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Song sharing and repertoire size in the sedge warbler, *Acrocephalus schoenobaenus*: changes within and between years

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The complex song of the male sedge warbler functions mainly in sexual attraction and the evolution of repertoire size is driven primarily by female choice. As male song ceases upon pairing, male–male singing interactions are relatively brief and have not been studied to our knowledge. This study shows that young males in their first breeding season shared significantly more syllables with their nearest neighbour than with their fathers or more distant males. Moreover, daily recordings revealed that rapid learning and modification of syllable repertoires occurred, resulting in a progressive increase in sharing within just a few days. This does not lead to a gradual increase in repertoire size as some syllables are dropped and new ones are acquired. This turnover process allows males to share syllables with their neighbours, whilst repertoire size, known to be important in female choice, remains relatively constant in any one year. Individual males were followed for several years and also showed considerable syllable turnover between years. However, in this case, repertoire size was found to increase between years, the largest increase occurring between the first and second years. We obtained a significant positive correlation between repertoire size and age, suggesting that females choosing males with larger repertoires may gain indirect (genetic) benefits for their offspring, such as good genes for viability. Whilst these results reveal a more flexible picture of repertoire turnover than previously suspected, the relative stability of repertoire size within a season and the increase with age suggests that repertoire size remains a likely target for sexual selection by female choice.

Keywords: *Acrocephalus schoenobaenus*; age; neighbour; sedge warbler; song sharing; repertoire

Although the complexity of bird songs has been the subject of considerable research and much debate concerning their function and evolution, there is now general agreement that male song serves two main functions; the repulsion of rival males and the attraction of females for mating (Catchpole & Slater 1995; Collins 2004). In evolutionary terms, a number of pressures including intrasexual selection through male–male competition, and intersexual selection through female choice, have helped to shape the diversity of form and function we now observe (Andersson 1994). Song structures in any one species may well be the result of these two evolutionary pressures and how they have interacted during evolution to fulfil the two main functions. There is now considerable empirical support that song complexity and the evolution of large repertoires, in particular, are driven by female choice (Searcy & Yasukawa 1996) and this is seen particularly in *Acrocephalus* warblers (reviewed in Catchpole 2000).

If repertoires are, indeed, the target of directional selection through female choice, then what are the benefits females obtain? Older males often show more developed sexually selected characters (Manning 1985; Andersson 1994), which would be expected if the expression of male ornaments is dependent on either condition (Rowe & Houle 1996) or even delayed learning (O'Loghlen & Rothstein 1993). In songbirds, it may be that females use repertoire size to select older males that have shown their ability to survive (Kokko 1998). If so, choosy females could gain indirect benefits such as heritable good genes for viability (Trivers 1972). An important study on the great reed warbler, *Acrocephalus arundinaceus*, Hasselquist

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et al. (1996) found that repertoire size was correlated with offspring viability, although this was not found in a German population of the same species (Forstmeier et al. 2006). The repertoire size of the sedge warbler is well known as a strongly sexually selected trait (Catchpole 2000) and in an earlier study, we found a significant positive relation between repertoire size and age (Birkhead et al. 1997). However, this was achieved by cross-sectional analysis, which can give misleading results (Gil et al. 2001; Forstmeier 2002). Therefore, one objective of the present study is to determine whether this finding can be confirmed by a more rigorous longitudinal analysis following individual males from year to year.

Although the emphasis has been on female choice in *Acrocephalus* warblers, there remains the possibility that, even with the complex song of the sedge warbler, there could still be some function in male–male competition for territories. Songbirds are some of the few animals that tend to learn their vocal signals and display a remarkable diversity of song-learning strategies, as recently reviewed in Beecher & Brenowitz (2005). As they point out, the other key target for selection, besides repertoire size itself, is song sharing between neighbouring males, and these two main functional hypotheses are not necessarily mutually exclusive. In the case of repertoires, song learning may lead to an increase in repertoire size, whereas with song sharing this is not necessarily the case, and indeed could even lead to attrition in final repertoire size. Most song sharing hypotheses focus on the supposed advantages of song sharing between neighbouring territorial males (Beecher & Brenowitz 2005), for example, by matching the songs of their rivals, males may be able to maintain territorial boundaries more effectively. If sharing song types with neighbours is the main target of selection, then this goal could well be achieved in species with small- or medium-sized repertoires. Hence, the sharing hypothesis, in general, helps to explain the prevalence of such species through advantages in male–male competition, thus acting to counter the selection pressure to increase repertoire size for female choice.

In the sedge warbler, a large literature has now accumulated which strongly suggests that the long, complex songs are largely the result of female choice (reviewed in Catchpole 2000). This, and the fact that males cease singing upon pairing after only a few days, would seem to mitigate against any significant male–male interactions leading to song sharing. However, males do aggressively interact and countersing at this time, and the final objective of this study was to follow territorial interactions in more detail than before to discover whether repertoire changes can lead to song sharing in just a few days.

METHODS

The study species was the sedge warbler, which has been extensively studied at Wraysbury Lakes, Berkshire, England from 1993 (Buchanan & Catchpole 1997; Buchanan et al. 1999; Marshall et al. 2003). Soon after arrival, males were caught in mist nets under appropriate U.K. licences and ringed with a unique combination of coloured plastic rings to facilitate individual identification.

Fifteen minutes of continuous song was recorded for each male using a Marantz CP430 tape recorder, with a ME67 Sennheiser unidirectional microphone mounted on a sprung handgrip. Each male was recorded for the first time either on or within the first few days of arrival. Songs were analysed using Avisoft-SASLAB Pro for windows (Avisoft Bioacoustics, Berlin, Germany) by a researcher who was blind to the identity of each recording. Repertoire size was calculated for each individual as the number of novel syllable types appearing in the first 20 uninterrupted songs within the sample (Catchpole 1980; Buchanan & Catchpole 1997). Syllables were identified, classified by type and stored electronically as a library for each individual male. Syllables were defined as the smallest unit of continuous song as in previous work (Catchpole 1980). Statistical analysis was conducted using SPSS (SPSS Inc., Chicago, IL, U.S.A.) and Minitab version 14 (Minitab Inc, PA, U.S.A.).

Song Sharing

To calculate the proportion of syllable types shared between two individuals, the repertoire libraries of males were compared by visual inspection. The proportion of repertoire sharing between two birds was then calculated using the formula developed by McGregor & Krebs (1982): $2N_s/(R_1 + R_2)$, where N_s is the number of shared songs and R_1 and R_2 are the repertoire sizes of the two individuals. From recordings made between 1993 and 1996 (Buchanan & Catchpole 1997), nine first year males (sons) and their fathers (recordings of which had been made in their first year) were identified. Sharing values for any siblings or half-siblings that shared the same father were averaged ($N = 3$ total) and any half-siblings that did not share the same father were excluded. The nearest and furthest neighbours of these first year birds were determined from territory positions that had been previously marked on scale maps. Nearest neighbours were defined as males on territories less than 5 m from the son's territory. Where the neighbours clustered around a particular territory were equidistant, one was picked at random to be nearest neighbour. Furthest neighbours were those judged furthest, which in all cases was at least 100 m away. The repertoire library of each son was then compared with his nearest neighbour, furthest neighbour and father to determine the proportion of syllables shared with each. To study changes over several days, pairs singing on adjacent territories were recorded once a day for up to 5 consecutive days. For each such male, a repertoire library was compiled for each of the days that he was recorded. The proportion of syllables shared between each neighbouring pair was then calculated for each of the days that they were both recorded. The fate of each syllable could then be followed to determine exactly what changes occurred over several days.

Four males that had been recorded for 3 consecutive years and two males that had been recorded for 4 consecutive years were used to study annual changes. As exact ages were unknown, when birds were first ringed and recorded they were designated as year 1, then if