A STOCHASTIC ANALYSIS OF THE MAINTENANCE BEHAVIOUR OF SKYLARKS

by

JUAN D. DELIUS [1)2)]
(Dept. of Zoology, Oxford, and Dept. of Psychology, Durham, England)

(With 24 Figures)
(Rec. 5-VII-1968)

INTRODUCTION

This paper, which is one of a series dealing with the behaviour and ecology of the Skylark *Alauda arvensis* (DELIUS, 1963, 1965) has a twofold aim. It describes, along the usual ethological lines, the maintenance behaviour of this bird. Although often neglected, non reproductive behaviour has lately attracted some attention perhaps mainly because of the frequent and seemingly irrelevant appearance some of it makes in the context of reproductive behaviour (*e.g.*, VAN IERSEL & BOL, 1958), but also because it challenges an explanation in being recognisably organised (*e.g.*, EWER, 1967), or because of its significance in comparative studies (*e.g.*, MCKINNEY, 1965). At the same time, however, the paper is an attempt of applying an analytical procedure which seems potentially useful for behavioural studies. While the desirability of quantitative behaviour descriptions has long been recognized, a confusing variety of descriptive frameworks have been used. Spectral functions would seem eminently suited to replace some of this variety since they usefully typify a wide variety of stochastic processes (BARTLETT, 1966). Over the last years techniques have been developed which make it possible to derive such for behavioural data. They are these techniques I am attempting to explore, although because of shortcomings in the data collected long before this analysis was envisaged, their application will remain in-

1) I wish to thank Professor N. TINBERGEN, F.R.S. for supervising the fieldwork, Sir W. PENNINGTON RAMSDEN Bart. and the Cumberland County Council for permission to work in Ravenglass. Mrs E. TEMPLETON for computing advice, Dr R. DAWKINS for providing a computer program used early in this study and my wife for preparing much of the data and manuscript. The work was supported by grants from the U.S. Air Force Office of Scientific Research through the European Office of Aerospace Research, and the Science Research Council.

2) Present address: Dept of Neurosciences, UCSD, La Jolla, Calif. 92037, U.S.A.

complete and imperfect. However, it is hoped that it may stimulate further and more consequent work.

OBSERVATION METHODS

The data were obtained from behaviour observations made on individually marked Skylarks of a population at Ravenglass Gullery in Cumberland, England, 54° 21′ N 3° 25′ W. They were watched with the aid of 10 × 50 binoculars, mounted with a ball-joint on a tripod. The territories of the Skylarks were located in dune valleys with scarce vegetation and so individual birds could be followed for virtually unlimited periods, interrupted only by rare absences from the territory, usually lasting less than a minute, or by bouts of incubation. When they were observed at the nest from a hide on the other hand, it was not possible to follow them when they were off the nest. In this way records of no less than 30 minutes and up to 5 hours (average 2 hours) were obtained from individual birds. Some 200 hours of observation are available of which some 120 consist of virtually uninterrupted periods. These provided the bulk of the data used in this study. Additionally more casual notes were made over some 15 months of field work, spread over 4 breeding seasons. The behaviour records were attempts to note all observable behaviour with a concurrent time basis. They mainly consist of strings of symbols, standing for the diverse behaviour patterns and their variations interspersed with timing notes at variable intervals between 2 and 3 minutes. Since however the durations of several behaviour patterns were fairly constant, it was possible to allocate behavioural events to particular one-minute-intervals with reasonable confidence.

The records relevant to this study were transcribed on punched tape so that all further processing could be done with a KDF 9 digital computer using programs especially written for the purpose by the author [1]).

ANALYTICAL METHODS

When attempting to describe the relationships between the input and the output variables of a linear system, one of the procedures used in system analysis is frequency analysis (MILSUM, 1966). This consists in driving the input with a sinewave of a given amplitude and varying its frequency from ideally zero to infinite, and measuring the output in terms of amplitude and phase relations to the input. From this information the transfer functions of

1) A comprehensive program deck for random event series analysis is now available for the IBM 360 (LEWIS, 1967).