A SIMPLE MODEL FOR COMPETITION BETWEEN BEHAVIOUR PATTERNS

by

P. J. B. SLATER 1)

(Ethology & Neurophysiology Group, School of Biology, University of Sussex, Brighton, U.K.)

(With 4 Figures)

(Acc. 25-III-1978)

I. INTRODUCTION

Many studies of the organisation of behaviour concentrate on one particular behaviour pattern or class of patterns, such as feeding, drinking or locomotion. By examining one pattern in some detail it is hoped to discover the rules which govern its organisation in time and thereby construct reasonable models of the sorts of mechanisms which might determine its occurrence. This approach has, for example, been successfully applied to feeding behaviour, sometimes revealing that it tends to take place in meals of fairly standard length (e.g., WIEPKEMA, 1968), that the size of a meal tends to correlate with the length of the gap between that meal and the next one (e.g., LE MAGNEN & TALLON, 1966), and that it tends to take place rhythmically (e.g., RICHTER, 1927). However, clear findings of this sort are by no means universal for feeding and are less common in the case of other behaviour patterns.

One reason why individual behaviours may not show a clear structure in their organisation in time is that the various possible activities in an animal's repertoire cannot usually be performed simultaneously. Thus, although a behaviour pattern might in theory be scheduled to take place rhythmically, other acts may take precedence over it so that its time of occurrence is far from regular. If the pattern is a very low priority one, its time of occurrence may be scheduled more by gaps left in other behaviour than by any organisation intrinsic to it. The temporal pattern of an act is the converse of the combined patterns of all other acts. The difficulty of looking at the temporal

1) I am grateful to Dr Peter Clifton and Nigel Lester for useful comments on the manuscript and, in particular, to Tony Ludlow who provided detailed criticisms and encouragement. This research is financed by the Science Research Council.
pattern of one act in isolation from others is thus clear; those behaviour patterns which have yielded to such treatment must be dominant in some sense so that their organisation shows through despite the competing demands of other actions.

The complications which arise from interactions between behaviour patterns have become apparent during the course of a long-term study of the behaviour of zebra finches (*Taeniopygia guttata*). Amongst the behaviour patterns shown by isolated males, the most common are locomotion, feeding, song and grooming. Each of these has been studied individually, but the success achieved in the search for the rules underlying their occurrence has varied. Though individual differences are substantial, the temporal pattern of feeding behaviour shows the most obvious structure: in most animals both meals and the gaps between them tend to be of typical length; meal length usually correlates with the length of the gap after; in more regular birds feeding follows a cycle 24-30 min long (Slater, 1974a). Locomotion, though a heterogeneous and therefore rather unsatisfactory category of behaviour, also shows fluctuations which may be regular: the cycle length found varies considerably both between individuals and from day to day, but is most commonly in the region of 30-40 min (Slater, 1975). Preening, though it occurs in bouts which are relatively easy to define, has a complex pattern in time, with no suggestion that either bouts or gaps tend to be of a typical length. Slater (1974b) argues that major bouts may take place regularly but that this pattern is complicated by briefer bouts, perhaps stimulated primarily by peripheral irritation, which occur during intervals between them. Less work has been carried out on song, but it does occur in bouts which tend to be of a typical length. Unlike feeding, bout length most commonly shows a correlation with the length of the preceding gap (unpublished observations).

A further behaviour pattern which has been studied is ruffling or feather shaking. In some ways this shows the most predictable pattern of all: it very seldom occurs in bouts of more than one act and these are regularly distributed, tending to occur about once every 5 minutes.

It has therefore proved possible to discover some rules which govern the occurrence of individual behaviour patterns. Other evidence suggests certain associations between them. The fluctuations in locomotion are accompanied by changes in the probability of other behaviour patterns, with feeding occurring primarily at high levels of activity and song, preening and rest succeeding each other as the bird becomes less active. The possibility that these relationships might be accounted for by a single, arousal-like, underlying variable did not stand up to close examination (Slater & Wood, 1977), and it seems more likely that these sequences result from competition between patterns