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THE MANY MEANINGS OF GREAT TIT SONG

by

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SUMMARY

Studies on Great Tit song investigated song characteristics mainly influenced by song learning. Great Tit song provides information on the origin of birds (e.g. song dialects), and on the habitat type in which the birds live. Experimental studies yielded a series of hypotheses about the functional meaning of song type structure and song repertoires. Detailed studies of individual differences in great tit singing performance, that are summarised here, revealed that variation in great tit song is not only caused by learning ability and learning opportunities, but could also be influenced by constraints in singing ability. These studies showed that great tit song reflects male quality.

Keywords : Song ; *Parus major* ; function ; review.

INTRODUCTION

Since the mid-seventies about 30 papers have been published on various aspects of great tit (*Parus major* L.) song in order to search for answers to the very complicated question why birds in general, and great tits in particular, would spend so much time and energy in singing. In this paper we review how the problem has been studied so far, with particular emphasis on the work carried out in Antwerp, and make some suggestions for future studies.

Male great tits sing a very simple song, which they repeat a great many times. The smallest unit of great tit song is a group of one to more than five different notes that is called a phrase. A phrase is rapidly repeated in a stereotyped way in a short burst of song that is called a strophe. A strophe may consist of one to more than 20 phrases, and lasts normally between one and five seconds. Great tits sing a strophe. Then they pause a few seconds, and start all over again. If they sing for several minutes they will probably change to a different version of the species-specific song (i.e. another song type), etc. (Fig. 1) (McGregor and Krebs, 1982 ; Lambrechts and Dhondt, 1988a).

VARIATION IN SONG TYPES AND REPERTOIRES

The first song studies in the great tit made detailed descriptions of what kind of song types are found in different populations, how song types are distributed within populations, and how many song types individuals sing. Different song types show differences in phrase structure (number of notes per phrase, note length, note frequency,...) that can easily be recognized on sound spectrograms (Fig. 1). Although in a given study population one may hear 30-50 different song types, each individual male only sings between one and six, rarely more different song types. Each individual has a unique song repertoire composition (i.e. the song types that constitute the repertoire). Birds learn most of their song types before their first breeding season. The composition of the repertoire is not random in that birds are more likely to learn (copy) song types from territorial neighbours. Therefore, neighbouring males are more likely to sing the same song type than other birds, and song types may differ between populations. Habitat type has an effect on song type structure, whereby in more open park-like habitats complex song types (i.e. with more notes per phrase) are more common (Eyckerman, 1979 ; Hunter and Krebs, 1979 ; McGregor and Krebs, 1982, 1989). Therefore, song type structure and the repertoire composition gives information about where an individual lives.

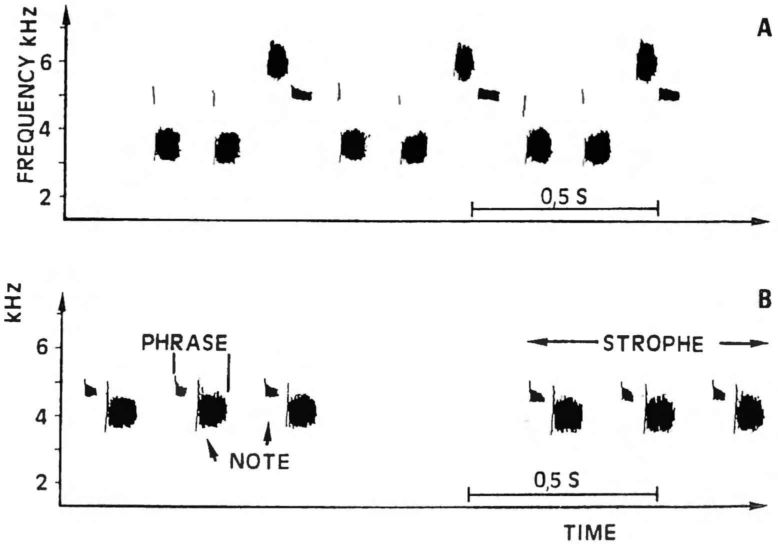

Fig. 1. — Examples of sonagrams (frequency against time diagram) of two songtypes of a Great Tit. Notes make up a phrase. Phrases are repeated in a strophe. Strophes of the same song type are repeated in a bout.

In A a complex four-note songtype is repeated three times.

In B two three-phrase strophes of a two-note songtype are shown, separated by an interstrophe pause. Drift can both occur within a strophe, by increases in interphrase pauses, as between strophes by increases in interstrophe pauses and reduction of strophe length.

Since song is mainly produced during the pre-breeding and breeding season one can reasonably assume it has to do with reproduction (e.g. EYCKERMAN 1979; MACE 1987), i.e. with territorial defence and with mate attraction or stimulation. This hypothesis is supported by a number of experimental studies. Great tits start to sing on their territory when they are presented with playback of the conspecific song (e.g. DHONDT, 1966). In territories with song intrusion is slower than in territories without song (KREBS, 1976a, 1977b). Finally, territorial males that lost their mate sing much more frequently than mated males (KREBS *et al.*, 1981a), and song stimulates sexual behaviour in females (BAKER *et al.*, 1986, 1987).

The detailed descriptive studies of song types and repertoires allowed investigators to ask very specific questions about the functional meaning of variation in great tit song : Why is great tit song simple in comparison with other species ? ; Why do great tits have a song repertoire ? ; Are some song types more effective in territorial defence than other song types ? ... Although in some species song types that are used in mate attraction differ from song types that are used in territorial defence in the great tit there is no evidence that different song types have a different functional meaning (KREBS, 1977a). The simple, stereotyped songs of great tits may facilitate individual recognition which could be important in territorial defence or in female choice. Indeed, male great tits respond differently to familiar song types (i.e. song types of neighbours) than to unfamiliar song types in a playback experiment. Therefore, great tits may use song type structure in neighbour-stranger recognition (FALLS *et al.*, 1982), even if the birds do not sing the song types themselves (MCGREGOR and AVERY, 1986). Also, a female is more likely to mate with a male that sings song types different from that of her father but similar to the song types he sings (MCGREGOR and KREBS, 1984a). BAKER *et al.* (1987) showed experimentally that local song types sexually stimulate females more than distant song types, which suggests that song type structure could be used in mate choice.

REPERTOIRES AND TERRITORY DEFENCE

KREBS *et al.* (1978) showed experimentally that song repertoires are more effective in keeping out intruders than single song types. MCGREGOR *et al.* (1981) found that males with larger song repertoires survive better, have a higher breeding success and a greater lifetime reproductive success. They suggested therefore that males with larger repertoires obtain better territories because they would be more successful in territorial defence. Several hypotheses have been proposed why song repertoires are more successful in male-male competition. According to the anti-habituation hypothesis the signal would lose strength unless the song types used are regularly changed (KREBS, 1976b). The Beau-Geste hypothesis assumes that song repertoires would mislead potential settlers into believing that the woodland is more densely occupied than it really is (KREBS, 1977a). A third hypothesis is that song repertoires allow birds to match song types with different individuals. In territorial conflicts males often match, which is the phenomenon that they select that song type in their repertoire that most closely resembles that of the opponent. Song type matching would improve territorial defence because it would be a mechanism (1) to direct a signal to a singing opponent, (2) to give information about the willingness to attack of the occupier that responds with the same song type (KREBS *et al.*, 1981b), or (3) to give information about the distance between singing birds (MCGREGOR and KREBS, 1984b). Finally females that mate with a male singing many song types could receive a reproductive advantage because song repertoire size reflects male or territory quality. This may explain why larger song repertoires sexually stimulate females more effectively than smaller ones (BAKER *et al.*, 1986).

HOW DO GREAT TITS SING?

The development of song of an individual can be divided into an input phase in which song types that are heard in the population are stored in the brain (memorized), and an output phase in which the song types that were learned are produced using a set of respiratory and syringeal muscles (KROODSMA and MILLER, 1982). Most of the song studies in the great tit (and in other species) were about those song features that are influenced by the phenomenon of song learning, such as the composition of song repertoires and the distribution of song types in populations : thus those features that describe what great tits sing. These studies were very successful in that they showed that song is for territorial defence and for mate attraction or stimulation, and that birds with large song repertoires were better at that.

In Antwerp we have less asked the question 'what do great tits sing' than 'how do they sing it ?'. As explained before great tits repeat in a very stereotyped fashion a particular song type, pause, then sing again. If one carefully listens to a strophe one can hear, in many strophes of many birds, drift. Drift is a slowing down of the rhythm within a strophe, caused by an increase in the pauses between notes and between phrases (LAMBRECHTS and DHONDT, 1987). Because a strophe only lasts a few seconds, it seems unlikely that this drift within a strophe would be the result of a change in motivation to sing, the more so, because a few seconds later the same bird will begin its next strophe again with no drift. If drift is not caused by a change in motivation it could be the result of, for instance, physiological or respiratory problems for the bird. We hypothesized therefore that drift might reflect a male's singing ability. Males able to sing well would show no drift, whereas males not able to sing well would show pronounced drift.

Our hypothesis about the causation of drift was supported by detailed descriptions of drift in different individuals (LAMBRECHTS and DHONDT, 1987). Comparing strophes with the same number of phrases some birds showed much more drift than others. In strophes longer than the bird's average strophe length there was pronounced drift, but in strophes shorter than the bird's average strophe length there was no or little drift. If drift would reflect a shortterm decrease in motivation to sing we expected to find the opposite, i.e. more drift when a bird produces strophes that are shorter than its average strophe length.

As measuring drift is very time consuming, and drift and strophe length are correlated, and as we needed to measure many song bouts from many birds, we used strophe length as a measure of male singing ability, rather than and instead of drift. As with drift we found that strophe length varies considerably between males. It also varied between song types and with season, although all measures of strophe length of a male were intercorrelated. In some males, with a high singing ability, the average strophe length of the repertoire was more than 10 phrases per strophe while in other males the average strophe length was not more than five phrases per strophe (LAMBRECHTS and DHONDT, 1987).

SINGING ABILITY AND FITNESS COMPONENTS

The next logical step was to investigate how far singing ability (defined by drift or by strophe length) reflected male quality, i.e. was related to fitness components. Social dominance in winter influences survival (KIKKAWA, 1980 ; ARCESE and SMITH, 1985 ; DE LAET, 1985). We therefore studied winter dominance and singing ability in the same males and found that dominant birds in winter were better singers in spring. This higher survival of the better singers was particularly clear between the first and the second breeding season, and better singers lived longer (LAMBRECHTS and DHONDT, 1986).

Social dominance, in many species, is related to early settlement, whereby individuals that settle first are more dominant (DHONDT, 1971a ; KREBS, 1982 ; BRAWN and SAMSON, 1983 ; DE LAET, 1985 ; HOGSTAD, 1987 ; NILSSON and SMITH, 1988). TEUNEN (1987) found, after a sudden massive mortality of the resident males in early January, that there was a clear correlation between date of settlement and strophe length : good singers settled significantly more rapidly than poor singers.

The second factor which influences fitness is the number of recruits produced in an individual's lifetime. We found that better singers were not more successful at recruiting offspring in a single breeding season, but did have a higher lifetime reproductive success (more recruits) because they bred in more different seasons.

A male's singing ability, as measured by strophe length and drift, is therefore a reliable measure of male quality (LAMBRECHTS and DHONDT, 1986). Male quality can thus be assessed easily just by listening to a singing bird.

SINGING ABILITY AND TERRITORY QUALITY

As song is used in territorial defence and female attraction, and song reflects male quality, we expected that birds with longer strophes and less drift would be more successful in male-male competition and in female attraction.

At the behavioural level strophe length seems to be important in male-male interactions. Thus when males were confronted with playback of long strophes (LAMBRECHTS and DHONDT, 1987) individuals naturally singing long strophes increased their strophe length in response to playback, while males with very short strophes started to sing even shorter strophes. This suggest that strophe length is used in territorial defence and that long strophes could inhibit territorial (aggressive) behaviour in some males. However, further experiments (cf. KREBS *et al.*, 1978) are needed to examine if longer strophes are more successful in keeping out intruders than shorter strophes.

Another suggestion why strophe length and drift could be important in male-male conflicts follows from the observation that in escalated conflicts, when the chance of a physical fight is high, males match. Matching is the phenomenon whereby males involved in a song duel countersing with a song type that closely resembles that of the challenger (KREBS *et al.*, 1981). Theory predicts that before starting a fight it may pay to determine as exactly as possible the actual strength of the opponent. In that way it is possible to avoid unnecessary fights if the strength of the opponents differs considerably. We found that strophe length and drift are not only influenced by the male but also by the song type. Only by matching and using a similar song type can opponents exclude the effect of song type on drift. Matching could then be considered to be mechanism of male great tits to estimate each others strength very accurately during the early stages of the territorial period. Territorial fights between birds of unequal strength could then be settled without escalated conflicts (LAMBRECHTS and DHONDT, 1987). This hypothesis is consistent with some of our observations that male great tits can match song types when they are very close together (e.g. within 5 m), i.e. when distance assessment between birds would not be necessary (see above).

Whereas at the behavioural level the predictions relating to the use of singing ability in male-male conflicts were supported, at the population level, and in contrast to former studies, our results suggest that there is no simple relationship between singing ability and territory quality. Thus, males defending a territory in a high quality subplot did not sing longer strophes nor more song types than males with a territory in a low quality subplot. Better singers, therefore, did not have a higher chance to obtain a high quality territory (LAMBRECHTS and DHONDT, 1988b ; LAMBRECHTS *et al.*, submitted). This observation was confirmed when we removed territory owners from their territories in the spring and allowed non-territorial birds to settle in a territory : replacement birds did not produce shorter strophes than birds of the same age that had acquired a territory in a natural way (LAMBRECHTS and DHONDT, 1988b). A possible explanation for this is that good vacant territories are rapidly occupied in late summer, and that locally born first brood males are at an advantage (DHONDT, 1971a). Once a territory is occupied it becomes very difficult to dislodge the owner (KREBS, 1982). Since Great Tits produce two broods that fledge 6 weeks apart, and since local born birds have prior residence to immigrants, possible advantages of male quality may be ofset by disadvantages of later presence. TEUNEN'S (1987) observation that after a sudden massive mortality of the resident males in early January, good singers settled significantly more rapidly than poor singers, supports this idea.

SINGING ABILITY AND REPERTOIRES

Finally, our study of great tit singing performance and the assumption that long strophes are important resulted in a new hypothesis for why birds may need a song repertoire (LAMBRECHTS and DHONDT, 1988a). Great tits that are very motivated will start a song bout with strophes that are much longer than their average strophe length, and these strophes are separated by very short intervals. After a short while the same bird will decrease its strophe length and/or the strophes will be separated by longer intervals. This means that great tits do not only show drift within strophes, but also throughout song bouts. The decrease in song output is more pronounced in shorter bouts, and in bouts that start with longer strophes or with shorter intervals. As for drift within strophes and strophe length, we therefore proposed that drift throughout song bouts is caused by constraints in singing ability. This hypothesis was supported by playback experiments, showing that great tits also show pronounced drift in song bouts in which males were regularly presented with a song stimulus (LAMBRECHTS, 1988 ; WEARY *et al.*, 1991). However, after a switch to a new song type, the birds could increase their song output again to levels that were similar to those observed at the beginning of the previous bout. To explain these findings we proposed that motivated great tits have physiological problems is using the same set of respiratory and syringeal muscles in a stereotyped way for an extended period at high rates. To avoid or reduce neuromuscular exhaustion birds would have to switch to a new song type, in which the respiratory and syringeal muscles are used in another way. Thus, a song repertoire would allow a bird to sing for extended periods at high rates, and high singing rates would increase the success in territorial defence or mate attraction. Our hypothesis does not exclude the idea, however, that great tit song repertoires have more than one function, depending on the context in which birds switch song types. Physiological and morphological studies of the sound apparatus will be necessary to test the « anti-exhaustion » hypothesis in more detail.

CONCLUSION

Initially most of the song studies looked at song characteristics that were mainly influenced by song learning. These studies showed that great tit song provides information on the origin of birds (e.g. song dialects), and on the habitat type in which the birds live. Experimental studies in the field and in laboratory conditions resulted in a series of hypotheses about the functional meaning of song type structure and song repertoires. More recently, even more detailed studies of great tit singing performance revealed that variation in great tit song is not only caused by learning ability and learning opportunities, but could also be influenced by constraints in singing ability. These studies showed that great tit song could reflect male quality, and resulted in a new interpretation of why great tits should have song repertoires. In the future, experiments related to mate attraction of different song lengths, functional studies of great tit singing performance, physiological research of the sound apparatus, and detailed studies of song characteristics that were not investigated before (*e.g.* volume) are required to know more about the many meanings of great tit song.

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