



Multiple signals for multiple messages: great tit, *Parus major*, song signals age and survival

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Birdsong is a well-known sexually selected trait that plays a major role in female choice and male–male interactions. Although birdsong has been studied for many years, it has only recently been suggested that it is a multifaceted signal that could encompass multiple sexually selected traits. According to the theories on the evolution and maintenance of multiple sexually selected signals, the different components of birdsong may signal multiple, redundant or unreliable information on male quality. We used a cross-sectional approach to examine whether the expression of song in the great tit was differentially related to any of three measures of quality: age, condition and survival. We analysed several informative characteristics in great tit song concerning diversity, output, performance and consistency to see whether different traits were simultaneously related to the studied quality parameters, or if, in contrast, each song trait was related to only one of the measures of quality. Song consistency and repertoire size were strongly related to only one of the studied parameters (age and survival, respectively), indicating that different song traits signal specific quality characteristics, and providing, therefore, evidence to support the multiple-signal hypothesis. Moreover, measures of song performance and song output (phrase and strophe rate) correlated positively with repertoire size, which might indicate that, at the same time, great tit song is signalling redundant information. In addition, some song characteristics did not correlate with any of the quality parameters measured, suggesting that those song traits might provide unreliable information.

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Sexual selection theory proposes that differential elaboration of traits can be explained by evolution of characters through intersexual preference or increased ability to fight rivals (Darwin 1871). Birdsong is a sexually selected trait that plays a major role in sexual selection in many bird species, either as a mating signal that influences mate choice, or as a trait that is used in male–male competition (Searcy & Andersson 1986; Kroodsma & Byers 1991; Searcy 1992). The relationship between birdsong and sexual selection has been studied for a long time, and it is generally accepted that birdsong is a multifaceted signal encompassing several messages (Gil & Gahr 2002; Podos et al. 2004; MacDougall-Shackleton et al. 2009). However, only a few studies have addressed the multiple expression of birdsong, and most research in this area has been carried out in isolation (Searcy & Nowicki 2005) while taking into account one or a few song characteristics at the same time (i.e. mostly repertoire size), which has limited our knowledge and understanding of the evolution and mechanisms of production of birdsong as a multifaceted signal.

Expression of multiple characters can be explained by means of three main mechanisms: (1) each trait reflects a single property of the overall quality and, therefore, expresses multiple messages, (2) each ornament gives a partial indication of condition, and hence all traits express redundant information or (3) the ornaments are unreliable indicators of condition but they are maintained because it is not costly to produce them, and consequently, they express unreliable information (Møller & Pomiankowski 1993). These mechanisms might have evolved by Fisherian selection (Fisher 1958; Møller & Pomiankowski 1993; Pomiankowski & Iwasa 1998), production of distinct signals for different intended receivers (Pryke et al. 2001) or dynamic evolution in relation to environmental fluctuations (Bro-Jørgensen 2010). In this respect, the analysis of the relationships between a multifaceted signal such as birdsong and several quality or fitness parameters may help to reveal whether the different components of the signal are sexually selected to encompass multiple or redundant information, or if, in contrast, there are components of the signal that provide unreliable information. However, the different components of a multifaceted signal can simultaneously carry multiple, redundant or unreliable information (MacDougall-Shackleton et al. 2009), and the hypotheses are therefore not mutually exclusive.

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Traditionally it has been assumed that age, survival and body condition reflect male quality in several taxonomic groups, especially songbird species. For example, it is well known that sexually selected traits are often more elaborate in older individuals than in first-year adults (Andersson 1994). Research on birds has shown that birdsong differs significantly between age classes in several species (e.g. Nottebohm & Nottebohm 1978; Cosens & Sealy 1986; Gil et al. 2001; Kiefer & Hultsch 2006). This age-dependent expression of a trait may be explained by enhancement of the expression through experience or learning (Eens 1997) or delayed maturation (Balsby & Hansen 2010). Body condition has also been used as a measure of quality in songbird species (reviewed in Podos et al. 2004). Song might reflect actual condition of the individuals, which could be affected by health status or parasitic infections (Garamszegi 2005), or it might signal condition as a result of developmental processes (Podos et al. 2009). In addition, survival or longevity has also been considered as a measure of male quality (Trivers 1972; Andersson 1994). As song production might be costly (e.g. energetically, by developing the necessary structures or by increased risk of predation, reviewed in Gil & Gahr 2002), theory predicts a positive correlation between the expression of the signal and survival, which may be mediated by the high cost of producing the signals, and the signals would be affordable only for high-quality individuals. However, theoretical evidence suggests that the exaggerated expression of a trait may have a detrimental effect on survival (Brooks & Kemp 2001; Kokko et al. 2002), and, therefore, low-quality individuals with a poor expression of a particular trait might survive better. Although aspects of birdsong have been related to age, survival and condition in several species (e.g. Searcy et al. 1985; Galeotti et al. 2001; Garamszegi 2005; Kiefer & Hultsch 2006; Garamszegi et al. 2007; Ballentine 2009) only a few studies have addressed the question of whether the multiple components of birdsong simultaneously relate to different quality parameters.

The analysis of the different components of a multifaceted trait may be confounded by the interrelation of the expression with multiple quality parameters. For instance, it is known that age-dependent expression of birdsong could covary with, or be potentially influenced by, between-individual differences in condition or phenotype-dependent survival (Kokko 1998) and, in addition, differential survival may confound the results of a cross-sectional study (Endler 1986). Disentangling the relationship of song with age, survival and condition may help us to understand the role of the different quality parameters in shaping song traits, and whether or not the different song characteristics interrelate to express quality in a variety of ways.

Great tit reproductive behaviour, including song, has been extensively studied. There is evidence that male song activity in this species is related to territorial defence, mate guarding and female attraction (Krebs 1977; Krebs et al. 1981; Mace 1987; Slagsvold et al. 1994). Although the song in this species has been the subject of several studies, only a few song characteristics have been considered simultaneously in studies of the relationship between song and male quality. In addition, few studies have considered several components of quality at the same time. McGregor et al. (1981) studied survival, age and reproductive success in relation to song, but repertoire size was the only trait measured. In addition, Lambrechts & Dhondt (1986) studied three song traits, repertoire size, strophe length and drift, in relation to age, body size and reproductive success in great tit males. Their results suggested that repertoire size and strophe length are related to reproductive success and survival. However, they did not examine whether the song parameters were intercorrelated, and they mainly focused on the role of dominance in survival and reproductive success, but the differential expression of song parameters was not disentangled.

We carried out a cross-sectional study on great tit song. In contrast to previous studies in this species, we simultaneously considered several song characteristics that could potentially vary in relation to male quality. Song traits related to diversity, output, performance and consistency were studied in a single year in 58 great tit males in a population in Belgium. We aimed to investigate how different song traits in the great tit relate to, or are expressed differently with, age, survival and condition, and whether the multiple-message hypothesis, the redundant-signal hypothesis and/or the unreliable-signal hypothesis apply. If great tit song carries multiple messages, we should find that (1) a particular song trait is related to, or expressed differently with, only one of the studied quality parameters (age, condition, survival) and, at the same time, the same song trait would not correlate with any of the other song characteristics. If great tit song provides redundant information regarding the quality of the males, we should observe that (2) several song traits are simultaneously related to, or expressed differently with, only one specific quality parameter, and the same song traits should be intercorrelated. If, in contrast, we observe that (3) the song traits do not correlate with any of the quality parameters and there is no correlation between song traits, we can conclude that great tit song provides unreliable information regarding male quality.

METHODS

Study Area and Standard Procedures

The data were collected between 10 March and 30 May 2008 in a suburban great tit population located in the surroundings of the University of Antwerp in Wilrijk, Belgium (51°9'44"N, 4°24'15"E). Since 1997 nestboxes have been installed and all the birds in the population have received a metallic-numbered ring and a combination of three colour rings that enables individual identification in the field. Nestboxes were checked during the winter at night to capture, ring and monitor individuals that used the boxes as a roosting place. Therefore, the great majority of great tit males were colour-ringed before recordings took place. Reproductive activity was monitored from March onwards and pairs breeding in the nestboxes were captured during the nestling period. Adult males were captured while feeding chicks, between days 7 and 10 after hatching; an electronic balance was used to assess body mass to the nearest 0.1 g and tarsus length was measured with an electronic calliper to the nearest 0.01 mm. Body condition index was obtained from the standardized residuals of a linear regression in which body mass was set as the dependent variable and tarsus length as the predictor (Schulte-Hostedde et al. 2005). Exact age was determined using hatching records for resident birds. Colour differences of primary coverts, grey for yearlings and bluish for older birds (Gosler 1993), were used to determine age of immigrant birds; individuals that did not arrive as yearlings were not included in the analysis. As previous studies have observed that adult great tits show high site fidelity after their first year (Krebs 1971; Clobert et al. 1988), we were able to determine survival from spring 2008 to spring 2009. All birds that bred in 2008 and were recaptured or observed alive in the study area between 1 March and 30 May 2009 were considered survivors, even if the birds did not use nestboxes to breed in 2009.

Song Recordings and Analysis

The largest peak of singing activity at dawn in great tit males coincides with the fertility of the female (Mace 1987). Great tit song activity at dawn increases as egg laying approaches, starting several weeks before egg laying (Mace 1987; Amrhein et al. 2008). Although dawn singing has been shown to decrease when the last

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