowed us to single out the effects of conducting a playback in general and of song type novelty in particular. Our main aim was to confirm the hypothesized ability to modify the song type repertoire in response to new neighbours in an experimental set-up. More insight into flexibility of repertoire size and composition for this model species is likely to affect our understanding of signalling potential in the context of sexual selection in general.

METHODS

Study Site and Species

We conducted the study in the contiguous urban area of Leiden and Oegstgeest (52°10′N, 4°27′E), the Netherlands, between 7 March and 15 June 2006. We selected 27 great tit territories with vocally active birds; only nonimmediate neighbours were included in the analysis. Consistent singing perches were indicated on detailed maps and used as identifiers for revisiting birds on 6–12 consecutive or semiconsecutive days. Male great tits hold territories and sing year-round, but song activity increases significantly during spring, especially at dawn (Mace 1987). They produce song strophes, which usually contain three to six (Slabbekoorn & Ripmeester 2008), but up to 20, repetitions of the same phrase (i.e. song type). Males sing several strophes of the same song type before changing the song type (eventual variation; see Collins 2004). Song types mostly contain two, three or four discrete notes, but may contain more (McGregor & Krebs 1982; Lambrechts 1996) or fewer (Slabbekoorn & den Boer-Visser 2006). A previous study on great tits in Leiden and Leiderdorp, immediately adjacent to the current study area, indicated that these song characteristics are also typical for Leiden and the surroundings (Slabbekoorn & Peet 2003).

Experiment Set-up

We tested subjects in sets of three individuals, and the different sets were tested during partially overlapping periods of time dispersed throughout the breeding season. We assigned each of the three individuals within a set to a different treatment (Novel, Own or Control). Experiments for each individual were carried out in three phases. During phase 1 we recorded at least 15 min of spontaneous singing (not triggered through playback) on 2–5 consecutive or semiconsecutive days. When phase 1 was completed for a set of three individuals, we initiated phase 2 for this set. During phase 2, we treated the first individual to be recorded for at least 15 min with playbacks of a novel song type (Novel), the second with playbacks of one of the song types in his own repertoire, recorded during phase 1 (Own), and the last individual was not treated with playbacks (Control). The songs sung in response to playbacks during phase 2 were recorded (only individuals in treatments Novel and Own). During phase 3, we recorded again at least 15 min of spontaneous songs from each individual on 2–5 consecutive or semiconsecutive days.

Recordings

For recordings we used a Sennheizer ME67/K6 directional microphone connected to a portable Marantz PMD670 solid-state digital recorder. All recordings were made between 1 h before sunrise and 1 h after sunrise. Each day during phases 1 and 3 we visited different territories. If the male in a territory was found singing we recorded him for as long as he continued singing; if not, we waited approximately 15 min before moving to another territory. During phase 1 of each set we focused on individuals recorded on previous days, to complete at least 15 min of recordings for three individuals. During phase 3 we focused on the individuals of the focal set, but we also started recording other individuals for phase 1 of the next set. Successive phases were separated by 0, 1 or 2 days depending on weather conditions.

Playbacks

We conducted playbacks to individuals in treatments Novel and Own between 45 min before sunrise and 45 min after sunrise. Each day, on 3 consecutive days, the same song type loop was broadcast three times in the vicinity of the territory of the focal individual. Each loop lasted 2 min, with a 3 min gap of silence between loops. The first loop started 3 min after the equipment was put in place, and was left running for a total of 12 min per experiment. We broadcast song type loops through a Visaton SC4ND speaker placed on an extendable pole extended into some available vegetation (pole height ranged from 1.5 to 5 m), and connected through a cable 10 m long to a Sony CDX-S2000 CD player. All song type loops used during playbacks were played at a sound pressure level of 90 dB at 1 m from the speaker (measured with a CEL 231 sound level meter). This volume is of a biologically realistic level.

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