

Song Structure
and
Syllable Repertoires
in the European Sedge Warbler,
Acrocephalus schoenobaenus

by
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I dedicate this thesis to the individuals who have enriched my life

in many non-material ways:

The Sedge Warblers of Wraysbury Lakes

My adviser, Professor Willem Ferguson

Professor Hugh Paterson

My late father, Leon

My mother, Marion; brother, Peter and sister, Cheryl

My sons, Simon and Ben

My partner, Annie

My late aunt, Ethel Gordon and late uncle, Boris Wilson.

“...And sedge-warblers, clinging so light
To willow twigs, sang longer than the lark,
Quick, shrill, or grating, a song to match the heat
Of the strong sun, nor less the water’s cool,
Gushing through narrows, swirling in the pool.
Their song that lacks all words, all melody,
All sweetness almost, was dearer then to me
Than sweetest voice that sings in tune sweet words.
This was the best of May – the small brown birds
Wisely reiterating endlessly
What no man learnt yet, in or out of school.”

From the poem, Sedge-Warblers by Edward Thomas
(Born London, 1878)

“science never imposes anything, science *states*. Science aims at nothing but making true and adequate statements about its object. The scientist only imposes two things, namely truth and sincerity, imposes them upon himself and upon other scientists.”

In Mind And Matter by Erwin Schrödinger, The Tarner Lectures, Trinity College, Cambridge, October 1956.

Summary

My thesis defines the temporal, acoustic frequency and sequential structure of Sedge Warbler song qualitatively and quantitatively in a rigorous way using a range of uni- and multivariate techniques. The implications of this definition are considered in terms of previous studies involving Sedge Warbler song structure, and the communication system of this species. Sedge Warbler song is extremely complex and variable and has provided fertile ground for the study of sexual selection by female choice. This complexity and variability present a formidable challenge for quantitative definition, which has not been achieved in a rigorous way in this species before. Despite this, structural features such as syllables, syllable types and songs have been used quantitatively to derive measures such as estimated syllable repertoire size and to test hypotheses about evolutionary function. Syllable types that comprise the repertoires of males have not been defined at all, yet are considered to play a central role in sexual selection as an honest indicator of male quality to prospecting females.

Quantitative evidence is presented to show that syllables and their component elements are the basic vocal units in Sedge Warbler communication and that songs are artificial units. This evidence has implications for the interpretation of Sedge Warbler communication and for studies that depend on a song as a discrete vocal unit. Element and inter-element durations are found to be within the limits of auditory discrimination in songbirds. The considerable variability in the cyclical behaviour of syllable, syllable type and mean inter-syllable duration rates, and out of phase variation between them in each male, indicate higher levels of variability and complexity in the structure of Sedge Warbler song than originally described. This variability and complexity may promote attention levels in prospecting conspecifics and may reduce specific neuromuscular activity and fatigue that will be important in sustaining the almost continuous singing over long periods, characteristic of male Sedge Warblers. The out of phase variation between syllable and syllable type rate cycles together with significant differences between song samples of different males in both these variables may provide a basis for them to function as independent multiple cues in female choice. Analysis of the relationships between inter-syllable duration, syllable rate and syllable type rate indicate that there are constraints on the possible sexually selected traits of syllable and syllable type rates. Significant differences between song samples of different males in element, inter-element, syllable and inter-syllable durations and syllable rate

may provide a basis for individual recognition, if differences shown reflect differences between males.

The size and composition of the complete estimated syllable repertoires of two male Sedge Warblers are determined by quantitative and qualitative analyses which yield very similar results, but appreciably higher estimates of size than previous qualitative studies. This discrepancy may be due to subjectivity of syllable type determination and insufficient song sample duration of the previous studies, which are likely to have produced inaccurate estimates of syllable repertoire size. This error may affect the significant relationships found between repertoire size and other variables in previous studies. Significant temporal and acoustic frequency differences found between syllable types are well within songbird auditory system resolving power, and form a basis for syllable types to function as fundamental units of syllable variation and for categorical perception of syllable types in the Sedge Warbler.

Quantitative and qualitative evidence is presented for structural distinctness of syllable types in a population of Sedge Warblers within and between breeding seasons. This evidence is consistent with syllable types functioning as fundamental units of Sedge Warbler vocal repertoires, and provides a quantitative basis for categorical perception and effective communication in this species. Structural constancy of a large proportion of syllable types in the population also is shown within and between breeding seasons. Differences in syllable type occurrence and repertoire composition found within males in the same breeding season may explain when they pair, and may have implications for determining syllable repertoire size in individual males. Differences in syllable type occurrence and repertoire composition found between song samples of different males in the same season and within males in successive years, provide scope for further work to gain a better idea about the biological significance of these differences. Shared syllable types found in the population together with distinctness and constancy of syllable type structure provide a basis for these types to function as part of the specific mate recognition system, which allows the recognition and bringing together of mating partners.

An important principle of my thesis is that fundamental problems of definition and description need to be resolved before hypotheses about biological significance can be formulated and tested. In line with this principle, syllables, their component elements, syllable types and the sequential structure of Sedge Warbler song are defined as objectively as possible in an accurate, transparent and verifiable way, after which their importance in Sedge Warbler communication is considered. This definition hopefully will enable and encourage repeatable

empirical studies involving Sedge Warbler song structure, including further research to determine whether the defined features of song structure, function as suggested in the specific mate recognition system, female choice and individual recognition in this species.

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