Studies on the Organisation of Bird Behaviour

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1. SLATER, P.J.B. & OLLASON, J.C. 1972.
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2. SLATER, P.J.B. 1973.
   Describing sequences of behavior.
   IN: Perspectives in Ethology, P.P.G. Bateson & P.H.Klopfer, eds. pp. 131-153. Plenum Press, New York.

3. OLLASON, J.C. & SLATER, P.J.B. 1973.
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7. SLATER, P.J.B. & WOOD, A.M. 1977.
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8. SLATER, P.J.B. 1979.
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14. SLATER, P.J.B. & CLEMENTS, F.A. 1981.
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15. SLATER, P.J.B. & LESTER, N.P. 1982.
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17. SLATER, P.J.B. In Press.
Sequences of song in chaffinches.
Animal Behaviour.

Note: While the papers are numbered and bound in chronological order, it would be most appropriate to read paper 15 between papers 6 and 7, and paper 17 between paper 8 and paper 9.

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ABSTRACT

This thesis includes papers in two main areas of bird behaviour: studies of temporal patterning and studies of song. These involve diverse approaches and findings which are drawn together by an introduction providing a guide to the individual papers and their main results.

The papers on temporal patterning are mainly concerned with the behaviour of zebra finches. The distribution in time of individual behaviour patterns and their sequential relationships are described using techniques for analysing sequences and bouts of behaviour developed by the author. The rules underlying the patterning in time of feeding and preening are described in some detail. The occurrence of short-term rhythms of behaviour, changes within which match those in the daily cycle, suggested that a single underlying variable might influence the occurrence of different behaviour patterns. However, this hypothesis was rejected following experimental manipulation of the short-term rhythms using cycles of sound and of light intensity. Instead, the results suggest that the sequential relationships found might result simply from competition between the behaviour patterns involved, an idea which computer simulations show to be plausible. A final paper on this topic concerns song in chaffinches and shows that, as with broader categories of behaviour in zebra finches, competition is an important factor in determining sequences of song types.

The remaining papers on bird song involve both laboratory and field work, largely on chaffinches. Hand-rearing experiments show that young male chaffinches can learn complete songs either as fledglings or in the following spring; learning is normally extremely accurate but sometimes involves errors. The frequencies of different song types and their distribution in the wild fit in well with these characteristics of learning, and it is argued that both local and geographical variation in song, as well as the way it has been found to change with time within a population, are simply a functionless byproduct of vocal learning. Possible reasons for song learning, and for the occurrence of song repertoires, have been explored and are discussed in relation to work on the chaffinch and on other species. Laboratory work on zebra finches suggests that learning is unlikely to lead song to provide a measure of kinship: the results of mate choice experiments show birds to prefer mating with a relative rather than a stranger, but these preferences are more likely to be based on plumage differences than on song.

INTRODUCTION

This thesis includes a selection of papers falling into two main fields: studies on the temporal patterning of behaviour and studies of bird song, with special reference to its development and cultural evolution. Such a diverse range of topics, involving observations and experiments in both field and laboratory, as well as some theoretical work using computer simulation, may be unusual within a single thesis. It is the aim of this brief introduction to provide a framework which will help to draw the papers together and may be used as a guide through them. The introduction is subdivided into the two main areas of the thesis. Papers included in the thesis are referred to by their reference numbers, by which they are labelled in the contents list and ontheir covers: other references are listed at the end.

Studies of Temporal Patterning

The past ten years have seen a tremendous growth of interest in the quantitative analysis of behaviour. Prior to that time, the quantitative methods used by ethologists had been very informally applied and were, quite often, misleading. This was excusable, because it is not at all easy to see how something as variable as behaviour should be quantified (Slater 1978). One area tha presented particular difficulties in this respect was that of temporal organisation. Generally speaking, animals only perform one behaviour pattern at a time, though they usually have a repertoire of many patterns which must vie with each other for expression. The aim of the papers on temporal patterning included in this thesis was to determine the rules which underlie the production of particular behaviour patterns at particular times. Quantitative treatment was essential to this and appropriate techniques had to be developed.

Traditionally, two methods have been most commonly used to look at the temporal organisation of behaviour. One is sequence analysis, which helps to determine which behaviour patterns lead to one another or occur in association. The other is the analysis of the distribution of a single behaviour pattern in time as is, for example, often done in the study of meals and the intervals between them. Sequence analysis is applied in papers 1 and 17, and paper 2 provides a discussion of its application and a critique of its earlier usage, pointing out the hidden pitfalls of application and interpretation, many of which had previously gone unremarked. An especially important point raised here was the difficulty of interpreting sequence analyses which included transitions between a given behaviour and itself; paper 2 describes appropriate methods for avoiding this as well as consideration of transitions that cannot, by the nature of the animal or of its environment, occur.

Papers 4, 5, 6 and 15 involve the analysis of the distribution in time of single behaviour patterns. Almost all behaviour occurs in bouts, many events of a given type occurring close together, while long intervals elapse without any events. For this reason, analysing behaviour in terms of bouts and the gaps between them has become a common technique. Just how useful it is, however, depends on the method used to define a bout. In the past the majority of studies used a criterion based on switching between behaviour patterns or on an arbitrary time interval, shorter gaps being considered as within a bout and longer ones as between bouts. The value of these methods depends critically on whether the criterion selected matches up to the real organisation of the behaviour of the animal. This is made clear by an analysis using various different time criteria described in paper 6. As papers 4 and 5 argue, a more objective criterion can be obtained using log-survivor functions to plot the distribution of intervals between events. This technique had been used less formally in studies of behaviour before these two papers were published (e.g. by Nelson 1964 and Delius 1969), but they established it firmly as the method of choice for bout definition (see, for example, appropriate chapters in Colgan 1978). It remains the best technique available, and is now widely used, although, as paper 15 points out, analysis in terms of bouts and the intervals between them, may not be useful if the slope of the log-survivor curve for a particular behaviour pattern changes gradually.

These were the main methods applied in initial work on the temporal organisation of zebra finch behaviour (papers 1, 4, 5 and 6). The animals studied here were placed in isolation in sound-proof chambers, the aim being to determine the temporal pattern that they would produce themselves, uninfluenced by changes in the external world. Sequence analysis showed that the birds tended to oscillate between periods of activity and ingestion, and periods of rest with which various grooming movements were associated (paper 1). These short-term changes were mirrored by those taking place during the course of a day: for example, the declining activity between morning and afternoon was accompanied by an increase in rest and in grooming (paper 3). This led to the idea that a single variable ("activation") might set the probabilities of different behaviour patterns and that oscillations in it might be responsible for the associations between them, both on the short- and the long-term. Despite considerable efforts, short-term cycles in behaviour proved particularly difficult to study because their period varied a great deal both between individuals and in the same animal from day to day. It was also technically difficult to separate them from the strong daily rhythm on which they are superimposed. External cycles were therefore used to entrain them (papers 6 and 7) and thus determine how different behaviour patterns fitted in to them. These studies showed the reality of short-term cycles of activity and inactivity, the duration of which could, to some degree, be manipulated. It was especially interesting that some birds fitted two behaviour cycles into one external one, while in other cases, where the external cycle was short, the behaviour cycle was twice the length of that imposed. The cycles were thus not simply being run by the external changes and were only flexible within limits. Similar short-term cycles in behaviour have been described in some other species, though they remain a relatively neglected and potentially very interesting phenomenon (Daan & Aschoff 1981).

The results of the experiments on the entrainment of cycles using varying light intensity failed to support the activation hypothesis (paper 7). It was possible to entrain one behaviour pattern without others and, where several showed cycles, their phase relations could vary depending on the imposed cycle length. Models of behaviour organisation based on hypothetical variables such as arousal, responsiveness and activation have been put forward on a number of occasions (see Andrew 1975): this paper provides one of the clearest experimental examinations of such an idea to date. What was suggested as a result of these experiments was that the normal sequence of behaviour, from activity and feeding, to song, to grooming, to rest and then back to activity again might instead result simply from competition between the behaviour patterns in question. For example, a possibility here was that the need to perform different behaviour patterns rose with differing speeds during a period of rest and that they were performed in order of priority when rest was over. Perhaps the observed sequences of behaviour might thus require neither activation nor direct sequential influences between the behaviour systems involved?

Although further experiments on zebra finches are planned, the most that can be said at this stage is that this hypothesis remains attractive. Some very simple computer simulations, loosely based on earlier zebra finch results, proved remarkably illuminating (paper 8). Simulated behaviour patterns, which alone would occur cyclically, but were made to compete for a single output pathway, showed a complex temporal organisation: some behaviour patterns ceased to appear cyclically, for example, and others showed cycles differing in length from their intrinsic one. The sequential relations between the different behaviour patterns were also far from random, suggesting that competition can indeed lead to such associations between acts without one directly stimulating another. The precise results of these simulations are unimportant as they depend a great deal on arbitrary assumptions. They do, however, make a number of important general points. First is the point that competition for a single output pathway can, on its own, lead to very complex output comparable to that of the behaviour of real animals. This gives some hope that the organisation of behaviour in animals may some day be understood in terms of relatively few basic rules if we just have the ingenuity to root them out. A second important finding was that the temporal organisation of behaviour patterns that happened for short periods was much less disrupted by competition than that of more time-consuming patterns. This may explain why behaviour patterns such as ruffling (paper 4) and feeding (paper 5) have proved much more tractable to temporal analysis than ones such as preening (paper 4). In the case of preening, its occurrence in time may be determined more by gaps left in other behaviour rather than by any pattern intrinsic to itself.

A final point of importance has emerged forcefully from these papers on temporal patterning, and this is the significance of individual differences in behaviour (see Slater 1981). The patterns of feeding of individual male zebra finches differed very greatly one from another but were found to fall roughly into two groups (paper 5). In one group the birds ate well organised meals at regular intervals; in the other feeding was much less structured with no clear rules of organisation. It was suggested that such differences could have arisen according to whether the birds fed in response to internal or external stimuli, those feeding mainly in response to internal factors being regular eaters while those that fed mainly at the random intervals when they came across food would show little clear pattern. A similar distinction between the effects of internal and of external factors, though not one that leads to differences between individuals, may account for some of the lack of clear pattern in grooming behaviour (paper 4). Here there are too many very short and very long bouts compared with random expectation: a likely reason for this is that the very short bouts occur in response to specific irritations which arise for one reason or another at more or less random intervals, while the longer bouts are internally driven, and perhaps regularly occurring, sessions of grooming the whole body. If this idea is correct, and more work aimed at examining it is planned, the organisation of grooming is complex because it is motivationally two distinct types of behaviour rather than one.

These papers on the temporal patterning of behaviour in zebra finches have helped to unravel some of the complexities of the factors affecting the organisation of behaviour in time. This is not an easy topic for analysis because different behaviour patterns may have quite different characteristics: for example, feeding depends on the presence of a specific external stimulus, while singing does not; in the case of grooming the relevant external stimuli are carried round with the animal, whereas with feeding they are not, and may be more or less localised in the outside world. The difficulties of dealing with such heterogeneous patterns of behaviour in sequence analysis are particularly great (paper 2). In paper 17, however, the different patterns considered are song types, a homogeneous category in which the different acts are equivalent to one another. The temporal pattern of bird song has been studied extensively, but with particular emphasis on its description in terms of Markov chain analysis (e.g. by Lemon & Chatfield 1971). Paper 17 argues that this may not be a very useful way of describing it given the way in which song sequences appear to be generated. A model involving some direct connections between song types may be necessary, because certain sequences are usually commoner than others. However, any realistic model must involve competition also, as the probability of a type is clearly related to the interval since it was last performed regardless of the position in which it normally appears in the sequence. This study of chaffinch song, together with recent studies on North American thrushes (Whitney 1981; Dobson & Lemon in preparation), suggest that song may be most appropriately described by a model remarkably similar to that put forward in paper 8. Indeed, in general, sequences of bird song, diverse though they are, have great potential for examining mechanisms of behavioural organisation because of their much greater simplicity than sequences of more heterogeneous categories of behaviour.

Studies of Bird Song

The remaining papers in this thesis are all concerned, directly or indirectly, with studies of bird song. While all the work discussed above, including paper 17 on song, was concerned with the causation of behaviour, the remaining papers are concerned with the other three questions which Tinbergen (1963) pointed out could be asked about behaviour, those dealing with development, function and evolution.

In one of the classic papers on behavioural ontogeny, Thorpe (1958) showed how young chaffinches learn the songs that they sing from other individuals during the first year of life. Thorpe believed that this learning was a continuing process, basic details being learnt as a fledgling and the full pattern acquired the next spring. However, his work left a number of questions. Much of the training he gave to his hand-reared birds was in autumn or winter when adults would not normally be singing. There is thus the question of how reasonable his conclusions are for birds in the wild. There is also the question of the implications of this learning process for wild birds. Several studies have suggested that chaffinches show dialects, the songs in one neighbourhood differing from those in another (e.g. Marler 1952; Metzmacher & Mairy 1974). However, no detailed study had been carried out of the songs of chaffinches within a small area in an attempt to understand the significance of the song learning process. It was primarily for this reason that the work on chaffinch song was initiated.

Despite three seasons of hand-rearing, laboratory studies on song learning proved exceedingly difficult because of very high mortality amongst nestlings and fledglings. However, the results from those birds that did survive were illuminating (paper 13). Clearly chaffinches can learn complete songs accurately either as fledglings or in the following spring. Differences may also exist between the song produced and that on which the bird was tutored, though learning is extremely accurate in other cases. These results tie in nicely with field observations made in Orkney and in Sussex. The same song type may be shared, in more or less identical form, by many birds in the population, while distinct song types often share several features suggesting that they are derived by miscopying from a common original (paper 9). Neighbouring birds within a wood share no more song types than those more distant from one another, suggesting that birds often learn songs before they set up their territories, as our laboratory results had shown to be possible (paper 13).

If chaffinches usually learn their songs accurately, but occasionally mistakes are made so that new song types are created, what are the consequences for the frequencies of different song types in the wild? This question is examined especially in papers 10 and 11. Paper 10 shows, both by application of a model for the distribution of neutral alleles in a population and by computer simulation, that the frequency of song types is much as would be expected if 85% of songs were accurately copied within the population and the other 15% either introduced from outside or created by copying errors. Thus the learning process itself, with a very high "mutation" rate, is enough to account for the relative frequencies of different song types in the population. Given that birds learn their songs in the general area where they breed, this process would also lead to the distribution of song types in one location being different from that elsewhere, as between Orkney islands (paper 9), and to total differences between more distant places, as between Orkney and Sussex (papers 9 and 10). Sharp dialect boundaries, which have sometimes been suggested and are found in some other species, do not appear to exist, and would not be predicted in the absence of geographical barriers to dispersal. Another prediction from this learning process would be that the songs present in an area should change slowly over time, some being uncopied and becoming extinct, others happening by chance to be copied by several birds and so spreading through the population. Comparison of the songs present in Stanmer Wood, Sussex, in two summers 18 years apart upheld this prediction (paper 10). Only three types were found which might have been considered the same between the two samples: a very close match to the number predicted from the computer simulations run with a 15% miscopying rate.

The only comparable study, recently published by Payne et al. (1981), shows that song in indigo buntings also changes through time. It seems parsimonious to suggest that this, and the changes in space which lead to geographical variation, are simply byproducts of the learning process rather than having any functional significance in their own right. This is unlikely to be a popular idea, however, given the huge amount of work that has gone into studying geographical variation in bird song (reviewed by Krebs & Kroodsma 1980). The very low rate of copying errors which is found, less than 15%, suggests that miscopying is not advantageous to the individual but may arise simply because individuals differ in their opportunities to learn, some being hatched later in the season or having fewer neighbours from which to copy than others. If this suggested reason for local, geographical and temporal variations in chaffinch song is correct, the important question is why song is learnt, not why it varies. This has been the most persistent question about bird song for a long time, but it is not one which there is at present a clear answer. Possible reasons are discussed in paper 16, which also places the chaffinch work in the broader context of the many other species that have been studied. It is clear that no single or simple answer is to be expected. However, as papers 13 and 16 point out, it is necessary to sweep away some common preconceptions. One is the idea that unlearnt behaviour is more fixed than learnt. The temporal organisation of singing is highly varied between individual male chaffinches, yet appeared normally in hand reared birds without tutoring. By contrast, the precision with which individual songs are learnt can be quite remarkable. it is on this basis that the suggestion is made that selection has favoured learning as the only means to achieve such high precision, while aspects of song which are unlearnt and vary considerably between individuals are so simply because they are of little importance so that a high degree of genetic variance is tolerated and there is no selection for learning to be involved.

A possibility considered at the outset of the chaffinch study was that song learning, if it normally took place from the father, as was likely where it occurred in fledglings, could enable song to be used as an indication of kinship. Thus, for example, females might be able to avoid inbreeding by selecting males with songs unlike those sung by their fathers. A similar idea, based in this case on selection between different odours, had been tested on mice by Gilder & Slater (1978), at about the same time as Bateson (1978) put forward the hypothesis that animals select mates to give an optimal degree of outbreeding. The idea that song can be used to assess kinship cannot be examined on wild chaffinches without a marked population followed for a number of years, but seems unlikely in view of the fact that learning often occurs well after fledging. A suitable alternative species is, however, the zebra finch, in which Immelmann (1969) showed close similarity between the songs of sons and their foster-fathers in the laboratory. An attempt was made to test this with a breeding colony of this species. Paper 14 resulted from this work and shows that, unexpectedly, individuals preferred to mate with a close relative rather than a stranger. It could, nevertheless, be that an individual of intermediate relatedness would have been preferred to either, as Bateson's model would predict. It is uncertain from the results whether song was the cue used in assessing relatedness, but it seems unlikely that it would be useful in the wild. The close match between father and son found by Immelmann depended on their being left together for 80 days; our birds were left with their parents for 50 and, while the songs showed recognisable similarities, the match was not exact; in the wild, young zebra finches probably leave their parents at around 35 days of age, suggesting that even less exactitude would prevail.

If there is one functional question about bird song which is as controversial as the significance of song learning, it is that of why birds have song repertoires. In some species individuals have only a single song type, but in others they may have many hundreds or even thousands. Individual male chaffinches have a modest repertoire, ranging from one to six types. Why this high variability in repertoire size persists amongst birds of the same species is also an intriguing question. The functional significance of repertoires has been much more extensively studied in other species (for example, by Krebs (1976) and Krebs, Ashcroft & Webber (1978) on the great tit), but preliminary examination suggests that there will be no easy answer for the chaffinch (paper 12). One of the aims of this paper was to examine the possibilities and issues involved to see which are the most plausible hypotheses and how they might be tested: while some hypotheses fit the data better than others, it is not possible to choose amongst them with any confidence at this stage. This is one of several aspects of chaffinch song on which more work is planned or in progress. For such an apparently small and trivial topic, the song of the chaffinch has proved an amazingly fruitful source of insights into the principles of animal behaviour in the past: there is every indication that it may continue to be so in the future.

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THE TEMPORAL PATTERN OF BEHAVIOUR IN ISOLATED MALE ZEBRA FINCHES: TRANSITION ANALYSIS

by

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(With 3 Figures)

(Rec. 15-VI-1971)

INTRODUCTION

In recent years many studies have been carried out within the broad field of temporal patterning. The methods of approach employed have varied widely, but most fall under three headings:

(i) Studies of the distribution in time of one act, or a restricted group of acts, under fairly rigorously controlled conditions (*e.g.* feeding in rats: LE MAGNEN & TALLON, 1966; strutting and gobbling in turkeys: SCHLEIDT, 1964a).

(ii) Ethological studies of a wider variety of acts specific to a given situation, but not usually in controlled surroundings (comfort movements in skylarks: DELIUS, 1969; agonistic behaviour of great tits: BLURTON-JONES, 1968; courtship of glandulocaudine fish: NELSON, 1964).

(iii) Studies of temporal patterning in social situations, which examine the effects of the behaviour of conspecifics on that of the individual rather than sequences within an individual (rhesus monkeys: ALTMANN, 1965; crayfish: HECKENLIVELY, 1970; canaries: MULLIGAN & OLSEN, 1969).

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[1] We are particularly grateful to Dr J. E. COHEN for drawing our attention to the iterative procedure employed here, and to Professor J. MAYNARD SMITH who had earlier worked out an alternative one for our use. Mr D. COOKE kindly gave advice on statistical methods, and other useful points emerged from discussion with Dr P. P. G. BATESON and Mr J. N. M. SMITH. Both research and manuscript have benefited greatly from suggestions by Professor R. J. ANDREW. Computing facilities were made available by the University of Sussex Computing Centre. This research is financed by a grant from the Science Research Council to P.J.B.S.

The first two of these are the most relevant here, as they involve analysis of temporal patterning within the individual. Both, however, have disadvantages. A major source of difficulty is in deciding the extent to which the pattern of behaviour shown in a social situation, or in the wild state, is modified by environmental influences. In most cases it is probably safe to assume that both endogenous and exogenous factors play a part in moulding it. On the other hand, when only one or two acts are examined, the analysis ignores the important possibility that their pattern is to some extent determined by interactions with acts which are not considered. SCHLEIDT (1964b) has shown, for instance, that the probability of strutting is greatly increased for a few seconds after the occurrence of gobbling, so that the temporal pattern of one is influenced by that of the other. In the present analysis an attempt has been made to marry these different approaches by studying a wide variety of behaviour patterns under rigorously controlled external conditions. While such a method is bound to lead to problems connected with the large amount of data to be analysed and the many possible ways of doing so, it does afford the prospect of being able to unravel some of the complexities of the pattern intrinsic to the individual. This can subsequently be compared with that shown when external conditions are varied.

The main features of the approach may be summarised as follows:

1. Birds to be studied were placed in total auditory and visual isolation from both other individuals and changes in the environment generally. In this way the patterning of behaviour can be examined under relatively constant conditions: the behaviour seen can be assumed to be generated within the individual, rather than in response to changing external cues.

2. As many behaviour patterns as possible were recorded and analysed. Acts were only lumped together where it was not practically possible to separate them, or where their association was so strong that to separate them would not be useful. Recording in this way enables one to look for *any* interaction between acts which may exist. Some workers have in the past tended to examine only those groups falling into a particular functional category (*e.g.* courtship or comfort movements). This is unfortunate, for acts which are functionally unrelated may have causal factors in common, or occur close together in time, even when the reason why they should do so is not obvious. The study of relationships between acts should therefore be approached with as open a mind as possible.

In this study *a priori* grouping of acts has been kept to a minimum.

3. A bird was chosen as experimental animal because of the relative ease with which they may be isolated from the visual and auditory stimuli which are most likely to modify their behaviour. Zebra finches are easily kept in captivity and their size allows them wide freedom of movement within a fairly small cage, such as must be used in a sound-proof chamber. They also have a number of relatively easily defined behaviour patterns, particularly those connected with care of the body surface and vocalizations.

The present paper deals with transitions between acts, mainly comparing the frequencies of particular pairs with those which would have been expected on a random model. This method has often been used in the past, but frequently the methods employed to analyse the data have been unsatisfactory. It is one of the aims of this paper to explore ways in which these difficulties may be overcome.

MATERIALS AND METHODS

The birds used were ten young adult male zebra finches (*Taeniopygia guttata*), all of which had been obtained from dealers shortly before use. Three weeks before testing, each bird was removed from the monosexual group in which it had been kept and placed in visual isolation from other birds. It was transferred to an observation cage in a sound-proof chamber one week prior to use. No chamber was opened less than 18 hours before a watch. Each bird was observed for two hours: from 9.15 to 10.15 a.m. on one day, and from 11.15 a.m. to 12.15 p.m. on the next (all times approximate). Lighting within the sound-proof box was provided by a 30 watt strip light controlled by a timeswitch to give 12 hours light daily (7 a.m. to 7 p.m.): all observations thus took place during the morning, at a time when this species is fairly active. Temperature within the box was in the range 22-24°C, and was controlled at this level by air-conditioning in the experimental room. Each box was equipped with a fan giving continuous ventilation.

The observation cages measured 28 × 30 × 39 cm. The back wall of each was wooden, and the front was made of glass with fine wire-mesh embedded in it. The other sides and top were of coarse wire-mesh to ensure adequate ventilation. The floor consisted of a metal tray with wire-mesh mounted 2 cm above it, so that seed dropping through it could not be retrieved. A single wooden perch ran across between the wire sides, and seed and water hoppers were fixed at either end of this. A photocell mounted behind each hopper was used to record when the bird pecked into the trough. A dish of sand was present on the floor and a piece of cuttlefish bone was attached to the wires.

The whole of the observation cage could be seen through a double glass window at the front of each box, but this was normally covered with a shutter. At least 18 hours before watches a microphone was put into the box and a television camera was placed outside the window facing into it. A black sleeve from the box to the camera excluded any other visual stimuli from outside. During each observation session two observers watched the behaviour of the bird on closed-circuit television, and each recorded the occurrence of up to five behaviour patterns by pressing buttons connected to different channels of an Esterline-Angus event recorder. Each observer also had an extra button with which mistakes could be corrected. Feeding and drinking were recorded automatically at the same time. The session was preserved on video-tape and this was later played through again and the timing of a further set of acts transferred to the paper chart. Each watch started with the depression of a button, which placed a light signal on the video-tape and a spike on the paper chart. These events were later used to synchronise the start of playback, and any slight discrepancies between the timing of the two runs were further allowed for by using a channel for song on both occasions. In this way the timing and approximate duration of 16 behaviour patterns were recorded on paper for each bird.

CATEGORIES OF BEHAVIOUR

Before proceeding further, it is necessary to list the behaviours included in this study, and to indicate where a particular category may be composite. The letters in brackets after each behaviour are the shorthand form used for it in the figures and tables.

Feeding (Fd): The food used was small panican seed to ensure adequate flow from the hopper. Occasional firing of the photocell without pecking into the trough was corrected by means of a cancel button. The photocell circuit was adjusted as far as possible to record individual pecks: sometimes two appeared as one on the record when the bird did not lift its head high enough between them. This is not, however, a problem in the type of analysis employed here.

Drinking (Dr): This is probably a composite category. While some birds could clearly be seen to drink, and only to drink, at the trough, others dipped their beaks in the water and subsequently raised and shook their heads, so spreading water widely about the cage. In some cases this behaviour was so common as to appear to be a stereotype. Its exact function is not known: it does not appear to substitute for bathing, as it is not eliminated by supplying a water bath as well, nor is it usually followed by preening. It could not be reliably separated from drinking as zebra finches, unlike most birds, suck water from the surface (IMMELMANN, 1965). It may, in any case, involve some ingestion.

Sand taking (Snd): recorded whenever the bird pecked into the sand dish.

Cuttlefish bone taking (CfB): Zebra finches do this rather frequently, and it is difficult to discern the extent to which it involves ingestion. It is similar in form to the gnawing at parts of the cage which is included in the category of stereotypes discussed below, and may be equivalent to this in some cases.

Locomotion (Loco): Ideally this would have been best recorded automatically, but no system could be devised to do so at the same time as letting the birds move freely about the cage. They could, for instance, perch on the walls, which had to be made of wire for ventilation. The locomotion button was pressed every time the bird flew or moved more than approximately two inches on the perch or floor. In general the decision to press the button was not difficult, as the birds seldom moved around slowly, but tended to be highly active or inactive. A wide range of variation was found between birds in the amount of locomotion shown in the test situation.

Stereotypes (Styp): The range of stereotypes shown was very similar to that described by SARGENT & KEIPER (1967) for caged canaries, though in no case did they appear to be so frequent or persistent. Route tracing was observed but is included under locomotion. Water spraying, which is described above, and very persistent eating of sand or gnawing at cuttlefish bone, which were shown by some birds, may also have been individual stereotypes. The following other behaviours definitely belonged to this category, and were recorded under it: gnawing and pecking at parts of the cage, persistent gnawing at the feet, and forcible pulling at feathers (this was only shown by one bird and was quite distinct from preening). This is, of course, a composite category.

Singing (Sng): This is the only vocalisation considered in this analysis. Both loud and soft call notes were also recorded, but occurred so often, especially during locomotion, that the behaviours with which they are associated are not most easily analysed in a transition matrix.

Bill-wiping (BW): The bill is wiped rapidly against the substrate.

Ruffling (Rf): This term is used for brevity: the behaviour can also be referred to as feather-settling. The feathers are raised, shaken and flattened again.

Wing-shaking (WS): This behaviour was only shown by four birds and so is not considered in detail here. It occurs mainly towards the end of long bouts of preening: the body is hunched and the wings are briefly extended and moved rapidly up and down.

Preening (Pr): This term is restricted to the grooming of feathers and legs with the bill. It was not feasible to record a distinction between the different areas of the body being preened.

Scratching (Scr): A leg is raised under the wing to scratch the side of the head; both sides of the body are considered together.

Stretching (Str): There are two types of stretching. One is the unilateral wing and leg stretch; the other is the bilateral stretching upwards of the closed wings. They usually occur in sequence and so were treated as a unit in analysis.

Gaps in behaviour (Gap): No method was required for recording these, but in analysis any interval between other acts of more than 10 seconds was classified as a gap. The preceding and following acts were regarded as going to and from this category rather than directly from one to the other. The aim in including this category was to exclude from consideration transitions between acts which were separated by longer time intervals, the intervention of which is assumed to make it less likely that the following act is influenced by the preceding. During a gap the animal may perform any behaviour which is not included in the other categories:

this covers activities as diverse as brief breaks in locomotion during which the animal is alert and producing call notes and long periods of drowsiness or sleep, although the latter are unusual in the morning. This is thus a heterogeneous grouping and does not simply indicate that the bird is resting.

It will be seen from the above list that not all behaviours can be separated into discrete categories: the consequences of this, and of omitting from consideration extremely common acts like call notes and head movements, will be discussed below.

TECHNIQUES FOR ANALYSING TRANSITIONS

The majority of previous analyses of transitions in the behavioural literature have considered all possibilities, from which a complete matrix of observed frequencies can be composed (*e.g.* WIEPKEMA, 1961; BLURTON-JONES, 1968; DELIUS, 1969). From this it is an easy matter to calculate the expected number of any given transition based on a random model:

$$\text{Expected} = \frac{\text{Row total} \times \text{Column total}}{\text{Grand total}}$$

The major drawback of the above method is that it includes consideration of transitions between a given behaviour and itself. While it is possible to devise a reasonably objective criterion for the point at which one act ceases and the next begins, the criterion chosen for one behaviour will not be comparable with that for another. For example, a single act of song might be taken as one phrase, or as a series of phrases separated from all others by a specified time interval. A choice of criteria is also possible for most other behaviours: in the case of locomotion it would be very difficult to decide upon one other than arbitrarily. If one is only interested in the temporal pattern of a single behaviour, the definition of an act does not matter much, as long as it is objective and consistently applied. But this is very far from being the case in a transition matrix. Here the number of song-song transitions might be greater than that of locomotion-locomotion, or *vice versa*, purely because of the criteria chosen. As the number of every transition contributes to the grand total, the criterion used for each behaviour will have an effect on all the expected values throughout the matrix. This makes any statistical tests applied virtually meaningless, except where the main concern is to demonstrate that certain behaviour patterns occur in bouts.

A second point is that most types of behaviour tend to occur in bouts, and this means that homogeneous transitions are likely to be more frequent than heterogeneous ones. This is often apparent in papers where the complete matrix of observed transitions has been published. Comparison of observed and expected figures thus gives high positive values on the descending diagonal of the matrix (A-A, B-B, *etc.*), and a tendency towards negative values elsewhere. The first of these two objections makes the whole procedure suspect; the second shows that it is predisposed to demonstrate that certain acts occur in bouts, and therefore to hide more interesting associations.

The answer to this problem lies in only considering those transitions which involve two different behaviours. WALLIS (1961) recognised the usefulness of this, but calculated expected values so that these added up to the correct totals in each row but not in each column. The model is thus only partially related to the data. GRANT (1963) followed WALLIS in part by eliminating the descending diagonal of his transition matrix, but subsequently calculated expecteds according to the formula given above: the row and column totals are thus correct, but only because expecteds have been calculated for the eliminated boxes. This is clearly invalid.

In the present analysis there are two reasons why certain boxes in the transition matrix cannot be occupied. Firstly, homogeneous transitions are not considered, so that no figures appear in any box on the descending diagonal. Secondly, the organisation of the experimental cage was such that no ingestive item (feeding, drinking and sand or cuttlefish bone taking) could follow any other without locomotion occurring in between. Thus twelve further boxes in the matrix are predisposed to be empty. Expected values for each box must therefore be calculated so that zero appears at all these points on the matrix. They must also add up to the correct row and column totals, so that the number of bouts of each type of act is kept equal to that specified by the data. The expecteds will then indicate the number of bouts which would follow one another were these bouts in random sequence.

GOODMAN (1968) gives a method for calculating transition frequencies which fulfils the above criteria. It is more complicated than that appropriate to a complete matrix, as the expected frequencies can only be arrived at by a process of iteration. It is, however, relatively easy to program, and in the present study, the raw data from each bird have been analysed in this way using an ICL 1905 computer. The program produced a 14 × 14 matrix for each bird (there being 14 categories of behaviour in the above list) giving both observed and expected frequencies. An example is shown in Table 1.

TABLE 1

The matrix of transitions shown by bird 27.
In each cell the observed figure is shown above the expected.
(For abbrevations see text)

	FOLLOWING ACT														
PRECEDING ACT	Str	Loco	Sng	Pr	Scr	BW	Snd	Styp	Dr	Fd	Gap	Rf	Wh	CfB	Total
Str	— —	3 7.2	3 2.0	3 0.8	0 0.2	2 0.5	0 0.0	0 0.3	1 1.1	0 0.6	1 0.2	1 0.4	0 0.1	0 0.5	14
Loco	5 7.2	— —	129 104.0	8 41.9	3 9.3	16 23.8	2 1.2	23 17.3	82 57.8	42 31.6	7 9.9	5 20.5	0 5.2	32 24.3	354
Sng	2 2.0	121 104.0	— —	21 11.8	2 2.6	3 6.7	0 0.3	4 4.8	1 16.2	3 8.9	2 2.8	11 5.8	0 1.4	4 6.8	174
Pr	1 0.8	19 42.4	18 11.8	— —	9 1.1	0 2.7	0 0.1	1 2.0	2 6.6	1 3.6	2 1.1	15 2.3	8 0.6	2 2.8	78
Scr	0 0.2	2 9.3	4 2.6	7 1.1	— —	1 0.6	0 0.0	0 0.4	0 1.5	0 0.8	1 0.3	1 0.5	2 0.1	0 0.6	18
BW	2 0.5	25 23.8	2 6.7	6 2.7	0 0.6	— —	0 0.1	0 1.1	6 3.7	2 2.0	0 0.6	2 1.3	0 0.3	0 1.6	45
Snd	0 0.0	2 1.2	0 0.3	0 0.1	0 0.0	0 0.1	— —	0 0.1	— —	— —	0 0.0	0 0.1	0 0.0	— —	2
Styp	0 0.3	18 17.3	2 4.8	0 2.0	1 0.4	1 1.1	0 0.1	— —	3 2.7	3 1.5	1 0.5	2 1.0	0 0.2	2 1.1	33
Dr	3 1.1	69 57.8	0 16.2	3 6.5	1 1.5	16 3.7	— —	1 2.7	— —	— —	2 1.5	0 3.2	0 0.8	— —	95
Fd	1 0.6	39 32.3	1 9.0	5 3.6	0 0.8	2 2.1	— —	1 1.5	— —	— —	3 0.9	1 1.8	0 0.5	— —	53
Gap	0 0.2	7 9.9	0 2.8	5 1.1	0 0.3	3 0.6	0 0.0	2 0.5	0 1.5	1 0.8	— —	1 0.6	0 0.1	0 0.7	19
Rf	0 0.4	16 20.6	12 5.8	8 2.3	2 0.5	1 1.3	0 0.1	0 1.0	0 3.2	0 1.8	0 0.6	— —	0 0.3	0 1.4	39
Wh	0 0.1	1 5.2	0 1.4	9 0.6	0 0.1	0 0.3	0 0.0	0 0.2	0 0.8	0 0.4	0 0.1	0 0.3	— —	0 0.3	10
CfB	0 0.5	33 23.7	3 6.6	2 2.7	0 0.6	0 1.5	— —	1 1.1	— —	— —	0 0.6	0 1.3	0 0.3	— —	39
Total	14	355	174	77	18	45	2	33	95	52	19	39	10	40	973

For statistical analysis, the data from each bird were kept separate. A common technique used by other authors is to mass the data from all individuals and thus boost the size of the figures in each box to make statistical treatment easier (WIEPKEMA, 1961; BLURTON-JONES, 1968; DELIUS, 1969). While this may be the only available course of action in field studies where individuals cannot be identified, it can lead to the data being markedly altered by one strongly aberrant individual, so that it is hard to draw conclusions about the population as a whole. It is usual also to test matrices such as these for non-randomness using χ^2. WORTIS (1969) pointed out that this may be invalid if the data shown in the contingency table do not represent truly independent trials. This may not be a serious objection, but the constraints of χ^2 (*i.e.* the necessity for the expecteds to be over a certain minimum value before the test can be used) make it difficult to apply to transition matrices without massing data or examining one individual very exhaustively, as did NELSON (1964). Neither of these methods is useful as a guide to population tendencies.

Two different methods of analysis were used here, and these will be dealt with in the following section.

RESULTS

1. GENERAL COMPARISON WITH THE RANDOM MODEL

The following technique was used to determine whether a particular transition was commoner than would have been expected on a random model. For each transition an index was calculated by subtracting the expected from the observed (O-E). This index followed an approximately normal distribution when the ten values (one for each bird) for each of several transitions were plotted. On a random model, the mean value of the index should be zero, observed being equal to expected. To determine whether the actual value diverged significantly from zero, the standard error of the mean value of the index for each transition was calculated and multiplied by student's t (for 5% probability and n-1 (= 9) degrees of freedom). If the mean was greater than this figure, it indicated that it was significantly different from zero ($p < .05$) (BAILEY, 1959). The measure of significance is, of necessity, an approximate one as no methods appear to be available at present for the rigorous statistical treatment of individual cells in a transition matrix.

Another possible index, which would theoretically be expected to follow a normal distribution more closely than O-E, is $O\text{-}E/\sqrt{E}$. This was also tried and yielded very closely similar results, though giving slightly more significant associations. It was decided to use O-E in preference because this index makes it less likely that transitions will be found to differ from random in situations where there is a wide spread of results amongst the birds.

This method is best at dealing with transitions which are common in absolute terms. Where a transition is rare, many birds may have zero as the observed and this is bound to be less than the expected. In such cases the distribution of the index diverges markedly from normality and effects which are apparently significantly negative occur rather frequently. These must be treated with caution, but as it is largely positive effects which are of interest, the test errs on the side of conservatism. In the 14 × 14 matrix considered here, 170 boxes could be occupied. Wing-shaking is included in this matrix, but was not shown by most birds and so should be excluded from discussion: this leaves 144 boxes. Of these possible transitions, 14 were found to be more common than random and 37 less common. No significant difference was found in the remaining 93. The general, but unexciting, conclusion that the matrix is not a random one can be deduced from the fact that more transitions differ significantly from random than would have been expected due to chance. However, the occurrence of positive associations in only 10% of boxes requires some explanation.

TABLE 2

Number of bouts of each behaviour recorded for each bird
(For abbreviations see text)

Bird number	14	29	6	23	25	12	5	22	27	26
Str	8	7	8	4	4	6	6	6	14	12
Loco	292	325	209	419	473	80	222	154	355	246
Sng	302	133	92	223	194	51	132	109	174	413
Pr	44	55	34	33	33	37	38	36	78	94
Scr	11	17	7	1	10	12	19	6	18	17
BW	62	45	73	33	41	7	46	34	45	77
Snd	2	1	28	6	23	6	6	57	2	4
Styp	1	60	13	11	34	3	96	28	33	108
Dr	18	101	119	15	27	12	26	14	95	45
Fd	19	92	12	107	166	7	52	7	53	48
Gap	2	29	21	5	33	67	22	56	19	19
Rf	29	33	37	38	43	23	30	37	39	51
WS	0	24	0	0	0	0	5	1	10	0
CfB	3	19	0	45	102	0	41	12	40	3
Total	793	941	653	940	1183	311	741	557	975	1137

The first point to be mentioned is that behaviour patterns differed greatly in their absolute frequency. In many birds locomotion was particularly common and the majority of transitions were to or from it (Table 2). If all transitions were like this, every second behaviour would be locomotion and the only possible sequencing of bouts would be that obtained: the expecteds would then be the same as the observeds. Thus the results of birds showing a very large quantity of transitions involving one particular behaviour will approximate to random. This is why it was not thought fruitful to consider call notes in the present context.

Secondly, with this method of analysis, fewer significant results might be expected than if χ^2 were performed on the massed data. One or two individuals showing a particularly high frequency of a transition can make χ^2 significant, whereas here all birds are equally weighted and individual variation will lead to a greater spread of results and thus a lower likelihood of achieving significance. Before this analysis was carried out, the massed data from three birds were examined using χ^2. Out of 110 possible boxes, 22 were significantly positive at the 1% level and two further at 5%. This suggests that the χ^2 technique tends to give a larger number of significant results and lower probabilities (only four of the transitions in Figure 1 were significant at the 1% level).

Thirdly, fewer positive associations might be expected here because of the heterogeneity of the behaviour patterns considered. While it is perhaps to be expected that courtship, agonistic or grooming movements will occur in ordered sequences, as they have been shown to do in many cases, it is less obvious that, for instance, preening, locomotion, feeding and singing should be other then randomly associated.

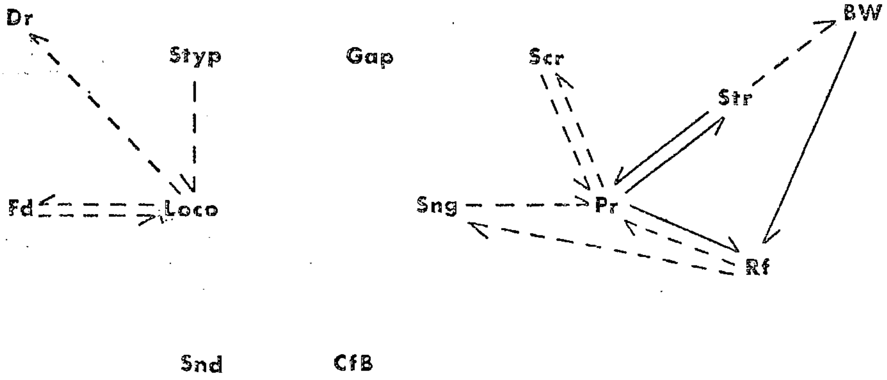

Fig. 1. Transitions which were significantly commoner than random. Complete arrows: $p < .01$; broken arrows: $p < .05$. (For abbreviations see text).

2. THE TRANSITIONS WHICH DIVERGE FROM RANDOMNESS

Figure 1 shows the significantly positive connections between acts found in this analysis. The majority of arrows are between the various acts concerned with grooming, and song also has one or two non-random associations with this group. The negative relations are too numerous to portray, but it is interesting that none exists between any one of the grooming movements and any other (*i.e.* preening, scratching, stretching, ruffling and bill-wiping). These behaviours do thus seem to form a group with some degree of shared causation as well as function. Song, however, has as many positive connections within the group as do scratch and bill-wipe. It tends not to lead to stretch, but otherwise has no negative relations with grooming movements. Thus, though functionally unrelated to these other behaviours, an objective classification into groups might include it with them on causal grounds. At this stage, however, we do not regard the massing of various behaviour patterns under single headings as being the best way of proceeding. Apart from anything else, it hides differences in causation and interaction within the group, and also differences between the grouped patterns in their interactions with other behaviours. These points have already been made by HINDE (1959, 1970) in his criticisms of the use of drive concepts, and by ANDREW (in press) who, on similar grounds, suggests the breaking down of behaviour into smaller units during preliminary analysis than has been customary in the past. The occurrence of certain behaviour patterns in a group need not necessarily imply a motivational similarity between them, although this is one possible explanation. The nature of the causal factors which lead them to be temporally related cannot be determined by purely descriptive studies such as this.

Because of the above considerations, we intend here to examine the interactions between behaviours as individual acts rather than as groups. Any further references to groups will be to certain defined combinations of behaviour patterns which are found to occur in association with one another.

This statistical analysis has shown that there are a number of significantly positive transitions amongst the grooming movements and song, and that other positive effects exist between locomotion, feeding, drinking and stereotypes. The polarisation of behaviour into two groupings, with some intermediates, is suggested by the fact that 29 out of 37 negative effects cross from one set of five acts (locomotion, drinking, feeding, sand, cuttlefish bone) to another (preening, scratching, stretching, ruffling, bill-wiping).

3. TRANSITIONS WHICH ARE COMMONER THAN OTHERS

Figure 1 was concerned only with those transitions which are significantly positive compared with random. For detailed analysis, this is not a very useful criterion because, in a transition matrix, the frequency of one transition depends to a large extent on that of others. As already mentioned, the high number of positive effects on the descending diagonal of a complete matrix tends to give negative effects elsewhere. In the truncated matrix used here, if a particular transition is commoner than expected, others involving one or other of the same acts will tend to be rarer. The most interesting information is whether a particular transition is commoner relative to the other possibilities rather than in relation to a random model. On the basis of this argument, Figure 2 is drawn to display all transitions having a mean index more than one standard error away from zero. This criterion selects the 39 transitions which are most common compared with their expecteds: any other criterion might have been chosen, leading to a greater or lesser number of arrows in the figure.

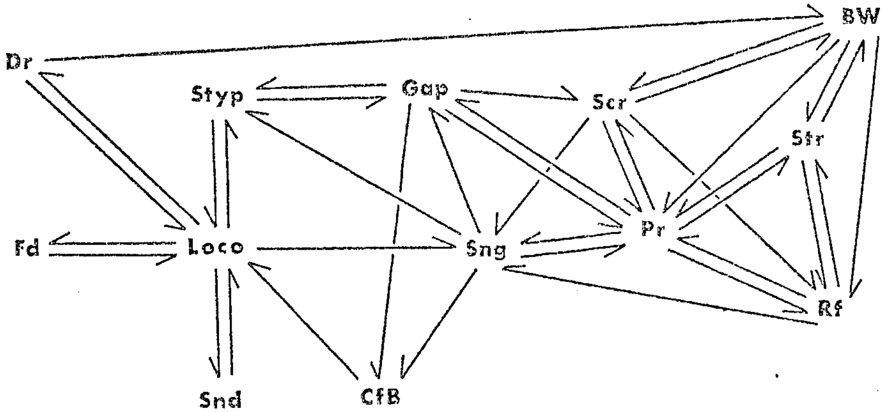

Fig. 2. The transitions which were commonest compared with their expecteds. These are all those having a mean index (O-E) more than one standard error greater than zero (For abbreviations see text).

The immediately striking thing about Figure 2 is that it can be drawn in such a way that few arrows travel very far. The polarisation of behaviour, which was suggested above, is supported here. We shall consider three groupings in turn:

a) Locomotion, feeding, drinking and sand taking.

Drinking, unlike other forms of ingestion, often leads to bill-wiping, presumably stimulated by water remaining on the beak. Figure 2 also shows that sand taking, feeding and drinking tend to be preceded and followed by locomotion. This could be because these ingestive items tend to group, but the constraints of the cage determine that locomotion must take place between them. The impression was certainly gained during observation that drinking tended to occur either during or shortly after feeding. No other connection between the four ingestive acts was obvious, however. On the other hand, the relationship between them and activity was clear: ingestion occurred during short breaks in flying around the cage and, in active birds, was frequently interrupted by short periods of locomotion. Whatever the relations between the ingestive items, which cannot be shown by the present analysis, feeding, drinking and sand taking tend to occur while the bird is active.

b) Stereotypes, cuttlefish bone taking, gap and singing.

These four categories form a very heterogeneous intermediate group with connections both with each other and with other acts. Stereotypes and gnawing at cuttlefish bone both have arrows from gap and song and to locomotion. This lends weight to the previously mentioned suggestion that pecking at cuttlefish bone may be a stereotype. One bird which was given cuttlefish bone after several days without, alternated pecking at it with flying to drink. This was not noted in others, and may indicate that they were not ingesting it, but gnawing it as they would other parts of the cage. The wide difference between birds in the number of bouts of gnawing at cuttlefish bone (Table 2) also suggests that it was a stereotype developed by some but not others.

Both gap and song share a number of connections, suggesting that they may have some causal factors in common. A gap in behaviour might be expected to indicate that the tendencies to perform any of the specific behaviours being recorded is low and also to herald a change in behaviour: the longer the gap, the less likely the behaviour after it is to be influenced by that before. The similarity in connections between gap and song prompts the suggestion that singing is a low priority act which only occurs when a gap in other behaviour allows it. Interestingly, this mirrors the conclusion of IMMELMANN (1968) that song in the Estrildidae is 'just a sign of a very tranquil mood, not influenced by any other motivation'. Song also bears a similarity to gap in that it often occurs between dissimilar and unrelated activities: seven behaviours are connected to it in Figure 2, but only one (preening) by arrows in both directions. Of all the behaviour patterns considered here, locomotion and preening show the strongest negative relation with each other. The most direct route form one to the other in Figure 2 is through song. In many of the birds tested it was particularly noticeable that a period of activity tended to end with singing, followed by an alternation between singing and preening. This again points to song being a transitional act.

If gap and song share some causal factors, and likewise stereotypes and pecking at cuttlefish bone, it remains to be pointed out that the first two tend to be followed by the last two. This suggests that stereotypes follow periods when other tendencies are low. That they are less common in a complex environment or a social situation (KEIPER, 1970) may stem from the rarity of this circumstance under these conditions. It should, however, be noted that the ordering of acts suggested here (singing and gaps being followed by stereotypes and cuttlefish bone taking) was not confirmed by the analysis of directional tendencies given below and this argument should therefore only be regarded as tentative.

c) Preening, scratching, stretching, ruffling and bill-wiping.

The fact that grooming acts tend to be associated has already been mentioned, as the strength of this association was sufficient to show up in Figure 1. Their outside connections are largely through gap and song (categories which were suggested above to be transitional), and through the fact that bill-wiping tends to follow drinking.

In summary then, it appears from this section that the behaviour oscillates between periods of high and low activity, ingestion occurring mainly in the former and grooming movements during the latter. Songs and stereotypes appear during the period of transition between these two phases. As an alternative to visualising the cycles of behaviour as being between active and inactive periods, they can be seen from Figure 2 to involve a change from self-orientated behaviour (grooming acts) to behaviour orientated to the outside (locomotion, including active inspection of the surroundings; gnawing and pecking at parts of the cage; ingestion). Such a switch in attention may partly explain why behaviours fall into these groups.

4. DIRECTIONAL TENDENCIES

A further method of analysing the transition matrix does not depend on the calculation of expecteds. If bouts succeed each other randomly, transitions of the type A-B and those of the type B-A would be expected to be equal in number. Slight divergences from this can be seen to occur in Table 1 where row and column totals are not the same, due to the inclusion of the first and last transitions in each observation period, but as these are small it seems safe to ignore them. By using a Wilcoxon matched-pairs test one can compare the frequency of A-B with B-A to decide whether transition is more frequent in one direction than in the other. The arrows in Figure 3 indicate the switches which are significantly commoner than their opposites.

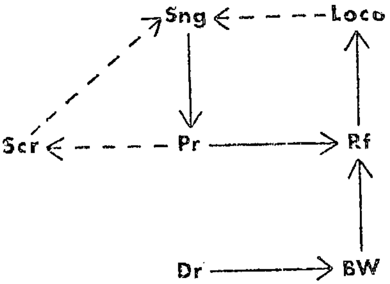

Fig. 3. Transitions which are commoner in one direction than in the other. Arrows indicate commonest direction. Complete arrows: $p < .01$; broken arrows: $p < .05$. (For abbreviations see text).

Eight of the 72 tests yielded a significant result: once again more than one would expect due to chance. Several of these mirror the discovery of arrows in one direction, but not the other, in Figures 1 and 2: for instance, drinking leads to bill-wiping more often than *vice versa.*

Two effects found here, and also present in Figures 1 and 2 are particularly striking. The first is that bill-wiping tends to be followed by ruffling ($p < .01$: Figure 1), and this transition is significantly commoner than in the other direction ($p < .01$: Figure 3). These behaviours are particularly common in birds with damp plumage, and ANDREW (1956) suggested that they are produced in response to foreign material on the bill and body feathers. In the present situation there was no such obvious common external stimulus for them, nor does it seem likely that bill-wiping produces the peripheral stimulus for ruffling (as it might if it led to derangement of the plumage). It would seem most probable that the link between them is at the neural level and that bill-wiping leads to a reduced central threshold for ruffling. Ruffling is a curious behaviour pattern as it shows no tendency to occur in bouts: if it is induced by a source of irritation on the plumage, it must be extremely efficient at removing this.

The second interesting combination is the sequence song-preen-ruffle, again apparent in both Figure 1 and Figure 3. This is thus a common sequence both relative to other possibilities and also to its own occurrence in the opposite direction. Strictly speaking one can only deduce from this analysis that each of the two pairs comprising the trio is common in this way, not the trio itself. However, observational evidence suggests that the trio is also common. Early in the inactive phase of the behaviour cycle, an alternation between singing and preening is particularly common, with the change from one to the other taking place at a rate of several times per minute. In these circumstances ruffle often follows preen and precedes song. The most likely explanation of this sequence is that each of them produces the peripheral state conducive to the performance of the next. Singing involves a raising of the feathers in certain areas of the body. On lowering again these may be locally displaced and so stimulate preening, while ruffling may serve to flatten them again after preening.

The conclusion from this section is that certain pairs of behaviour patterns are more likely to occur in one order than in the other. In some instances it is possible to suggest a reason why this might be the case, based on the hypothesis that the performance of one generates peripheral stimulation appropriate to the performance of the next. In other instances the connection is less clear, and it is possible that the pattern is to some extent centrally determined.

DISCUSSION

WIEPKEMA (1961) went on from his analysis of transitions in the courtship of the bitterling to carry out factor analysis on the results, in an attempt to explain the behavioural interactions in terms of major underlying variables. An index was calculated for each transition (O/E), and these were then ranked either across or down the matrix, depending on whether preceding or following was being considered. The factor analysis was based upon correlations of the ranks between all pairs of behaviours either for following or preceding. Thus two behaviours were considered to share causation if their relations with other acts were similar, in the same way as has been argued here. Depending on which set of correlations was used for factor analysis, two separate models could be devised: WIEPKEMA's subsequent causal analysis was based on that for following.

One problem with factor analysis based on transitions is that there are differences between following relations and preceding ones: WIEPKEMA's model would have been rather different had the latter been chosen rather than the former for further discussion. The reason for this is probably that courtship responses tend to occur in chains, and transitions in a particular direction will be very different in frequency from the same in the reverse direction. Only to the extent that behaviours tend to both lead to and come from a similar range of other acts will the two models be equivalent. A striking divergence from this is found in our zebra finch data: song tends to be preceded by a very different range of behaviours from those that follow it (Figure 2). If these are ranked in order of likelihood (given here by Mean Index / Standard Error, but essentially similar to WIEPKEMA's measure), and the ranks for preceding and following correlated with one another, the coefficient obtained is insignificant (Spearman rank correlation coefficient, $r_s = + .098$). Thus the correlations with other behaviours would be expected to be quite different for preceding from those for following.

A further problem with factor analysis is a general one, which has been pointed out by ANDREW (in press). This is that the use of the method assumes the usefulness of describing causation in terms of a few variables, or factors. The nature of these factors is open to question: some behaviour patterns may appear together because they are pushed into a group by the close relations between other acts or, indeed, because of the constraints of the environment. Similarity of motivation cannot be inferred. Furthermore, as ANDREW comments, it is easy to explain the occurrence of behaviours with loadings on two factors in terms of a conflict theory of motivation. This tends to confirm preconceived notions.

The transition analysis used here has revealed those acts which are most likely to succeed one another, and has given a general picture of the groups of behaviours which occur in association. This provides a useful basis for comparison with the pattern of behaviour after experimental manipulation. It is also a fruitful source of hypotheses concerning underlying causation and a pointer to certain relationships which deserve closer study. From the point of view of causal analysis, it appears particularly important to realise that acts may be closely associated because of common causation (*i.e.* A-B and B-A occur more than expected and/or A and B have similar links with other behaviours) or because one generates the other in some way, either central or peripheral (*i.e.* A-B more than B-A). Associations between behaviour patterns may arise by a combination of the two mechanisms (as may be the case here with singing and preening which are linked by a double arrow in Figure 2 suggesting common causal factors, while also present in Figure 3 showing that song tends to lead to preening more often than *vice versa*). It is also possible that in some cases two acts may appear to share common causal factors because each generates the other, but occurrences of this type could not be detected without experimental intervention.

As far as a full understanding of the temporal pattern of behaviour is concerned, transition analysis must of course be supplemented by other methods. As the inclusion of homogeneous transitions tends to bias the data and involves unwarranted assumptions, the method used here has avoided this. It thus gives no information on the organisation of acts of a particular type into bouts. Nor can the analysis of pairs be used to examine sequences of behaviour longer than two patterns. Triplet analysis would be useful here to determine whether longer sequences can be explained adequately by the frequencies of the pairs, as in a first-order Markov chain model, or whether higher order dependencies are in operation. If the results from different animals are not massed and several animals are tested, this necessitates the collection of a massive quantity of data. There are 1983 possible types of triplets in the data presented here. The treatment of triplets is rather easier than that of pairs: the expected frequency of A-B-C can be calculated from the observed frequencies of A-B and B-C (NELSON, 1964). As a rough guide this has been carried out on the massed data of all the birds used in the present study. Even from such a crude measure it is apparent that the behaviour does not approximate to a first-order Markov process, as judged by the strong tendency for the observed numbers of triplets of the general form A-B-A to be greater than their expecteds. As well as suggesting that more detailed analysis of triplets would prove fruitful, this confirms our earlier rejection of χ^2 for the analysis of pairs as clearly each pair is not independent of those that surround it.

The mechanism of switching between different behavioural acts is an important problem (McFARLAND, 1966, 1969). Further analysis of some of the commoner sequences revealed here may help towards an understanding of such mechanisms.

SUMMARY

A transition analysis has been carried out on the behaviour of single male zebra finches, isolated as far as possible from all varying environmental stimuli. As wide a variety of behaviour patterns as feasible was included and grouping of these was kept to a minimum. The dangers of grouping acts on functional rather than causal grounds are stressed.

The method of analysis differs from most of those used previously in the following ways:

1. Data from different individuals are not massed for statistical treatment. This avoids a source of bias which makes it difficult to reach conclusions about the population as a whole.

2. Transitions between one act and itself are not considered. It is argued that models including such transitions have a strong arbitrary component and are predisposed to demonstrate merely that certain acts occur in bouts. A method is employed for calculating the expected frequencies of transitions which does not appear to have been used before in this field. It is based on a random model which excludes from consideration homogeneous transitions and any others which cannot occur because of environmental constraints.

The analysis suggests that zebra finches show cycles of behaviour having active and inactive phases, with ingestion occurring mainly in the former and grooming in the latter. Song appears to be transitional between the two and to occur during periods when other tendencies are low, while stereotypes often follow such periods. Certain pairs of behaviours which occur frequently in sequence are discussed. In some cases one probably generates the peripheral state appropriate to the other and in others the pairing appears to have central causation. Triplet analysis on the massed data from all birds suggests that for most behaviours triplets of the form A-B-A are commoner than would be expected from the frequencies of the pairs A-B and B-A.

It is suggested that factor analysis is not a very useful method for dealing with transition data. Detailed closer study of particular interactions, and of the temporal pattern of individual behaviours, are likely to prove more fruitful.

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RÉSUMÉ

Une analyse transitoire a été effectuée sur le comportement des Diamants mandarins mâles, isolés aussi loin que possible de tous les stimuli variables de l'environnement.

Une variété aussi grande que possible de types de comportement a été étudiée et on a évité autant qu'on a pu de les grouper. Le danger de grouper des actes sur des bases fonctionnelles plutôt que causales est sérieux.

La méthode d'analyse diffère de toutes celles qui ont été employées auparavant sur les points suivants:

1. Les données relatives aux différents individus ne sont pas réunies en un travail de statistique. Ce qui permet d'éviter de tomber dans des préjugés qui rendent difficile l'énoncé de conclusions sur la population dans son ensemble.

2. On ne tient pas compte des intermédiaires entre une action et elle-même. Il a été prouvé que les types qui comportent de tels intermédiaires sont très arbitraires et qu'ils ont tendance à montrer simplement que certaines actions apparaissent groupées.

On emploie, pour calculer les fréquences attendues des intermédiaires, une méthode qui apparemment n'a pas été utilisée avant dans ce domaine. Reposant sur le hasard, elle exclue tous les intermédiaires homogènes et tous ceux qui ne peuvent apparaître à cause des contraintes de l'environnement.

Cette analyse suggère que les Diamants mandarins ont un comportement cyclique avec des phases actives et inactives. L'ingestion a lieu principalement dans le premier cas et le grattage dans le deuxième cas.

Le chant sert de transition entre ces deux actions et il semble qu'il apparaisse dans les périodes où les autres motivations sont réduites. Des comportements stéréotypés suivent ces périodes.

Certaines phases de comportement, couplées et apparaissant souvent l'une après l'autre, prêtent à discussion. Dans certains cas l'une engendre un état périphérique propre à l'autre et dans d'autres cas, il semble que les deux sont liées centralement.

Une analyse de trois phases faite d'après toutes les données fournies par les Oiseaux fait penser que, dans l'ensemble, les séries de comportement de la forme A. B. A. sont plus communes qu'on ne l'attendrait des fréquences des séries couplées A. B. et B. A.

On pense que l'analyse des facteurs n'est pas une méthode très concluante pour étudier à fond les données des intermédiaires. Il est probable qu'une étude plus serrée et plus détaillée des interactions particulières et des types de comportement tout court dans le temps serait plus fructueuse.

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Chapter 5

DESCRIBING SEQUENCES OF BEHAVIOR[1]

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I. ABSTRACT

A review is given of the methods currently available for analyzing sequences of behavior. Simple flow diagrams based on the frequencies or conditional probabilities of individual transitions are considered to be of restricted usefulness except where the sequence is highly ordered and the different patterns occur at similar frequencies. It is more helpful to compare the data with a random model provided that repetitions of the same behavior, and any transitions which cannot occur, are excluded before the expected number of each type of transition is calculated. Such comparisons are most likely to be helpful if the behavior patterns included are closely related and fall into discrete homogeneous categories. The fact that most behavioral data are unlikely to be stationary is considered to be the main factor limiting this approach. It is suggested that first-order transition analysis and correlative techniques are the best current methods for examining such data. The search for higher-order dependencies is useful only in stationary data, where grouping of acts due to changing causal factors can be assumed to be unimportant. Additional difficulties involved in the analysis of sequences of interaction between individuals are briefly discussed. The major complicating factor here is that the behavior of an individual is likely to be dependent both on that of others and on its own previous behavior.

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Some ways of improving current techniques to take account of this are put forward. It is emphasized that sequence analysis provides only a description of the behavior under study and that there are dangers in making causal inferences on the basis of such descriptions alone.

II. INTRODUCTION

The analysis of sequences occupies an important position among the methods available to ethologists, particularly those interested in the causation of behavior. By borrowing and adapting mathematical techniques from other branches of science, they have been able to achieve precise and quantitative descriptions of behavior, and on these to base hypotheses about the causal mechanisms involved.

How can sequence analysis help in the study of causation? It is generally considered by ethologists that the occurrence of two behavior patterns close together in time indicates that they have some causal factors in common. This may not always be the case, for one of the behaviors may bring the animal into a situation appropriate to the other, but in many instances the explanation seems plausible. The causal factors shared may be of two types. First, both behaviors may depend on a particular bodily state, such as the presence of a hormone. Second, both may appear in response to the same or related external stimuli and thus be shown only when these are present. Sequence analysis cannot differentiate between these possibilities, but it can indicate in an objective way the groupings in which behaviors occur and so define the relationships which need to be explained.

Its objectivity is perhaps the greatest asset of the approach. Before such methods were developed, observers depended on their own judgment to determine the affinities between behavior patterns. Because activities which are similar in function, such as courtship and grooming movements, often appear close together in time, this subjective classification led to explanation in terms of specific unitary drives (e.g., courtship or grooming drives). The fact that behaviors of different function sometimes occurred in the midst of these groupings could be accounted for only by assuming their causation to be different, and they were labeled as "displacement activities." These early theories thus depended on the acceptance of a rule and the development of theories to account for exceptions to it. The rule, it should be noted, was based on the doubtful assumption that causation and function are equivalent The inference that functionally related behaviors occurring close together in time were expressions of a common internal drive also neglected the possibility that their grouping was due to the constraints of the external world courtship movements may occur only when a female is present and thus appear to be grouped. This point was appreciated by Tinbergen (1951), whose model of causation stressed the role of external stimuli in leading to the grouping of behavior patterns, though he still felt it necessary to argue that each functional group shared a particular drive.

With the appreciation that drive concepts are of limited usefulness in the explanation of causation (Hinde, 1970), it has become necessary to arrive at objective ways of examining associations between acts empirically, so that more realistic models of their causation may be constructed (Slater, in press). Sequence analysis was one of the first methods to be employed in this context, and its continuing attractions make an appraisal of its usefulness long overdue. That such methods are preferable to the rather subjective assessments of the interrelations between behavior patterns which were previously common seems beyond dispute, but one must be aware of their limitations and not be overimpressed by their precision. The mechanisms underlying the sequence of acts shown by an animal are likely to be complex, and to analyze them using methods appropriate to simpler situations, such as the sequence of cars passing along a road, will inevitably involve some rather sweeping assumptions. The less valid the assumptions, the less realistic will be the results. But it is perhaps even more important that the questions asked should be framed with the nature of the behavior, rather than the nature of the mathematical tools available, in mind. It is, unfortunately, only too easy for research using sophisticated mathematical methods to give very little insight into behavior.

The purpose of this chapter is to review the methods which have been employed by ethologists to analyze sequences, to assess their validity and usefulness, and to point to the conclusions which may be drawn from their application. Its main concern will be with the role of these methods in helping to outline the relationships between successive acts shown by the same individual, but, as they have also been used in studies of interactions between animals, additional points raised by this application will be more briefly considered.

III. SEQUENCES WITHIN THE INDIVIDUAL

A. Methods of Analysis

The methods used for analyzing sequences vary according to the complexity of the data and how structured the behavior appears to be at first sight. Basically, they may be split into two groups depending on whether or not they involve comparison with a random model.

1. *Analysis of Transition Frequencies and Conditional Probabilities*

The simplest type of sequencing of events is a deterministic sequence: in this, the events always follow each other in a fixed order, so that the nature of the preceding act defines precisely the nature of that which will follow Such sequences are rarely studied in normal behavior, partly because tw acts always occurring in a particular order tend to be regarded as a singl behavior pattern. An instance of a sequence parts of which are deterministi was, however, described by Isaac and Marler (1963). They found the song o a mistle thrush (*Turdus viscivorus*) to be composed of some 21 possibl syllables; within a song, each of these could be followed by only a smal range of others and often, deterministically, by only one. Fabricius an Jansson (1963) observed that pushing by courting pigeons (*Columba livia* was always followed by nest demonstration, but it was useful here to regar the two activities as separate because nest demonstration often occurre without pushing preceding it.

Most behavioral sequences are probabilistic rather than deterministi in form, meaning that while the probability of a given act depends[2] on th sequence of those preceding it, it is not possible to predict at a particula point exactly which behavior will follow. Some such sequences are onl marginally less precisely ordered than deterministic ones, and these ar usually referred to as "chained responses." In these cases, the probabilit of a particular event is so markedly altered by the nature of that immediatel before it that a flow diagram indicating the frequencies with which differen transitions occur provides a good impression of the organization of th behavior. This has proved particularly true of goal-directed sequences, suc as courtship, in invertebrates and lower vertebrates (e.g., Brown, 1965 Parker, 1972; Baerends *et al.*, 1955; Hinde, 1955/56). Noirot (1969) ha applied a similar technique to the maternal behavior of mice: she looke at the order in which different acts occurred during an observation session disregarding repetitions of the same act.

Where sequences are not so highly ordered, some transitions may b observed between almost every behavior and every other, so that simple flo diagrams become complex and hard to interpret. A way around this is t include only those transitions which have a high probability of occurrenc a method which was used by Fabricius and Jansson (1963). For each se quence of two acts, they worked out the conditional probability ($p\ B|A$, th probability that B will occur given that A has just occurred), and only wher this exceeded 0.1 was an arrow from A to B included in their flow diagram For each type of act, an impression is thus given of those other behavior most likely to follow. This method has also been employed to show up differ ences in sequences between two groups of animals (isolated and sociall

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[2] The expression "one behavior depends on another" is used throughout this chapter in th statistical sense: the occurrence of the first alters the probability of the second. Where it intended to imply that the first is in some way causal to the second, this will be referred t as a "sequence effect" rather than a "dependency."

eared guinea pigs, *Cavia porcellus*) by Coulon (1971). It is perhaps best uited to situations like this where comparisons are to be made, for the ndividual flow diagrams obtained are hard to interpret when behaviors differ trongly from each other in frequency. A large number of transitions, yielding comparatively complex diagram, may result even from sequences in which he events are independent of one another. This is because the expected conlitional probability of a rare act following a common one is low, whereas hat of a common act following a rare one is high. In a sequence of 1000 acts, f act A is observed 100 times and B is observed 10 times, and A and B are ndependent, then one would expect the sequences $A \rightarrow B$ and $B \rightarrow A$ to occur nce each (100 × 10/1000), but the expected conditional probabilities are uite different: $p\ A|B = 0.1$ (100/1000); $p\ B|A = 0.01$ (10/1000). In the ight of this complication, it is difficult to assess the importance of the differnt sequences found by Fabricius and Jansson (1963), as they do not give the requencies of the individual acts.

These simple ways of looking at sequences are thus likely to prove useful nly where sequencing is strong and where the different behaviors considered ccur at roughly equal frequencies.

. *Comparison with a Random Model*

The shortcomings of descriptions based on frequencies and conditional robabilities have led many workers to adopt some of the techniques of arkov chain analysis. A sequence of behavior can be described as a Markov hain if the probabilities of different acts depend only on the immediately receding act and not on any earlier ones (Cane, 1961). This model is thus ppropriate to describe the sequence $A \rightarrow B \rightarrow C$ if the probability that C will llow B is not in any way altered by the nature of A or events prior to A. uch a sequence of events can also, more generally, be referred to as a "first-rder" Markov chain, to differentiate this model from ones in which more f the preceding events affect the outcome: in this case, an rth-order Markov hain is one in which the probability of a particular event is significantly ffected by the r preceding events (Chatfield, in press). Thus if the probability f C depends on A as well as B, the first-order model is inadequate to account r the structure of the sequence and second-order dependencies can be said be in operation. If the probability of an event does not depend on any revious events, the events can be said to be independent, and this is somemes referred to as a "zeroth-order" Markov chain.

Most sequence analysis in behavior is concerned with establishing the istence of, and identifying, first-order dependencies. Here, the matrix of bserved transition frequencies is compared with that which would be exected if all acts were independent of one another. For these first-order ansitions, the expected values are calculated as for a contingency table (assuming that it is possible for any of the behaviors considered to follow an other), and comparison between the matrices can then be made either in th usual way, using χ^2, or by the use of information theory (Bolles, 1960; Chat field and Lemon, 1970; Fentress, 1972).[3] If the difference is found to be signif icant, the hypothesis that the behavior consists of a sequence of independen acts can be rejected. This discovery is not, in itself, surprising; it would b more so if a sequence of independent acts were found, which has not so fa been the case. Further analysis is required before any useful description o behavior is obtained, and here two different approaches are possible.

First, the sequence can be analyzed more closely as a whole to decid whether the first-order model is adequate or whether higher-order dependen cies affect it. It can be tested, as a start, whether a second-order model is mor precise: in the generalized sequence $A \rightarrow B \rightarrow C$, is the probability of obtainin C after B significantly altered by the nature of A? In a first-order Marko chain, this is not the case, and the frequency of $A \rightarrow B \rightarrow C$ is that predicte from the frequencies of $A \rightarrow B$ and $B \rightarrow C$. A difficulty arising here is that different types of behavior will give N^3 triplet types, and so very extensiv data are required before reasonable numbers of each of these are expecte In two cases where triplets have been examined, however, a first-order Ma kov model has been found to be satisfactory: the frequency of triplets of eac type corresponded closely to that predicted from the first-order relationshi (Nelson, 1964; Lemon and Chatfield, 1971). As will be seen below, rathe special conditions, which are unlikely to arise often in behavioral data, ma have to be met before sequences of this type are discovered. The statistic comparison of first- and higher-order models has been thoroughly explore by Chatfield and Lemon (1970; Lemon and Chatfield, 1971; Chatfield, i press).

A second approach to finer analysis is an attempt to detect those firs order transitions which are significantly commoner than their expected value This is done when the groups in which behaviors occur and the exact relatio ships between different behavior patterns are the main points of interes Because such discoveries are behaviorally more interesting than the detectio of higher-order dependencies, this approach has greater currency. It carri with it, however, the necessity to examine the discrepancy between the o served and expected values in individual cells of the transition matrix. B cause many cells often contain rather low figures and because the observe value in each cell depends on those in others, this is difficult both to car out and to interpret. The commonest method is a condensation of the who matrix into a 2 × 2 table about the cell of interest, followed by a χ^2 test t detect whether that particular transition is more frequent than expected (e.g

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[3] Strictly speaking, a transition matrix is not a contingency table, as the events included it are not independent of one another, the second act of each pair being the first act of t next. The use of χ^2 on such data has, however, been validated by Bartlett (1951).

Stokes, 1962; Blurton Jones, 1968). Other techniques have been employed by Andrew (1956), Weidmann and Darley (1971), and Slater and Ollason (1972). In this last case, an attempt was made to overcome the biases involved in massing data from different animals, which is a usual practice where χ^2 is employed in order to boost the figures in individual cells. Perhaps the safest method is a simple inspection of the data, as recommended by Lemon and Chatfield (1971).

Whichever of these tests is used, pairs of behaviors which are commoner than expected can be extracted and a flow diagram constructed along the lines of those used in frequency and conditional probability analyses. This flow diagram has the advantage, however, that the relationships in it are not biased by the frequencies of the individual acts.

A further method may be used if it is of interest to detect asymmetry in particular sequences. If the row and column totals of the transition matrix are the same, then the expected values of the generalized sequences $A \rightarrow B$ and $B \rightarrow A$ will be the same, and tests can be carried out to see if the observed values differ (Blurton Jones, 1968; Slater and Ollason, 1972). While sequence analysis is not the only, or necessarily the best, way of looking for associations between acts, it is certainly the simplest way to detect such asymmetries.

B. Some Comments on the Methods Used

Having given a general outline of the commonest approaches to sequence analysis, it is now appropriate to consider the assumptions underlying them in the wide range of circumstances in which they have been used. Three main points are important here: the validity of using complete matrices, the choice of categories of behavior, and the problem of stationarity.

1. Complete vs. *Incomplete Matrices*

Comparison with a random model is easy if the matrix considered is a complete one, as shown in Table IA. The expected number of transitions between any pair of behaviors is calculated in the same way as for a contingency table (row total × column total/grand total; Table IB). This then gives the expected number of acts which would succeed each other if all acts were independent of one another. Two considerations are liable to make such a model unreasonable:

a. Repetitions of the Same Act. The complete matrix includes transitions which are repetitions of the same behavior. Figures thus appear on the descending diagonal of the matrix indicating the frequency of transition between A and A, B and B, etc. For each behavior, the observer must develop a criterion with which he can decide when one act ends and the next begins before he can reach a figure for the number of these repetitions. This may be easy for some behaviors: they may almost never be immediately

Table I. Artificial Data Showing the Observed Number of Transitions Between Three Behavior Patterns and the Number Which Would Be Expected If All Acts Were Independent of Each Other

A. Observed Matrix

	A	*B*	*C*	
A	10	20	5	35
B	15	4	6	25
C	10	2	8	20
	35	26	19	80

B. Expected Matrix

	A	*B*	*C*	
A	15.3	11.4	8.3	35
B	10.9	8.1	6.0	25
C	8.8	6.5	4.7	20
	35	26	19	80

repeated, or, if they are, a consistent time interval may separate succeeding events so that they can be simply distinguished. Other behaviors pose more difficult problems: when, for instance, does one act of locomotion end and the next begin? Here, it would be necessary to select some arbitrary time interval during which the animal did not move as indicating a gap between two acts.

In zebra finches (*Taeniopygia guttata*), other behaviors which highlight this problem are preening and singing (unpublished observations). These birds tend to groom in sessions several minutes long, during which preening of the feathers with the bill is interrupted little by other acts, with the exception of scratching of the head. A preening bird lowers the head to a small area of the body, preens one or a few feathers, and raises the head again. The next series of preening movements is most likely to be directed to the same area of the body as the last. There are thus at least three ways of defining an act of preening:

1. The preening of a single feather, several such acts often taking place between each raising of the head.
2. The series of movements between each raising of the head, which may involve several feathers.
3. The series of movements directed to the same area of the body, which may be interrupted by several instances of head raising, depending on how an area of the body is defined.

In the case of song, a series of almost identical phrases is produced, followed by a gap usually lasting for more than 2 sec before the next such eries. An act here might be defined as each individual phrase, or as each eries of phrases separated by longer than a certain time.

It is clear from these examples that defining an act other than arbitrarily vill often be impossible. For some purposes, this may not be a hindrance, s long as the definition used can be consistently applied, but this is certainly ot the case with sequence analysis. Here, two observers might apply differ- nt criteria, each in themselves perfectly reasonable, to the same data and so each quite different conclusions. This is illustrated by Table II, where the ame data as in Table I are shown except that the number of $A \to A$ transitions as been boosted from 10 to 100, as might happen if an experimenter with different criterion for what constituted an act of *A* had collected the same ata. A comparison of the expected values in Table IIB with those in Table B shows that this difference, in only one cell of the observed matrix, would ead to a totally different set of expecteds.

The results of sequence analysis in relation to a random model using a omplete matrix will usually depend on such arbitrary criteria selected by the xperimenter. It is interesting to note, for instance, that each of the behaviors tudied by Wiepkema (1961) was recorded as being repeated often, whereas his was seldom the case with the data given by Blurton Jones (1968). This ells one more about the criteria chosen by these workers than about the ehaviors which they studied. Most of the matrices published in the literature re rather similar to that of Wiepkema in that the act definitions chosen lead o relatively high figures on the descending diagonal (e.g., Bolles, 1960; aerends *et al.*, 1970; Lemon and Chatfield, 1971). Carrying out sequence nalyses on matrices such as these will tend to show just that these acts occur n bouts rather than more interesting relations between different behaviors.

Table II. The Same Data as in Table I But with the Number of $A \to A$ Transitions Boosted from 10 to 100

A. Observed Matrix

	A	*B*	*C*	
A	100	20	5	125
B	15	4	6	25
C	10	2	8	20
	125	26	19	170

B. Expected Matrix

	A	*B*	*C*	
A	91.9	19.1	14.0	125
B	18.4	3.8	2.8	25
C	14.7	3.1	2.2	20
	125	26	19	170

If arbitrary act definitions are involved or if behavior patterns tend t fall into bouts, the analysis of the complete matrix of transitions will thus b of little help in elucidating the interrelationships between activities. Unde these circumstances it is more fruitful to eliminate the entries on the descen ing diagonal before analysis so that only transitions between different b haviors are considered.

b. Cells Which Cannot Be Occupied. In some sequences of behavio there may be transitions which cannot occur, particularly because of enviro mental constraints. Thus the matrix of Slater and Ollason (1972) could n include transitions from feeding to drinking, as locomotion, another categor of behavior included in the study, had to occur between the sources of foo and water. Likewise, Baerends *et al.* (1971) recognized in their matrix that herring gull (*Larus argentatus*) could not show "looking down while not o nest" immediately after "sitting on nest" as well as certain other transition These constraints may not occur in many sequences, but they should be re ognized where they do so.

While many workers eliminate the descending diagonal from the transition matrices and some remove other cells which cannot be occupie few realize that the calculation of expected values must then be altered s that the row and column totals add up correctly without figures appearin in the empty cells. Goodman (1968) gives a method whereby this may b done, and a simpler, though more approximate, method has been develope by Lemon and Chatfield (1971), whose study of song in cardinals (*Richmo dena cardinalis*) was the first to use this technique on sequential data. Tabl IIIA shows the same data as in Tables I and II but without the descendin diagonal. The expecteds in Table IIIB are calculated according to the Goo man method; they add up to the correct row and column totals despite th

Table III. The Same Data as in Tables I and II but with Expected Values Calculated Ignoring Transitions Between Each Behavior and Itself

A. Observed Matrix

	A	*B*	*C*	
A	—	20	5	25
B	15	—	6	21
C	10	2	—	12
	25	22	11	58

B. Expected Matrix

	A	*B*	*C*	
A	—	17.8	7.2	25
B	17.2	—	3.8	21
C	7.8	4.2	—	12
	25	22	11	58

resence of empty cells. These expected values give the number of bouts of ach type of behavior which would succeed each other type if all bouts were ndependent of one another. A "bout" is here defined as a sequence of a given ype of behavior not punctuated by the occurrence of any of the other types onsidered.

As these methods are available, there is no hindrance to the analysis of ransition matrices in which repetitions of the same act and transitions which re impossible are not considered. While only Lemon and Chatfield (1971) nd Slater and Ollason (1972) have so far used them, it is clear that most ata on sequences of behavior would benefit from their application.

. *The Choice of Categories of Behavior*

An important preliminary to any study, and especially to the analysis f sequences, is the classification of behaviors into discrete categories. ome acts are almost invariant in form and intensity and can easily be defined nd recognized; others are more problematic and may require more or less rbitrary definition. However the categories of behavior are defined, it is nportant that they should be mutually exclusive and that the observer hould "be prepared to treat all members of a given category as equivalent" McFarland, 1971). Several factors may make these conditions hard to comly with. First, several different behaviors may frequently occur simultaneusly, making it difficult to cast the data into a transition matrix. Data of is kind are more appropriately analyzed using correlation techniques (e.g., elius, 1969), and Golani (unpublished manuscript, cited by Golani and endelssohn, 1971) has also applied multidimensional scalogram analysis this problem. Second, the equivalence of behavior patterns within a ategory may be doubted where they differ greatly in form (as where all rooming movements are grouped under a single heading) or where there is a ide spread of bout lengths within a category. In this instance, long and short outs may differ in context so that grouping them in one category clouds eir different relationships with other activities.

Studies differ a great deal in the diversity of behavior patterns considered nd the ways in which these are classified. It is common, for example, for ansition matrices to include mainly behaviors from one functional category omfort movements: Andrew, 1956; Delius, 1969; Fentress, 1972; courtship ehavior: Nelson, 1964; Wiepkema, 1961; Coulon, 1971; song syllable pes: Isaac and Marler, 1963; Lemon and Chatfield, 1971). Certain other ehaviors may be included, but these are mainly taken as markers indicating e beginning and end of sequences of the group under study (e.g., in studies f comfort movements: resting and locomotion by Andrew, 1956; "other ehavior" by Delius, 1969). Where such markers are not included, it is often nclear how a sequence is defined, though the careful study of Nelson (1964) an exception. He established the time interval between two events for the succeeding to be independent of the nature of that before it and took interva longer than this to be between, rather than within, sequences. Other matric avoid the problem of sequence definition by including all behaviors shown a particular situation regardless of function (e.g., at the nest site: Baeren *et al.,* 1970; at a food source: Blurton Jones, 1968; in isolation from co specifics: Bolles, 1960; Slater and Ollason, 1972). The range of behavio included can therefore vary from a wide spectrum of very different ac (e.g., sleep, grooming, and feeding) to a variety of very similar acts (e. grooming different areas of the body, different song types). All the behavio included in a matrix of the latter type may be lumped as a single catego in matrices of the former type.

For a number of reasons, the application of Markov chain analysis the whole matrix is likely to prove more fruitful if the behaviors studied a homogeneous within categories, distinct between categories, and yet closely related to one another:

a. Cane (1959) comments that "If the states of a Markov chain a grouped, the resulting process is not in general a Markov chain Homogeneity within each category of behavior will make it le likely that such a grouping has been made.
b. If the behaviors considered are all closely related to each other, may be possible to split them into categories which are, at lea approximately, at the same level of organization. If the categori considered are very dissimilar, this may affect the order of tl Markov chain found. Birds, for example, tend to wipe their beaks aft drinking, presumably stimulated to do so by water left on the ou side. If drinking and beak wiping were included in a matrix wi various small bodily movements, some of the latter would often interpolated between them, making it necessary to invoke highe order relationships to explain the sequencing.
c. It is useful to work out the order of the dependencies governing sequence only if the rules are the same for the whole matrix. This more likely to be the case if the different categories can be taken be distinct from each other and yet closely related. One determinist sequence in a matrix of acts which are otherwise independent of o another could lead the observed and expected matrices to diff significantly.
d. Markov chain analysis presupposes that the animal is in a stea state (i.e., that the system is stationary), which is much more like to be the case during sequences of closely related acts which a considered motivationally similar. The problem of stationarity h more widespread repercussions, however, and these will be discuss in the next section.

. *Stationarity*

A stationary sequence is one in which the probabilistic structure does ot change with time (Cox and Lewis, 1966; Delius, 1969). Nonstationarity an lead to very complex transition matrices: while the rules underlying equencing may be simple on the short term, if they are not the same throughut the observed data in a transition matrix the matrix will be a complicated um of the various simple processes involved and extremely hard to interpret.

Checking to see that the data are stationary is therefore a first requireient of rigorous Markov chain analysis as well as of other methods for xamining sequences. It is a condition likely to be met seldom in behavioral ata, which is one reason why this type of analysis is not often taken far. he use of concepts such as "drive" and "arousal" to explain behavior Bindra, 1959; Hinde, 1970) and the discovery of daily cycles (e.g., Palmgren, 950; Aschoff, 1967) and of short-term cycles (Richter, 1927; Wells, 1950) l speak for the long-standing realization among those studying behavior iat the data they collect are not stationary. In certain situations, the steadyate assumption may be valid, but this will not often be the case. The shorter ie observation period, for example, the more reasonable the assumption, ut the more difficult it becomes to obtain adequate data for analysis.

The most likely source of nonstationarity is the existence of a trend with the data, such as might be caused by daily cycles. The effects of such ends may be minimized by testing only for short periods at a consistent me of day, and methods are also available for detecting trends so that the tent to which they affect the data may be assessed. Perkel *et al.* (1967) ggest breaking the data into segments, analyzing each separately, and then sting to see if they are drawn from the same population. Especially where e types of act considered are heterogeneous, most behavioral data will fail pass this test: sporadic periods of sleep or long bouts of grooming, which ay take place only a few times per day, will tend to occur in some segments ut not others.

Moore *et al.* (1966) point out the complexity of rigorous criteria for tablishing stationarity in a simple system such as the firing pattern of a ngle neuron. Very few workers on sequences of behavior attempt such ecks, and the frequent interpretation of results in terms of changing motivaon suggests that nonstationarity is accepted. Rough tests for stationarity ve been performed in two cases. Nelson (1964), working on courtship in h, was able to carry out Markov chain analysis on one species studied *orynopoma*) after excluding intersequence intervals from the data, but he jected the possibility of sequence analysis on another (*Pseudocorynopoma*), the probabilities of different acts showed marked temporal fluctuations. mon and Chatfield (1971) proceeded with Markov chain analysis after finding no significant differences in the probabilities of different song typ between the first and second halves of the records they analyzed.

The fact that these workers were able to satisfy at least some of t criteria for stationarity with their data and the fact that in both cases t behavior was found to follow a first-order Markov chain may be no coi cidence. Moore *et al.* (1966) point out that "the distinction between seri dependence (with an overall stationary sample) and actual nonstationari is an arbitrary one." Thus data which appear to follow a Markov chain high order could also be interpreted as nonstationary and *vice versa.* In so behavioral data, triplet sequences of the general form $A \rightarrow B \rightarrow A$ have be found to be commoner than expected (Slater and Ollason, 1972; Fentres 1972), indicating the inadequacy of a first-order Markov model. It is possib here that a second-order model might be satisfactory, but shortage of da precludes testing for this. Another interpretation would be that periods time exist during which the two acts involved in the sequence are of hi probability, while that of all other behaviors is low, thus leading to altern tion between them. This interpretation assumes nonstationarity, i.e., fluctua ing probabilities.

C. Alternative Methods of Approach

It will be apparent from the above discussion that there are many reaso why the techniques of Markov chain analysis should be applied only wi caution to behavioral data. The most obvious reason for this is that t probabilities of different behavior patterns tend to change with time. Giv this difficulty, it is worth considering briefly other methods which, while n primarily concerned with sequencing, may be used to detect associatio between behaviors.

Factor analysis is particularly interesting in this context, as it has al been employed by ethologists for the treatment of data in transition matric (Wiepkema, 1961; Baerends and van der Cingel, 1962; van Hooff, 197 Baerends *et al.,* 1970). Using this method, a small number of hypothetic variables are extracted, the existence of which as causal factors could accou for most of the observed correlations between acts, without the acts the selves being directly related. It is assumed that the measured variables, in t case behavior patterns, do not depend causally on each other but only the postulated factors (Blalock, 1961). This assumption highlights the sha contrast between this method and Markov chain analysis. The choice which of these approaches is used appears to depend mainly on whether t research worker believes "sequence effects" or "motivational states" to the more important in determining the relationships between behavio In the former case, it is thought useful to describe the probability of an a t a particular instant in terms of the sequence of acts which preceded it. he animal is assumed to be in a steady state, which is tantamount to ignoring he possibility that motivational changes occur. On the other hand, if nterpretation is in terms of motivational states (underlying variables which re postulated as changing more slowly than the switching in overt behavor), the same data can be treated quite differently using factor analysis. n association between acts is here taken to be indicative of common causal actors underlying the behaviors involved, and the factor on which they have high loading may be argued to represent a motivational state (e.g., "aggressive," "sexual," "nonreproductive": Wiepkema, 1961; "affinitive," play," "aggressive," etc.: van Hooff, 1970). If factor analysis is based on a ansition matrix, two different models may be derived, depending on hether the frequency of acts following each other or preceding each other taken as a starting point. The method assumes that sequence effects are nimportant, as these will make the two models differ from one another Slater and Ollason, 1972). As both motivational changes and sequence ffects are likely to occur in most behavior, each of these two descriptions is ecessarily imperfect, and cases where either is valid in the strictly mathematical sense may be hard to find.

Factor analysis is open to several other objections, some of which have een discussed by Overall (1964), Andrew (1972), and Slater and Ollason 972). The use of the method supposes it to be useful to describe behavior n terms of a few underlying variables, and yet it is not altogether clear what hese may represent. While Wiepkema (1961) referred to his factors as tendencies," thus identifying them with a drive type of model, Baerends 970) gives them weaker status as "areas of higher density within the causal etwork," thus recognizing that their existence may depend on external s well as internal variables. It is doubtful whether the extraction of factors hich are themselves of complex causation advances understanding. At the escriptive stage of analysis, it appears preferable to examine the relationhips between individual acts, as these can be directly assessed without theoetical implications and do not place constraints on the type of model of rganization which may emerge from subsequent experimental work.

Analysis based on transitions between behaviors is not the only way of etecting associations between individual acts: an alternative approach hich has much to recommend it is the use of correlation techniques. This nvolves measuring the frequencies of different behavior patterns within a eries of time units and then correlating between each pair of acts to determine whether they are positively or negatively associated. Stationarity emains a problem here, though perhaps a less acute one, while some of the ther objections to sequence analysis are not important: two behaviors which ccur concurrently are no problem, nor does it bias the results if acts at different levels of organization are included in the analysis. The main difi culty is that the results may depend on the choice of time unit. While tw acts may be significantly correlated over 1-hr periods, this is not necessari true when their correlation is assessed over 10-sec units. To allow for thi it is therefore preferable to analyze the data separately for a number different time intervals, as has been done by Baerends *et al.* (1970). With th approach, it becomes possible to detect much looser associations than wou be achievable with sequence analysis.

Ordinary correlation techniques give no indication of whether ac tend to follow each other in a particular order. If one behavior leads another, correlations of this type can only indicate that they are in some w associated. A modification of the method can, however, extract such info mation; this is the cross-correlation procedure which is discussed in detail Delius (1969). Here the frequencies of different acts are correlated, not ju for the same time unit, but with progressive lags introduced between ther Thus if behavior *B* tends to occur 5 sec after behavior *A* and the time un used is 1 sec, a positive correlation will be found when the data for *A* a moved forward 5 sec in relation to *B*. Heiligenberg (1973) has carried o the most elegant study to date employing this procedure and, using 1-s time units, has been able to demonstrate both sequence effects and loos associations between seven behavior patterns in a cichlid fish (*Haplochrom burtoni*).

Correlative techniques can thus give useful information on a numb of facets of behavioral organization, including sequence effects. They a particularly suitable where the behaviors under study are diverse and whe their associations are liable to be due to common causation rather than s quencing. A full analysis of this sort requires a considerable amount of da (Heiligenberg's results were based on 360 hr of observation), and, unlike t simpler forms of sequence analysis, the amount of calculation involved mak the use of a computer essential. Where an approximate guide to associatio is required, or where sequencing is strong, analysis of first-order transitio between acts is clearly more practicable.

IV. SEQUENCES OF INTERACTION BETWEEN INDIVIDUALS

The discussion so far has centered around sequences of behavior with the individual in contexts where the external world is presumed to be relativ ly unchanging. Some of the examples used were concerned with animals in social situation (e.g., the studies of fish courtship by Wiepkema, 1961, ar Nelson, 1964); in these cases, the assumption was made that the presence other animals, while perhaps stimulating the behavior under study, h

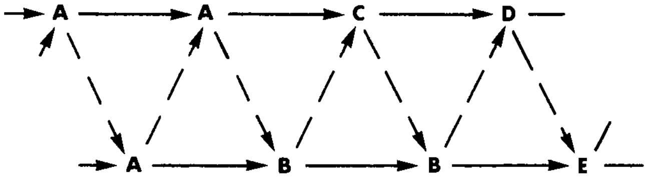

Fig. 1. A simple model of an interactive sequence involving two individuals.

ittle effect on its sequence. Nelson (1964), for instance, stated that the part played by the female in glandulocaudine courtship is slight, and therefore felt ustified in examining sequences within the male as if he were in a constant environment.

Most studies of social sequences have a different primary aim: to demonstrate that the behavior of one animal *is* affected by that of others, and so obtain evidence for the role of different behavior patterns in communication. At first sight, this is an easier task than the analysis of within-ndividual sequences, for data of this sort can easily be cast into a complete matrix such as Table I, the acts listed down the side being those shown by one individual and those along the top being the subsequent behaviors of another. The objections to including figures on the descending diagonal do not apply: these entries refer to those cases where the performance of a behavior by one animal is followed by the same behavior from the other.

Other difficulties do, however, arise, including those concerned with the choice of categories and with stationarity which have already been discussed. Stationarity may be a particularly serious problem, for as MacKay (1972) points out, many of the most interesting behaviors in communication are hose which change in probability as the interaction proceeds. A further difficulty, which is often neglected, is that the behavior of an animal in a social situation is likely to depend partly on the sequence of acts that it has already shown as well as on the behavior of others. Figure 1 shows a simple model of an interaction between two animals designed to take account of both these influences.[4] Studies of within-individual sequences, such as those of Wiepkema (1961) and Nelson (1964), suppose that the effects portrayed by dotted lines are of little importance, whereas some studies of interactions between animals pay only passing attention to the possible influence of the effects illustrated by complete lines (e.g., Hazlett and Bossert, 1965). The most thorough analysis of interactive sequences, that by Altmann (1965)

The model is, of course, too unsophisticated for many purposes. It assumes, first, that each behavior depends only on those shown by the individual and by his companion immediately previously and, second, that the interaction is like a game of chess, the animals making alternate moves.

on social communication in the rhesus monkey (*Macaca mulatta*), doe not attempt to differentiate between these two possible influences. Hi transition matrices are based on the order of events within a group o monkeys, making no distinction between animals; thus two consecutiv behaviors may be by the same or by different individuals. Using data of thi sort, Altmann has taken Markov chain analysis further than any other worker, his examination extending to quadruplets of acts (third-order relationships). The confounding of these two effects was perhaps inevitable in field study where several animals might be in view and each could show an one of 120 different behavior patterns, but it means that his results cannot b interpreted easily. In common with a number of other studies, some of sequences within the individual (e.g., Chatfield and Lemon, 1970; Fentress 1972) and some of interactive sequences (e.g., Hazlett and Bossert, 1965) Altmann's analysis used the techniques of information theory. Such method can also be used to assess the relative importance of within- and between individual influences. This can be done by deriving measures of informatio transfer separately for the transitions shown in Fig. 1 as dotted lines an those shown as complete lines, and comparing the two values so obtained The study by Dingle (1969) includes such calculations: his conclusion tha the two influences were of equal importance in interactions between manti shrimps (*Gonodactylus bredini*) warns against ignoring the effects of eithe of them. It should be noted in passing that measures of information transmission, while a useful way of expressing the correlation between events do not necessarily imply a causal relationship between them (MacKay 1972).

Consideration of a whole matrix of interindividual transitions ca indicate only that the behavior of one animal is in some way linked to tha of others. Ethologists usually want to ask more specific questions: e.g., doe one animal tend to perform behavior *B* more often than expected after another has shown behavior *A*? If within-individual effects are of no importance an unlikely finding, this could reasonably be tested by comparing the numbe of times an event of *B* follows an event of *A* with that expected on a random model. But if, as is quite possible, *A* and *B* tend to fall into bouts, the numbe of such occurrences may be high purely by chance. If a bout of *B* happen to start just after a bout of *A*, many transitions between the two behaviors wil be scored even though the animals may be acting independently of one another. Thus if successive events of *B* are not independent of each other, it i clearly invalid to suggest that each of them was separately stimulated by *A* It is more valid to ask whether more *bouts* of *B* started during or just afte each event of *A* than expected. A bout of *B* must be defined so that the firs event in one bout is statistically independent of previous occurrences of tha behavior in the same animal. Approximate methods for determining th nterval between events necessary for this to be the case have been provided y Duncan *et al.* (1970) and Wiepkema (1968), but have not yet been used in equence analysis. The closest attempt has been in the study by Wortis (1969) f interactions between ring dove (*Streptopelia risoria*) parents and their hicks. She accepted that only the start of a particular behavior should be cored, but took a gap of only 2 sec as indicating a gap between bouts. This riterion was apparently chosen arbitrarily, and it seems unlikely that 2 sec ould be adequate for the second event to be independent of the first. A ifferent way of getting around this problem has been used by Heckenlively 1970), who examined encounters between pairs of crayfish (*Orconectes irilis*). For each encounter, he scored only a single transition, that between he first act of one animal and the response to it of the other, and all transi- ons could thus be considered truly independent of each other.

The analysis of interactive sequences is clearly a more difficult task than hat of sequences within the individual because of these additional complica- ons. Furthermore, in this case other methods do not afford the prospect of chieving an improvement. Sequence analysis seems an obvious first step in he study of communication, for here the suggestion is being made that the ehavior of one animal is in some way causal to the behavior of another, hile this is not necessarily true of two successive behavior patterns shown y the same individual.

. DISCUSSION

In this chapter, I have mentioned various ways in which sequences of ehavior can be analyzed and some of the assumptions which underlie each f them. It is now pertinent to outline the circumstances in which they are kely to prove helpful and to discuss the conclusions which may be drawn s a result of their application.

The simplest form of sequence analysis, that in terms of frequencies or onditional probabilities, can usefully be applied only in circumstances here sequence effects are strong, the acts following each other in an almost xed order. If the behavior is less structured than this and, in particular, hen the different acts considered occur at markedly different frequencies, better approach is to compare the observed first-order transition frequencies ith those which would be expected on a random model, a method equivalent o the initial stage of Markov chain analysis. This is preferable because it akes into account the frequencies of the individual acts and thus extracts hose transitions which are commoner than expected, rather than those which re common in absolute terms. In the past, ethologists have not applied this ethod as carefully as they might have done, particularly those who have based their analyses on complete matrices of transitions. But, while th methodological problem can be overcome, other difficulties are harder t cope with.

There are several reasons why two behaviors may tend to succeed eac other more often than expected. Of these, the two most likely are that the both share causal factors and so occur only when these are present, or th the first act stimulates the second in some way. Data in which behaviors a grouped due to changing causal factors fail to fulfill the statistical requir ment of stationarity and will thus be unsuitable for rigorous Markov chai analysis. Despite this, the examination of first-order relationships will provid a rough guide to the groupings into which different activities fall. Whi first-order transition analysis may therefore be of some usefulness in no stationary data, the extraction of higher-order dependencies is here pointles for the statistical dependencies between successive acts may be just a b product of their shared causation rather than indicating that rules gove the sequence as such. Correlative techniques using various different ti units offer a more effective way of assessing the associations between ac when these are thought to result from changing causal factors.

In situations where internal and external causal factors are thought n to change with time, the data are more likely to pass the test of stationarit and here it is probable that the sequential dependencies found result fro causal dependencies between the successive acts, or between the states which they are the overt indicators. In these circumstances, the analysis first-order dependencies is a first step toward discovering the rules governin sequencing. These may then be fully elucidated by a search for higher-ord dependencies.

Many behavioral sequences will not fall neatly into one of these cat gories or the other; perhaps the most profitable approach here is to combin first-order transition analysis to look for associations liable to result fro sequence effects, with correlation techniques, to find the looser associatio which might result from shared causal factors.

It is important to stress that none of these methods provides more tha a description of the behavior under study. That two acts tend to occur i sequence need not imply a similarity of causation, nor that one generat the other in some way: they could be associated by exclusion, or because particular characteristics of the experimental situation. The choice descriptive method may bias the researcher toward a particular type explanation. For example, if $A \rightarrow B$ more than $B \rightarrow A$ in a transition analysi it suggests that A generates a state appropriate to B, or increases the prob ability of B. This result can, however, also be explained on a motivation model in which the acts differ in threshold (Bastock and Manning, 195 Hinde and Stevenson, 1969). Conversely, a symmetrical relationship betwe wo behaviors such that both $A \rightarrow B$ and $B \rightarrow A$ are common could be taken as indicating common causation or that each of the two acts stimulated occurrence of the other. The description of behavior provides hypotheses but not explanations; a frequent mistake made by those using factor analysis s the attempt to provide a causal explanation based on purely descriptive data. On the other hand, the detailed knowledge of the associations between behaviors made possible by the other methods discussed here may prove an invaluable source of hypotheses; the way in which these associations change in response to experimental intervention can then be used to build models of the causation of behavior.

Similar arguments apply to the description of interactive sequences. Even after valid ways have been found of demonstrating that behavior B by one animal tends to occur after behavior A by another more often than expected, this discovery is not evidence that A causes B, though this is one possible explanation. Other possibilities are that a behavior occurring close o A in time stimulates B, or a behavior associated with B, or even that the wo behaviors tend to occur synchronously due to some event in the more distant past, such as social facilitation of other activities or the onset of daylight (Andrew, 1972). Experiments are essential if communication is to be demonstrated. Nevertheless, the analysis of sequences of behavior in normal interactions is a useful initial stage before such experiments are carried out to indicate the acts which are likely to be important in communication. The fact that most studies on this topic have failed to distinguish clearly between intra- and interindividual effects does not argue against the usefulness of the general approach.

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CHANGES IN THE BEHAVIOUR OF THE MALE ZEBRA FINCH DURING A 12-HR DAY

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Abstract. Isolated male zebra finches show a daily cycle of locomotion similar to that of other birds. During a 12-hr day (07.00 to 19.00 hours) approximately 75 per cent of movement between perches occurs between 08.00 and 14.00 hours. Trends are also apparent in other behaviours, as assessed by the number of 30-s time units in which they are recorded. Soft call notes, singing, drinking and taking of sand and cuttlefish bone all decline during the day. Sitting still and preening rise. Despite these changes the associations between acts are similar at different times of day. In general the behaviours previously found to be associated with locomotion during the morning decline with it during the day, whereas those not associated with it rise.

Slater & Ollason (1972) commenced a study of the temporal patterning of behaviour in isolated male zebra finches with an analysis of transitions between different pairs of behaviours. This work suggested that the behaviour of these birds fluctuates between two interrelated groups of acts: on the one hand locomotion and ingestion and on the other various grooming activities. Some behaviours, such as singing and stereotyped pecking at parts of the cage, were found to have connections within both these groups and were considered to occur during transition between the two. The present paper examines further the relations between various acts in a similar situation but using rather different techniques; the long-term objective of these studies is to obtain an understanding of the organization of behaviour in individuals isolated from external change as an aid to understanding the actions of internal and external factors on it.

Transition analysis is mainly useful for examining the behaviours which immediately precede and follow one another. While analysis of triplets and quadruplets has sometimes been attempted (e.g. Nelson 1964; Lemon & Chatfield 1971), this necessitates the collection of a very large quantity of data. It also assumes the usefulness of describing the probability of a given act in terms of the sequence of acts which preceded it. In many behavioural situations motivational changes may be at least as important as sequential influences in leading to the grouping of patterns (Slater 1973). It is therefore important to supplement sequence analysis by looking for looser associations between acts, such as might arise where they shared causal factors without necessarily following one another directly.

The technique employed here is to record the presence or absence of a number of behaviours in a series of 30-s time units. This method yields a score for each act: the number of time units in which it occurred. It also allows the detection of associations between acts, which can be done by comparing the number of time units in which two types of behaviour coincide with that expected on a random model. The counts for individual behaviours will be referred to as 'scores' because they are not, strictly speaking, measures of frequency, as a single 30-s period will be rated the same whether it contains one or many acts of a given type. As Baerends et al. (1970) point out, however, scoring in this way may provide a better measure of the tendency to perform a particular behaviour than counts of individual acts: a single long bout will lead to very high figures with the latter method and correlations between acts will tend to be negative because high levels of one behaviour will lead to low levels of others purely by exclusion. These effects are less strong with the technique employed here. Long bouts will only score more than short ones where they continue into two or more 30-s time units. The chances of detecting associations are also enhanced because, within a 30-s period, short bouts receive the same scores as long ones and are less likely to exclude other behaviours.

One problem with the study of associations, as with that of sequences, is that the system under study may not be stationary, i.e. its probabilistic structure may change with time. The effect of this can be minimized by observing for only a brief period at a consistent time of day. For this reason the 2 hr of observation which we use to detect associations has been split into ½-hr sessions carried out at the same time on four consecutive days. It is, however, of interest to determine how these associations change with time of day to see if those found at one time hold true at others. Comparisons between times of day may also help in understanding the interrelations between behaviour patterns and how these change with their frequencies. We have therefore repeated the basic observations at four different times of day to look for such changes. That locomotor activity in birds shows a strong daily pattern is well known for a number of species (e.g. Aschoff 1967). Data from automatic recording of perch changes will be given to indicate the form of this rhythm in the zebra finch as a background to the behavioural observations on daily changes in individual acts and in their associations with one another.

Methods

Subjects and Maintenance

The subjects were adult male zebra finches (*Taeniopygia guttata*) selected at random from monosexual groups. All birds were bought from dealers several months before use. They were kept on a 12-hr day (07.00 to 19.00 hours B.S.T.) in the stock cages and during the observation period. Supplies of seed, water, sand and cuttlefish bone were present throughout.

Procedure

Each subject was isolated auditorily and visually in a cage inside a sound-proof chamber. Lighting inside the chamber was provided by a 30-W strip light controlled by a time-switch. Each box was equipped with a fan giving continuous ventilation and the temperature within was kept in the range 22° to 24°C by air conditioning in the experimental room.

Locomotion records. A record of the locomotion of each of ten subjects was made for 1 day. Every animal was isolated in a sound-proof box 3 days before testing. The cage used was of metal but with a front consisting of wire bars: it measured 61 × 37 × 28 cm. Three perches ran from front to back of the cage. These were joined by two connecting bars in such a way that the two outer perches, which were 45 cm apart, pivoted about the centre perch. Visits to the outer perches were recorded by two micro-switches beneath one of the connecting bars. These were wired up to Sodeco counters which printed out the total count every 3 min. The measure of locomotion used is thus based on visits to two of the three perches in the cage, and as the aim was to compare locomotion between times of day, this was considered to give a sufficiently accurate measure. The great majority of the movement of caged zebra finches is between perches if these are available.

Behavioural observations. Each of ten subjects was isolated inside a sound-proof box in an observation cage measuring 28 × 30 × 39 cm. The back wall of this was wooden, the front wall made of glass with a fine wire mesh embedded in it. The sides and top were of coarse wire mesh. A single wooden perch ran across between the wire sides.

The whole observation cage could be seen through a glass window in the front of the sound-proof box. There was a microphone inside the box and a television camera in front of the window, with a black sleeve running from it to the box to exclude external visual stimuli. The subject was placed in the box for 4 days before observations began and then watched on closed-circuit television for each of the next 4 days at the following times: 09.05 to 09.35, 11.35 to 12.05, 14.05 to 14.35 and 16.35 to 17.05 hours. These ½-hr watches were split into sixty 30-s periods and, using a stop-clock and record sheet, an observer noted the presence or absence in these of ten behaviours. In this way a score for each act, with a maximum possible value of sixty was obtained for every ½-hr watch.

The following ten behaviours were included (abbreviations are those used in the Figures): preening (Pr) (grooming of the feathers and legs with the bill); singing (Sng); soft call notes (SCN); locomotion (Loco) (in this case scored as all movements involving a change in the position of the feet); feeding (Fd); drinking (Dr); sand taking (Snd); cuttlefish bone taking (CfB). Sitting alert (S[A]) was scored at the end of a 30-s period in which the birds showed none of the above behaviours but remained alert. An alert bird, as defined here, maintains a sleek posture with open eyes and may move its head. Sitting drowsily (S[D]) was scored for 30-s units in which none of the previously listed behaviours were shown: in such periods the feathers are fluffed out, the head still and the eyes may be closed. This category includes sleeping.

Results

Locomotion Records

The total locomotion count in 12 hr varied

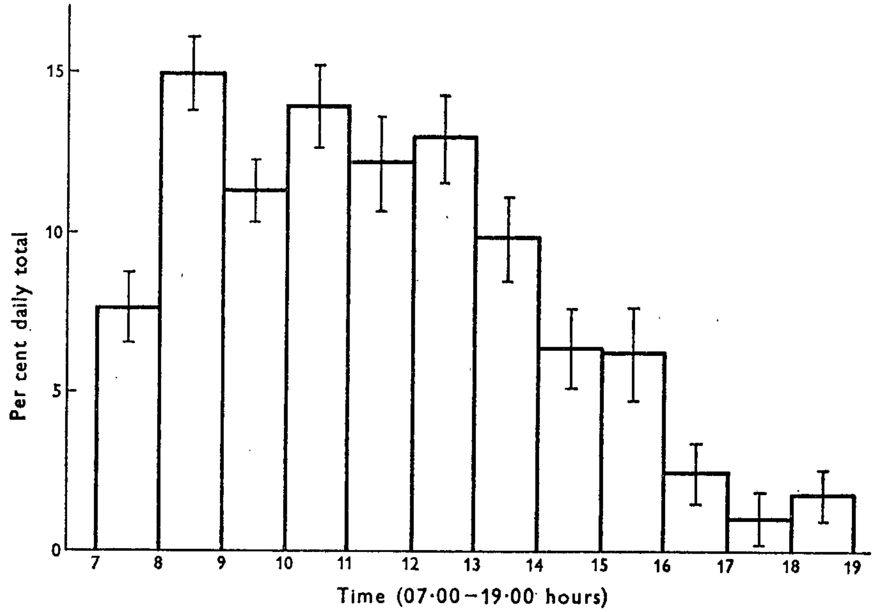

Fig. 1. The mean locomotion of ten individuals in each hour of a 12-hr day as measured by perch changes. Results are expressed as the percentage of the daily total for each bird. The ranges indicated are standard errors.

greatly between individuals (range 3378 to 31750). We have independent evidence from direct observation that individual zebra finches differ by at least an order of magnitude in the amount of locomotion that they show, and Sossinka (1970) reports a similar finding. The differences in the present case may be accentuated by the tendency of some birds to fire the microswitches several times for each movement between perches, as a particularly vigorous departure made the perches bounce. It is thus not realistic to compare scores between birds, but there is no reason to believe that scores within a bird differ for reasons other than differences in the amount of locomotion. This would only be likely to occur if the distribution of movements about the cage varied with time of day.

Figure 1 shows how locomotion, as measured in this way, changes during the course of the day. The data have been split into hourly totals and that for each bird expressed as a percentage of its total figure for the day to allow for the individual differences mentioned above. The most active part of the day is clearly between 08.00 and 14.00 hours; on average 75 per cent of the day's locomotion takes place during this period. Comparison between the raw counts at the times of day when the behavioural observations were made was carried out using a two-tailed Wilcoxon matched-pairs test. Locomotion at 09.00 to 10.00 hours was not significantly different from that at 11.00 to 12.00 hours. Birds were more active at 11.00 to 12.00 hours than at 14.00 to 15.00 hours ($P<0{\cdot}01$), and at 14.00 to 15.00 hours than at 16.00 to 17.00 hours ($P<0{\cdot}05$).

Behavioural Observations

Before treating the data gained from observations, the results from the four watches at the same time of day were massed for each bird, so that the score which it achieved for a behaviour was the number of 30-s periods, out of a maximum possible of 240 in which that act was noted. Massing of the data in this way was felt to be justified, as a Friedman two-way analysis of variance for each behaviour at each time of day (forty tests in all) only revealed a difference between the days in one case (there was a rise in the score for drinking at 09.05 hours over the four days: $\chi_r^2=8{\cdot}2$, $P<0{\cdot}05$). With so many tests, such a finding can probably be attributed to chance.

Scores for individual behaviours. Figure 2 shows the mean number of 30-s periods in which each of the ten behaviour patterns was recorded.

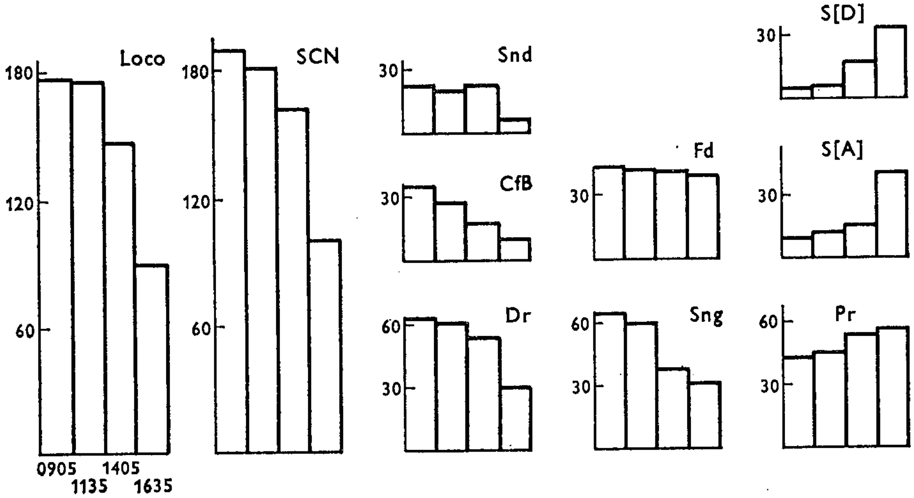

Fig. 2. The mean number of 30-s units, out of a total of 240 at each of four times of day, in which ten different behaviour patterns were recorded as occurring. Data from ten birds. Abbrevations used are: Loco (locomotion), SCN (soft call notes), Snd (sand taking), CfB (cuttlefish-bone taking), Dr (drinking), Fd (feeding), Sng (singing), S[D] (sitting drowsily), S[A] (sitting alert), Pr (preening).

The Friedman two-way analysis of variance was used to assess differences between the four times of day.

Significant differences, involving a decline in score during the day, were found in the case of six behaviour patterns: locomotion ($\chi_r^2=19\cdot8$, $P<0\cdot001$); soft call notes ($\chi_r^2=18\cdot7$, $P<0\cdot001$); sand taking ($\chi_r^2=15\cdot8$, $P<0\cdot01$); cuttlefish bone taking ($\chi_r^2=14\cdot8$, $P<0\cdot01$); drinking ($\chi_r^2=15\cdot0$, $P<0\cdot01$) and song ($\chi_r^2=12\cdot4$, $P<0\cdot01$). Significant increases took place in sitting alert ($\chi_r^2=9\cdot0$, $P<0\cdot05$) and sitting drowsily ($\chi_r^2=15\cdot9$, $P<0\cdot01$). The only behaviours to show no change were feeding and preening, although the slight upward trend in the latter behaviour is significant when the massed morning ing data are compared with the massed afternoon data on a Wilcoxon matched-pairs test (two-tailed: $P<0\cdot05$). Wilcoxon tests were also carried out on consecutive pairs of observation times: the major additional piece of information which this yielded was that there was no significant difference between the score at 09.05 hours and that at 11.35 hours for any of the ten behaviours. The changes detected by the Friedman tests are thus largely attributable to trends setting in after midday.

Associations between behaviours. Delius (1969) has demonstrated that frequency correlations between behaviours can vary markedly depending on the time unit over which frequencies are assessed. This is also true of associations as measured here, and the time unit chosen is therefore critical. In this study 30 s was chosen as being a period in which several, but not all, types of behaviour would be expected to occur. With a time unit of this length the fact that the four ingestive behaviours could only occur with locomotion between them is unlikely to be of consequence, as a bird can fly from one side of the cage to the other in a matter of 1 s. In considering associations the two categories of sitting still are excluded as they cannot occur in the same unit as any other acts.

The four observation periods at the same time of day have once again been massed. The number of time units, out of the total of 240, in which two acts which are independent of one another would be expected to occur together is given by $(ab)/240$, where a and b are the numbers in which each of the two acts occurs respectively. Taking first the 09.05 to 09.35 hours observation time, for each possible pairing of acts an expected value was calculated using this formula for every bird. The association between the two acts was then recorded as either positive or negative for each bird depending on whether the observed was greater or less than expected. On the hypothesis that the two acts were independent, as many birds would be expected to give a negative as a positive result. Whether the number differed significantly from this was determined using the sign test (Seigel 1956). With ten individuals a significant effect is obtained if nine or more show the same direction of difference between observed and expected ($P<0{\cdot}022$, two-tailed).

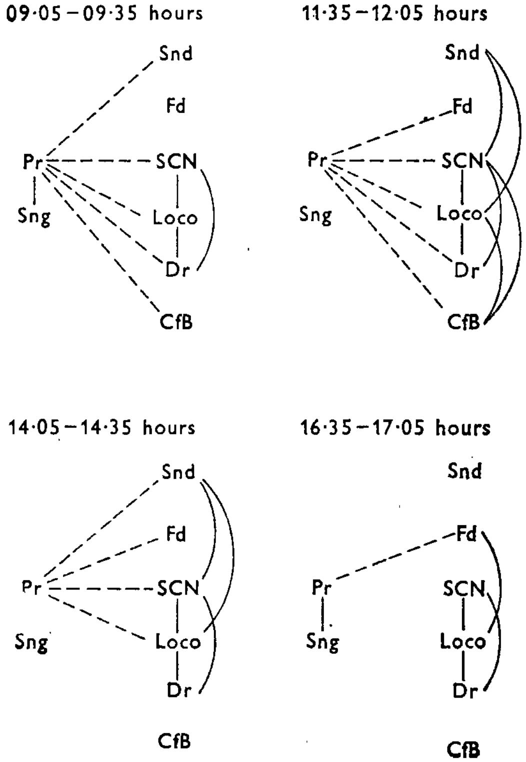

Fig. 3. Significant associations between acts at four different times of day. Dotted lines indicate negative relationships and complete lines positive relationships ($P<0{\cdot}022$). Abbreviations used are the same as for Fig. 2.

Figure 3 shows the positive and negative associations between behaviours worked out in this way for each of the four times of day. Despite the rigorousness of the criterion for significance, it is apparent that many more connections are included than would be expected due to chance. In general the four times of day give similar patterns and no connections are positive at one time and negative at another. From the actual numbers of birds showing negative and positive associations at each time it is even more clear that the patterns remain similar: every effect, both positive and negative, shown in Fig. 3 was true of five or more birds at all times of day.

Certain points in Fig. 3 are worth noting. Firstly, none of the ingestive acts is positively connected with any of the others although all are, at one time or another, associated with locomotion. Secondly, preening and singing are significantly associated at 09.05 and at 16.35 hours despite the fact that their scores, as shown in Fig. 2, change in opposite directions during the day. Certain other differences between the four diagrams in Fig. 3 are, however, attributable to the changes in scores of individual behaviours. For instance, that there is only one negative connection in the diagram for 16.35 hours is partly due to the prevalence of sitting still at this time of day, which tends to push all other acts into loose association with one another. Failure to find connections between sand and cuttlefish-bone taking and other acts is mainly due to shortage of data: at each time of day some birds failed to show these behaviours and so their associations could not be assessed for these individuals.

Discussion

Both by direct observation and by automatic recording, we have found zebra finches to show most locomotion during the morning and a progressive decline thereafter. This is in keeping with the findings of many workers on other species (e.g. Aschoff 1967; Delius 1969), although we did not find the minor peak at dusk which has often been reported elsewhere (e.g. Palmgren 1949; Aschoff & Wever 1965). Curiously, the pattern found is at variance with the only previous data on the zebra finch: Sossinka (1970) found both domesticated and wild-type birds to show more peaks of locomotion in the afternoon using a very similar technique. The reason for this difference may lie in the fact that Sossinka's birds were not auditorily isolated from other individuals. As grouped birds tend to sit quietly and close together in the afternoon, individuals close to a group may strive more actively to reach it in the afternoon than in the morning.

Slater & Ollason (1972), on the basis of a transition analysis on data all collected in the morning, suggest that the behaviour of zebra finches fluctuates on the short term between active and inactive phases, with ingestion largely in the former and grooming in the latter. In general the data on associations reported here follow the pattern which would have been expected from transition analysis, with locomotion and ingestion falling into a group which is negatively related to preening. Most of the differences in associations between times of day can be accounted for by the changes in the levels of the individual acts. The various ingestive behaviours tend to be associated with locomotion but not with each other, thus confirming the impression from observation that all of them occur during active periods but not in close temporal proximity. Soft call notes have almost identical relationships with other behaviours to those of locomotion, reflecting the fact that they take place largely during and shortly before movement.

The findings of transition analysis and the associations discovered here suggest a more general hypothesis: that the probability of occurrence of each behaviour at any given time is related to the prevalent level of locomotion. While this hypothesis is based on short-term changes in behaviour, predictions from it can be tested against the data on daily changes obtained in this paper.

The changes in scores of individual acts show some agreement with this hypothesis. The decline in locomotion during the day is associated with a fall in the score of most of the acts occurring during the active period (i.e. soft call notes, drinking, sand taking, cuttlefish-bone taking). Song was previously found to take place during the transition between the active and inactive phases, so that the hypothesis would not predict whether it would rise or fall: it was found to show a decline. The only behaviours to rise during the day were sitting still (both alert and drowsily) and preening, though the latter effect was not strong. A swing towards inactivity would have predicted these changes. Feeding, on the other hand, goes against the hypothesis in that, unlike other ingestive acts, it does not show a decline. Despite this discrepancy, it seems that many of the short- and long-term changes in behaviour could be accommodated in a fairly simple model involving a single (arousal-like) variable showing a 24-hr cycle onto which short-term fluctuations are superimposed. The usefulness of such a model will depend on its ability to predict changes in individual behaviour patterns under a variety of experimental conditions; at present, on the basis of purely descriptive data, it can only remain tentative.

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BOUTS AND GAPS IN THE BEHAVIOUR OF ZEBRA FINCHES, WITH SPECIAL REFERENCE TO PREENING

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Résumé

On donne une technique pour fragmenter le comportement en « bouts » avec des intervalles entre eux. La meilleure technique consiste à traduire les intervalles entre les événements sous formes d'une fonction logarithmique spéciale. Cependant même alors il existe des comportements du mâle qu'on ne peut scinder de cette façon ; l'auteur admet que les événements sont bien groupés, mais que leur répartition temporelle est trop complexe pour se prêter à l'analyse sous forme de « bouts » et d'intervalles. Il existe un type de comportement (« ruffling ») qu'on peut considérer comme très dispersé plutôt que groupé ; on a trouvé aussi un élément très dispersé entre les séquences de chant. On propose des mécanismes rendant compte des causes de ce groupement et de cette dispersion.

La répartition temporelle d'un toilettage a été analysé avec plus de détail, car cette activité se prête aisément à la fragmentation en bouts. La probabilité d'un nouveau toilettage reste constante avec le temps ; on ne peut trouver de corrélation entre la longueur des bouts et la longueur des intervalles qui les encadrent. La distribution de la longueur des bouts d'autre part est loin d'être aléatoire ; il y a trop de bouts très courts et très longs pour qu'on puisse les décrire sous forme d'une distribution mathématique simple. Il semble que ces résultats peuvent le mieux s'expliquer suivant l'hypothèse que le toilettage survient dans au moins deux contextes différents et que la distribution de la longueur des bouts dans les deux contextes est différente. Une preuve en est dans l'observation que les bouts de toilettage sont plus courts quand ils sont immédiatement précédés par la locomotion que lorsqu'ils ne le sont pas.

Summary

An account is given of methods for splitting behaviour into bouts and the gaps between them and it is argued that the most precise technique is provided by plotting the intervals between events in the form of a log survivor function. Even so, some behaviours shown by isolated male zebra finches cannot be easily split up in this way and it is suggested that, while events of these behaviours are clustered, their temporal pattern is too complex for analysis in terms of bouts and gaps to be useful. One behaviour, ruffling, is overdispersed rather than clustered and an element of overdispersion between outbursts of song has also been found. Causal mechanisms are proposed to *account fort he occurrence of clustering and overdispersion in behaviour.*

The temporal pattern of preening has been analysed in more detail as this behaviour is relatively easily split up into bouts. The probability of a new bout starting remains constant with the passage of time between bouts and no consistent correlation could be found between bout lengths and the lengths of th esurrounding gaps. The distribution of bout lengths, on the other hand, departs strongly from randomness with too many very short and very long bouts to be adequately described by simple mathematical distributions. It is argued that these results are best explained on the hypothesis that preening occurs in at least two different contexts and that the bout length distribution in each is rather different. Evidence for this comes from the observation that preening bouts are shorter when they are immediately preceded by locomotion than when they are not.

Acknowledgements

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INTRODUCTION

Many of the behaviour patterns shown by animals are relatively stereotyped. By ignoring the slight differences in form and intensity of separate occurrences, it is possible to study their temporal pattern as if they were point events (Delius, 1969). A common finding of this type of study is that acts of most behaviours occur in bouts. This implies that several acts tend to follow each other in quick succession, while long intervals elapse without the occurrence of any acts. Splitting behaviour into bouts and the gaps between them simplifies analysis, but it is most valuable if the criterion for doing so bears a close relationship to the way in which the behaviour itself is organised. The two ways most commonly used to define a bout often leave something to be desired in this respect :

Bout Definition Type I. A bout is considered as a series of events of a particular class not punctuated by those of any other type. This « common sense » definition is widely used (e.g. Morris, 1954 ; Sevenster, 1961 ; Feekes, 1972) and, in particular, it is that implicit in analysis of transitions between acts (e.g. Bolles, 1960). It has several difficulties. First, the numbers and lengths of the bouts found depend on the range of other acts considered. The more types of behaviour that are included in the analysis, the more will each be interrupted by others, thus giving more bouts of shorter length. Second, a difference between two treatments in the number of bouts of a particular type recorded does not necessarily indicate that this behaviour has been affected : changes in the frequencies of other acts may cause it to be interrupted more or less often in one situation than in the other. A third difficulty stems from the finding that triplet sequences of the general form A-B-A are much more frequent in zebra finch behaviour than would be expected from the frequencies of A-B and B-A (Slater and Ollason, 1972). The same has been found true of sequences of grooming in mice (Fentress, 1972). This suggests that behaviour A is not entirely switched off during interruption by behaviour B so that successive bouts of A, defined in this way, are not independent of each other.

Despite these objections, the method is probably adequate in cases where behaviours follow each other in a strongly ordered sequence (Bastock and Manning, 1955 ; Hinde, 1958 a). It is also the obvious method to use where interactions between only two behaviours are being studied (e.g. McFarland, 1970). The difficulties largely arise where the behaviour is less structured and where many different types of act may occur and are being recorded. In this situation, and in those where the temporal pattern of individual behaviours is being analysed, the next type of definition is clearly preferable.

Bout Definition Type II. A bout can also be defined according to a critical time limit. All acts separated by a period of less than t seconds are considered to be within a bout and gaps of more than t seconds are defined as between bouts. Using this method act B may occur during a bout of act A, and bouts of two different behaviours may take place concurrently if they alternate with one another. The main difficulty here lies in the choice of the time limit such that it represents as closely as possible a genuine switching point. That this has not always been achieved is apparent from studies of rat feeding behaviour in which criteria as disparate as 40 minutes (le Magnen and Tallon, 1966), 20 minutes (Thomas and Meyer, 1968) and 10 minutes (Levitsky, 1970) have been selected. Sometimes the criterion chosen is stated to be arbitrary (Rowell, 1961 ; Baerends, 1970) but, where this is not the case, it is usually chosen by examination of an interval histogram. With this type of plot some workers have found a bimodal distribution of interval lengths, indicating the position of the trough between the modes as a clear changing point (Isaac and Marler, 1963 ; Ewing, 1969 ; Lemon and Chatfield, 1971). More often the histogram shows a fairly uniform decline in numbers with increasing gap length.

From the point of view of defining a bout, a more useful way of plotting interval distributions, and that which will be used here, is as a log survivor function. This method has been used surprisingly little in behaviour (exceptions being Nelson, 1964 ; Wiepkema, 1968 ; Delius, 1969) so some account will first be given of the rationale behind it. After this its application to several behaviours in the zebra finch will be described and preening, which is one of the most appropriate behaviours for analysis in terms of bouts and gaps, will be singled out for detailed consideration. An equivalent analysis of feeding behaviour will be found elsewhere (Slater, in press).

METHODS

Most of the data used in this analysis were obtained by observing each of ten adult male zebra finches (*Taeniopygia guttata*) for eight hours. Each bird was isolated in a cage measuring 28 × 30 × 39 cm inside a sound-proof chamber for three weeks before observation and eight one-hour watches were then carried out during the ensuing two weeks, all between 11 a.m. and 12.30 p.m. This method was employed to avoid as far as possible differences due to daily rhythms (Ollason and Slater, 1973). Observations were made on closed-circuit television and the data transcribed onto paper charts with an Esterline-Angus pen recorder.

A detailed description of the behaviour patterns recorded is given by Slater and Ollason (1972). Briefly, those considered here are as follows (abbreviations are those used in the Figures) : preening (Pr) (grooming of the feathers and legs with the bill) ; singing (Sng) ; locomotion (Loco) (all movements greater than approximately 5 cm) ; feeding (Fd) ; drinking (Dr) ; feather settling or ruffling (Rf) ; scratching of the head (Scr) ; stretching of the wings or legs (Str) ; bill-wiping (BW).

The recording button appropriate to each behaviour was depressed for as long as it was continuously performed. Thus for feeding individual pecks at food were scored ; for preening breaks were recorded when the beak was no longer in contact with the feathers ; for song, breaks of a fraction of a second between individual phrases were recorded. This allowed the duration of inter-event intervals for each category of behaviour to be determined as accurately as possible. Gaps were measured from the pen recorder charts in whole numbers of seconds : thus a gap recorded as 0 seconds long was less than 1 second in duration, a gap recorded as 1 second long was between 1 and 2, etc.

The log survivor function

If events of a given type are distributed at random (i.e. forming a Poisson process), the histogram of intervals between them will follow a negative exponential distribution (Duncan et al., 1970). It is not, however, easy to compare such a theoretical distribution with the observed distribution of gap lengths. This is considerably easier if the intervals are cumulated backwards and plotted on a semilogarithmic scale as in Figure 1. In this case the gaps between independent events yield a straight line, the slope of which is proportional to the probability of an event at any given time after the last event. In Figure 1, 1000 intervals have been recorded in all, 100 of these are greater than 10 seconds long, 10 are greater than 20 seconds and 1 is greater than 30 seconds. The probability of an event occurring in each 10 second interval after the last event thus remains constant at 0.9 (900/1000 = 90/100 = 9/10 = 0.9).

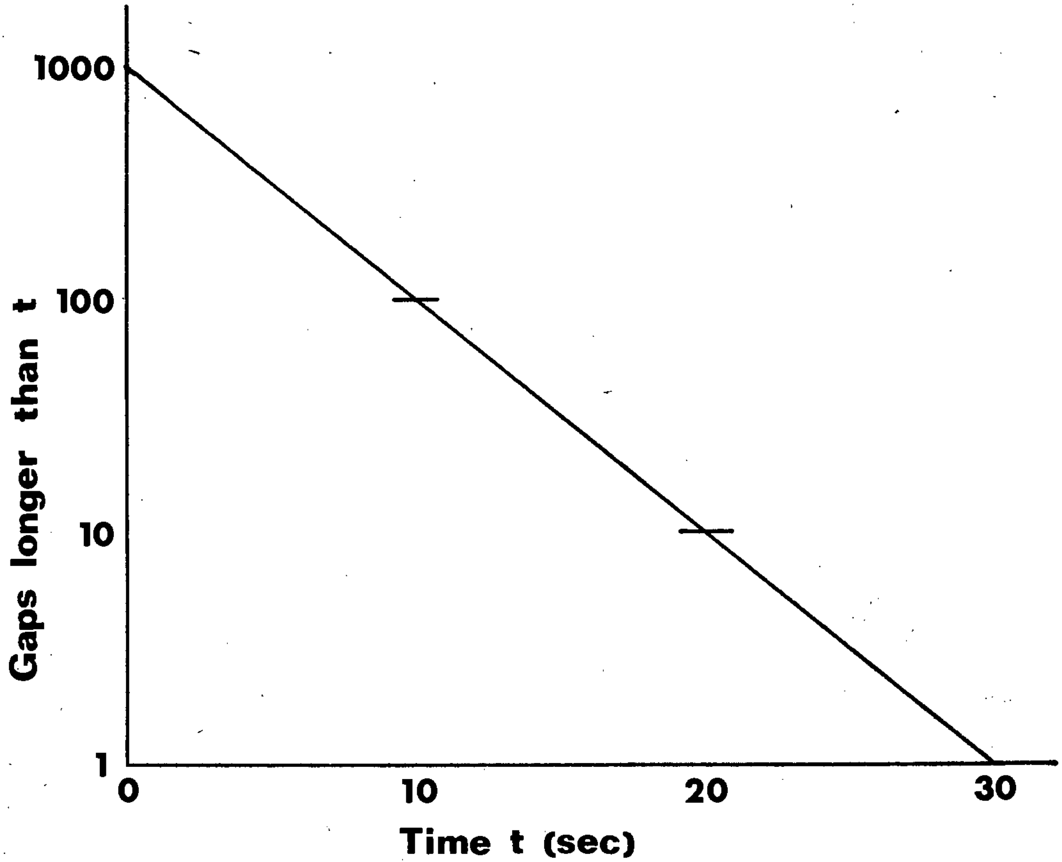


Figure 1

Hypothetical log survivor function for 1000 gaps between events which are distributed at random.

Of course real data seldom approximates to such a straight line, but plotting it in the form of a log survivor function has several advantages. Most obviously, it is much easier to compare the actual form of the data with the expected straight line than it is to compare an interval histogram with a negative exponential curve. Further, as the slope of the plot is proportional to the probability of an event with the passage of time since the last event, this changing probability can readily be assessed by inspection of the graph. If a sharp change in probability (slope) occurs at a certain point, this point can be used as a time limit for bout definition, as will be explained later with reference to data on various behaviours.

A slight technical problem arises in the analysis of intervals between behavioural events because of the fact that observation periods are usually rather short. This means that the number of complete long intervals observed is less than it should be because they tend to overlap the beginnings and ends of watches. This has the effect of making the log survivor plot curve downwards at large interval lengths (Delius, 1969). This effect can, however, be minimised by adding the time before the first event in an observation period to that after the last and including this composite interval in the data. This procedure is followed in the treatment of data presented in this paper : it does not affect the data greatly as only eight of the many intervals recorded for each animal are of this type.

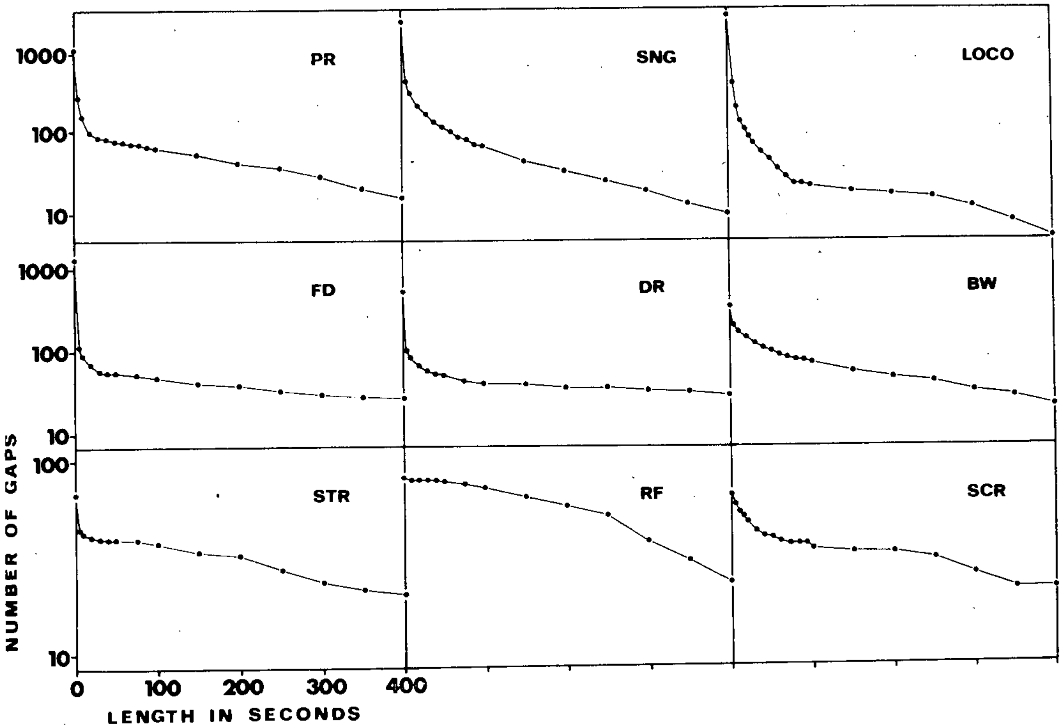
RESULTS

The temporal pattern of several different behaviours

Figure 2 gives log survivor functions of the intervals between nine different behaviours

Figure 2

Log survivor functions of the gaps between events for nine different behaviour patterns shown by bird 13 *during eight hours of observation. All plots are up to a maximum of* 400 *seconds, each point indicating the number of gaps recorded which were longer than the time shown on the abscissa. The abbreviations used are explained in the Methods section.*



for one of the birds tested. Similar plots for the nine other individuals are of the same general form but differ in some details which will be referred to below. In most cases these plots diverge so markedly from a straight line that statistical comparison with such a random model is unnecessary. Instead, the type of plot shown falls into two categories :

1. *Overdispersed.* Remembering that the slope of the log survivor function gives a measure of the probability of occurrence of an event, ruffling can be seen to be a behaviour which is overdispersed. The probability of the next event increases with the passage of time since the last one. In some birds there is a slight initial peak in the log survivor function of ruffling, indicating some tendency for the events to occur close together, but in the majority this is absent, as it is in Figure 2. This is illustrated by Figure 3, which is based on earlier data involving only two hours of observation on each of ten birds. The probability of ruffling can be seen to rise with the passage of time and is significantly greater 300 - 400 seconds after its last occurrence than 0 - 100 seconds after ($p<.02$, two-tailed Wilcoxon matched pairs test).

2. *Clustered.* For the other behaviours shown in Figure 2 the probability of an event is high to begin with and falls later. This is also true of these behaviours in all other birds studied and they can thus be said to be clustered.

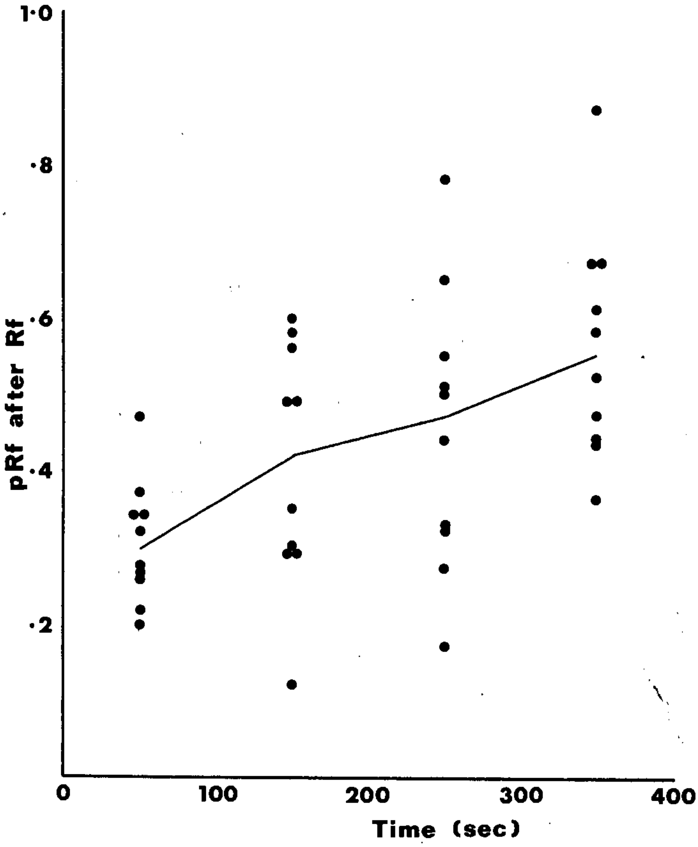


Figure 3

The probability of ruffling in the four consecutive 100 second intervals immediately after its last occurrence, based on two hours of data from each of 10 birds. The line joints the medians.

As a general description it seems preferable to refer to these behaviours as clustered, rather than as occurring in bouts, for a number of reasons. The bout concept expresses a particular notion about the structure of behaviour : that within a bout he probability of occurrence of an event in any particular time unit is high, whereas between bouts the probability of an event (i.e. of a new bout beginning) is low. In the simplest hypothetical case, where these two probabilities are constant, a switch between then taking place at the beginning and end of each bout, the log survivor function will be a composite of two straight lines. That with the steepest slope will describe the probability of an event within a bout ; that with the gradual slope will give the probability of a new bout starting with passage of time between bouts (Nelson, 1964). While there are various reasons for thinking that the assumption that the two probabilities are constant is an oversimplification, if the behaviour is realistically to be described as falling into bouts, the log survivor plot should resemble the sum of two simpler processes. Several of the graphs in Figure 2 encourage this interpretation, with the probability of a further event being great at first and then changing rather rapidly to a relatively low and constant value. In these cases (e.g. preening, feeding and stretching in the bird illustrated), it seems reasonable to regard the behaviour as organised in bouts. Then, assuming the between bout probability to be constant, a time limit for bout definition can be chosen as the point where the graph starts to rise up more steeply to meet the ordinate. While this depends to some degree on judgement, it has the merit of greater objectivity than does the examination of interval histograms.

Even where behaviours do appear to fall into bouts it is possible that this is not the most economical was of describing their temporal pattern. A simpler alternative is that after each event the probability of a further event decays in the manner shown by the log survivor function regardless of the lengths of previous gaps. Such a process, known as a renewal process, would be equally capable of explaining the form of the curves found here ; it has also been found adequate by Heiligenberg (1973) to account for the organisation of gaps between behavioural events in a cichlid fish. He found that the length of a particular gap was independent of that of the gap preceding it, and concluded therefore that no more complex processes were necessary to account for the intervals between successive events than a decay in probability following the same pattern after each event.

The possibility that the temporal pattern of some of the behaviours considered here could be adequately described by a renewal process has not been explored in detail, but it appears unlikely for two reasons. First, the rather sharp change in probability found in some cases suggests that a switch takes place at this point. Second, if the data were generated by a renewal process, splitting the behaviour into bouts and gaps would give rise to bout lengths following a geometric distribution. While this it the case for feeding in some birds, it is not for most of them (Slater, in press) and as will be seen it is certainly not the case for the preening of those birds studied here. Analysis in terms of bouts and gaps therefore seems more attractive than the search for a simple mathematical rule to describe the distribution in time of single events.

For some behaviours (e.g. song in Figure 2 and locomotion in most other birds) splitting into bouts and gaps cannot be easily achieved. In these cases it appears that the underlying processes are more complex with no sharp changes in probability which can be used to give a time interval for bout definition. For locomotion this is not surprising as this behaviour occurs in so many different contexts that one might expect its probability to fluctuate widely, rather than fall simply into a bout/gap model. Bill-wiping and scratching also often show a gradually changing probability rather than a sharp switch at a particular time interval. Observation suggests that, if a realistic bout model could be constructed for these behaviours, it would probably have to take account of two different levels of bout. Behaviours such as these may take place in very quick succession (tightly organised bouts) ; may be generally common over a period of time, as is scratching during long preening bouts (loosely organised bouts) or may not take place for long periods (between bout intervals). Such a model, which assumes the log survivor plot to be a complex of three or more processes (in the example just given (lines of high, medium and low slope), is hard to derive simply from the graph and also difficult to differentiate from a model which assumes the probability of an event to fluctuate freely between broad limits. For the moment therefore it seems better to refer to these behaviours as being clustered rather than as occurring in bouts.

Song is another behaviour which appears to have two different levels of organisation. In this species song, consists of a series of similar phrases which follow each other in quick succession with gaps of less than 1 second between them. Following each series there is a longer gap but, as can be seen from Figure 2, the probability of further singing may remain high for over 1 minute after the last series of phrases. Thus individual phrases take place in tightly knit bouts and these bouts are themselves clustered in time.

A further feature of the singing of some birds is that each series of phrases is followed by a period of about 3 seconds during which the start of a new series is less likely than it is subsequently. This could be accounted for by the fact that song is very frequently followed by preening and, where this is so, a new song cannot begin until this preening has finished (Slater and Ollason, 1972). However, the probability of song is still lower 1 - 4 seconds after the last song than subsequently when only gaps between songs containing none of the other behaviours being recorded are considered (Fig. 4).

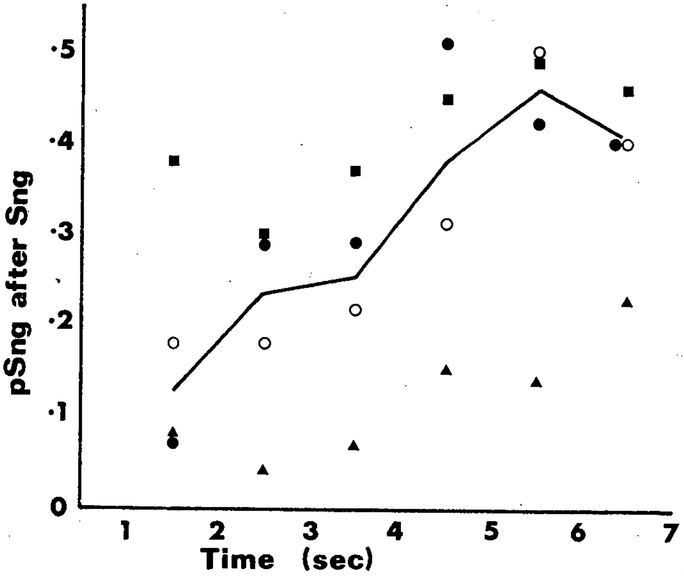


Figure 4

The probability of singing in six consecutive 1 second intervals from 1 - 7 seconds after its last occurrence for those occasions when none of the other behaviours being recorded intervened (i.e. the bird was sitting still), based on two hours of data for four birds. Each bird's results are represented by a different symbol. The line joins the medians. Note that for each of these birds the first three values are all lower than the subsequent three.

From these results it can be seen that the temporal pattern of song is a complex phenomenon showing tightly-knot bouts which are clustered in time, while the bouts within the clusters tend to be overdispersed in some birds. The high frequency of alternation between song and preening reported elsewhere (Slater and Ollason, 1972) may occur in these birds because preening is disinhibited during this period of song inhibition.

Bout organisation of preening

Introduction.

Preening is a behaviour which falls fairly clearly into bouts for all individuals so far studied and takes place frequently enough for sufficient data to be available for detailed analysis. For the purposes of this analysis preening is restricted to bill to feather grooming movements. Although this is a fairly heterogeneous class of events, they tend to be closely associated in time, and as they take place rapidly, it is not easy to subdivide them according to the different areas of the body being dealt with. Other comfort movements, such as scratching and ruffling, are associated with preening (Slater and Ollason, 1972), but their relationship to it will not be considered in detail here. A preening bird grooms a few feathers and then raises the head briefly before grooming again or changing to some other activity. A single event of preening is defined as the series of movements between occurrences of head raising; during this the beak is in constant contact with the feathers.

The bout criterion.

A separate bout criterion was derived from the log survivor function of preening for each bird. The criteria chosen varied between 25 seconds and 70 seconds depending on how rapidly the probability of a further event fell to a relatively constant value.

The distribution of gaps between bouts.

If bouts, as defined from the log survivor functions, were really independent of each other, the probability of a new bout starting would remain constant between bouts. There are two reasons why this might not be the case. Firstly, gaps between bouts might tend to be of a typical length, as one might expect if the behaviour recurred cyclically. Secondly, if the time limit used for bout definition was too short, too many new bouts would appear to start a short time after the last one finished. Comparison of the gap length distribution with that expected on a random model is therefore of some interest. This was done in the following manner :

The expected distribution of interbout intervals was calculated from the number of these and their mean length assuming a negative exponential distribution between t (the time limit used for bout definition) and infinity. The time between t and infinity was then split into eight units, in each of which an equal number of gap lengths would be expected to fall. The number actually found in these time periods was then compared with this expected value.

As an example, bird 12 showed 81 gaps greater than 70 seconds (the bout criterion) long. The mean length of these gaps was 295 seconds. From this it was calculated than one-eighth of them (10.1) should end in each of the following time units : 70-99.9 ; 99.9-134.6 ; 134.6-175.5 ; 175.5-225.7 ; 225.7-290.3 ; 290.3-381.3 ; 381.3-537.0 ; over 537.0 seconds. The actual numbers ending in these units were : 7, 9, 13, 10, 9, 15, 6, 12. Comparing this distribution with the expected gave $\chi^2 = 6.41$ (d.f. 7, $p > .25$). There is thus no evidence in this bird that gap lengths tended to cluster round a particular length.

The same conclusion holds for the other nine birds ; in no case was there a significant difference between the distribution of interval lengths and that expected from the negative exponential distribution. One can conclude, firstly, that the time interval used for bout definition was not too short and, secondly, that gaps between preening bouts do not tend to be of a typical length.

The relationship between bout and gap lengths.

While the distribution of gap lengths may appear close to that expected, it is possible that the length of a bout (here measured as the number of events which in includes) is related to the length of the gap after it or the length of the gap before it. Likewise, short-term rhythms may exist whereby a series of gaps or bouts tend to be of a similar length. This type of effect was tested for by correlating gap lengths with bout lengths in the four ways shown in Table 1. While four of the 40 correlation coefficients are significant, there is no evidence for a consistent effect of this type.

The distribution of bout lengths.

The simplest type of bout length organisation would be one in which the probability of a further event was constant regardless of the number of previous events. In this case the bout length distribution would be a geometric one. A more complex possibility is that the probability of continuing rises as the bout length increases, a model for this being the logarithmic distribution (Lemon and Chatfield, 1971). Figure 5 shows the number of bouts of lengths up to 10 events shown by one bird compared with that expected from each of these two distributions (expected values were calculated following Lemon and Chatfield 1971, for the geometric, and Williamson and Bretherton 1964, for the logarithmic). It is clear in this example that the geometric distribution gives an extremely poor fit to the data while that of the logarithmic is much closer, though with rather more bouts of one or two events than might be expected. Table 2 gives data for all ten birds on these

TABLE 1

Correlations between bouts and gaps of preening using the Spearman rank correlation coefficient. N reprensents the number of figures on which the first three correlations were based ; the fourth was on N — 8 (* = p.<05 ; ** = p<.01).

BIRD	BOUT WITH BOUT AFTER	BOUT WITH GAP AFTER	GAP WITH BOUT AFTER	GAP WITH GAP AFTER	N
9	+.14	+.07	—.05	+.06	31
25	—.03	+.18	+.27 *	—.04	58
5	—.09	+.03	—.04	+.01	57
13	+.03	+.36 **	+.10	+.16	65
12	+.17	—.26 *	—.07	+.05	67
28	+.13	—.07	—.13	—.003	56
6	—.14	—.21	—.14	+.02	52
11	—.20	+.06	+.07	+.09	55
2	+.14	—.12	+.17	+.16	67
22	+.21	—.30 *	—.001	—.07	45

TABLE 2

The number of bouts of preening consisting of only one or two events (Obs) compared with that expected from geometric (Geom) and logarithmic (Log) distributions. The expected values were calculated from the total number of bouts and the mean bout length shown in the second and third columns.

BIRD	NUMBER OF BOUTS	MEAN BOUT LENGTH	BOUTS OF 1 and 2 EVENTS		
			OBS	GEOM	LOG
22	53	30.4	19	3.4	15.6
6	60	6.9	38	16.2	27.3
12	75	10.8	31	13.3	29.3
25	66	20.9	26	6.2	21.4
11	63	29.2	30	4.3	18.8
5	65	29.6	26	4.3	19.3
28	64	28.3	29	4.5	19.3
2	75	5.5	57	24.9	37.2
9	39	49.9	21	1.6	10.3
13	73	20.0	28	7.2	23.9

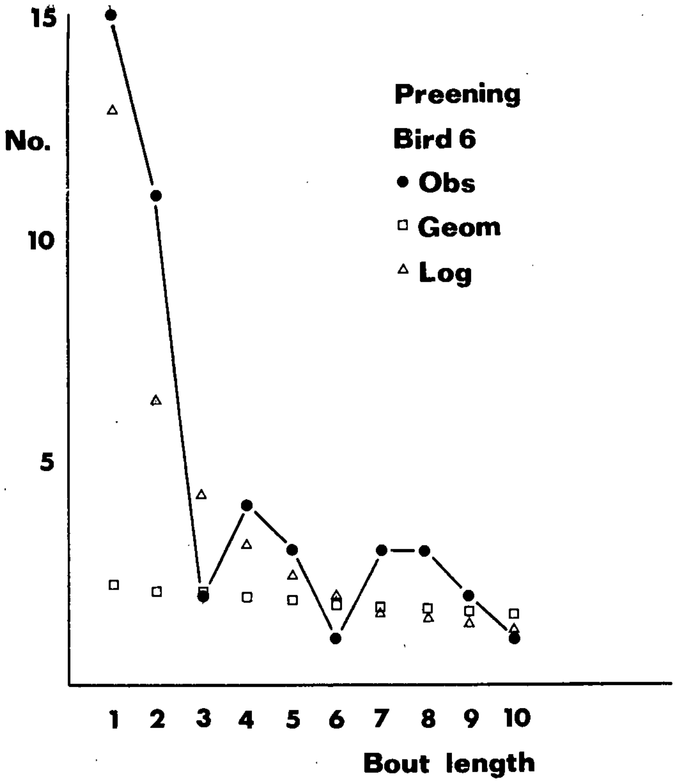


Figure 5

The number of preening bouts of 1 - 10 events in length shown by bird 6 during eight hours of observation (Obs). The number of each length predicted from the geometric distribution (Geom) and the logarithmic distribution (Log) are also shown.

short bouts. Their number is consistently considerably higher than that predicted from a geometric distribution. While in all cases the logarithmic distribution gives a much better fit for each bird, it always underestimates the number of these short bouts ($p = .002$, two-tailed Sign test). There are thus too many very short bouts (and, following from this, too many very long ones) for the data to be simply accounted for by either of these two mathematical distributions.

At first sight, the only explanation for this finding is that rather complex changes in the probability of continuing take place during the course of a preening bout. This explanation rests, however, on the assumption that all the observed bouts of preening are causally similar so that it is valid to mass them for analysis. This is in some ways equivalent to the mathematical assumption of stationarity (see Slater, 1973). An alternative possibility is that the data are not stationary. This might result if preening occurred in more than one behavioural context and the context determined to some extent the duration of the bout. Thus the temporal structure of bouts found in each context might be simple but when they were massed the resultant distribution of bout lengths would appear complex. A consideration of the context of preening does suggest that this latter type of explanation may be more accurate.

The context of preening.

Isolated zebra finches vary a great deal in the amount of locomotion that they show (Ollason and Slater, 1973), but in general, with the exception of one or two very inactive individuals, they have been found to spend periods of many minutes flying round their cages interspersed with feeding and drinking. During the morning, which is the active part of the day, these periods are separated by shorter intervals of inactivity which typically include a long bout of preening and the behaviours associated with it. In some birds this fluctuation between activity and inactivity is regular enough to be termed a cycle: this is very variable, but autocorrelations of locomotion tend to peak at around 45 minutes, suggesting a cycle of this length. Preening is not, however, entirely restricted to the inactive phase. An active bird will sometimes stop suddenly, make a few quick preening movements, and then move off again.

These observations suggest that bouts of preening occurring during locomotion may be shorter than those found when the bird is inactive. To see whether this is the case, Table 3 shows preening bouts for all the birds studied split into those which were preceded by locomotion within 15 seconds of their start and those which were not. The mean bout length following locomotion is significantly shorter ($p < .01$, two-tailed Wilcoxon matched-pairs test). The only bird going against the general trend was bird 12, the most inactive individual.

TABLE 3

Mean bout length of preening depending on whether or not locomotion took place in the 15 seconds before the bout began.

	LOCOMOTION BEFORE		NO LOCOMOTION BEFORE	
BIRD	NUMBER OF BOUTS	MEAN BOUT LENGTH	NUMBER OF BOUTS	MEAN BOUT LENGTH
6	26	3.3	34	9.7
28	20	26.3	44	29.2
11	21	18.5	42	34.6
9	15	1.8	24	80.0
25	15	2.2	51	26.3
5	14	3.4	50	33.6
22	12	8.5	41	36.8
2	36	2.0	39	8.7
12	7	14.4	68	10.8
13	26	8.5	47	26.4

On the basis of this finding it does not seem reasonable to regard preening as a unitary phenomenon with a complex within-bout probabilistic structure. It seems that it occurs in at least two different behavioural contexts and that bout length distributions in each are rather different. It is also possible that preening in different contexts differs in speed or in its constituent movements. Certainly the brief bouts of preening during locomotion do give the impression of being hurried, a feature more typical of the later events in long bouts. The present data are, however, unsuitable for quantitative analysis at such a fine level.

DISCUSSION

This paper has been concerned with an analysis of the temporal pattern of individual behaviours in the zebra finch in terms of bouts and the gaps between them. Bouts are often defined in a rather arbitrary and not always explicit way and it has been argued that a sharper definition, which bears a closer relationship to the structure of the behaviour concerned, is made possible by plotting the intervals between successive events in the form of a log survivor function. For several of the behaviour patterns considered such plots reveal a sharp change in the probability of a further event at a certain time interval after the last one, suggesting that gaps longer than this should be considered as between bouts and shorter gaps as within bouts. These behaviours can then be analysed further using the comparatively simple methods which have been applied here to the temporal pattern of preening and elsewhere to that of feeding (Slater, in press).

For other behaviours the change in probability with time is more gradual, suggesting that more complex underlying processes are in operation : while these behaviours are clustered, they do not take place in easily defined bouts. Any attempt to fit such behaviours as these into a simple bout/gap model would involve ignoring some of the complexities of their temporal pattern. Song is a particularly interesting case of this type. The individual phrases occur in tightly grouped bouts ; these bouts are in turn clustered in time but, in some birds, after each bout a new bout tends not to start some seconds. There is thus an element of overdispersion between the bouts. Overdispersion has only been found in one other behaviour, ruffling, and in this case it is the major feature of the temporal pattern.

There are several reasons why acts of a particular type may be grouped in time, as where they are clustured or occur in bouts. The most obvious of these is that the external stimulus or internal state appropriate to the behaviour may be present at some times but not at others. Unless a single act of the behaviour removes the stimulus, its persistence is likely to elicit further acts. It is also possible that positive feedback as a result of performance may lead to continuance of the behaviour (Wiepkema, 1971), or that interaction with other behaviours may cause the grouping of acts : part of the reason for bill-wiping being clustered may be that it is often stimulated by drinking and acts of drinking are themselves clustered. Given these considerations, it is rather suprising to find a behaviour, like ruffling, which does not usually show clustering. As this behaviour is probably stimulated by dishevelment of the plumage, it must be very efficient at removing this.

There thus seem to be good reasons why behaviour patterns should be clustered in time. Why then should some of them show overdispersion, which is the opposite of clustering ? In the case of song the overdispersion is very short-term, involving as it does a tendency for the behaviour not to start up again within 4 seconds of ceasing. A similar effect has been found by Hinde (1958 b) in the song of chaffinches and seems to be fairly general in vocal behaviour as evidenced by the frequent finding that gaps between events of song follow a bimodal distribution (Lemon and Chatfield, 1971 ; Isaac and Marler, 1963). This may be for the very good functional reason that song is a signal and a period of silence following its production will allow the singer to listen for a response which it would not hear if it continued to sing itself (Ollason, personal communication).

The overdispersion of ruffling is a more long term effect with the probability of an event increasing progressively over a matter of minutes after the last event. As ruffling is not usually clustered, this type of effect is particulary easy to detect, but it may also be true of the intervals between bouts or clusters in other behaviours. One might expect overdispersion to be found if causal factors for a particular behaviour rise during non-performance so that its probability of being elicited by the appropriate stimulus becomes greater. While there was no evidence of this for preening, in the majority of birds bouts of feeding are overdispersed (Slater, in press), the intervals between bouts yielding a convex log survivor function like that for ruffling in Figure 2.

The more detailed analysis of preening reported here was stimulated by the fact that preening could be split into bouts and gaps more objectively than could most other behaviours. Despite this apparent simplicity of organisation, in no bird did the distribution of gaps between bouts depart from random nor could any consistent relationship be found between the lengths of bouts and those of the gaps surrounding them. No simple rules could therefore be discovered which would help to predict the timing and size of preening bouts. By contrast, the analysis of bout lenghs revealed a strong departure from randomness : the rewere too many very short and very long bouts of preening for the bout length distributions to be adequately described by either the geometric or the logarithmic distribution.

The simplest present hypothesis to account for these findings is that preening takes place in two different behavioural contexts : during brief breaks in locomotion when bouts tend to be short and during periods of inactivity when the mean bout length has been found to be longer. If the behaviour in these two contexts is causally different any simple rules which govern its occurrence in either may be lost when an attempt is made to analyse all bouts of preening as if they were examples of the same phenomenon. One possible way in which short and long bouts might differ in causation would be if short bouts deal with specific sources of irritation which may arise at any time, whereas long bouts result either from generalised irritation, perhaps building up slowly between them, or from a central program. Short bouts in this case would be expected to deal more often with those areas of the body most prone to being dishevelled by other activities, whereas long bouts would cover all areas. Another possibility is that short bouts are disinhibited by ongoing behaviour in the same way as has been proposed for displacement activities (Andrew, 1956 ; van Iersel and Bol, 1958 ; McFarland, 1966). Being brief and giving the impression of hurriedness these bouts of preening do have a similarity to behaviour normally classed as displacement. On the other hand, there is no evidence to suggest that they arise because the animal is in conflict or thwarted, and such an explanation would be tenuous in the case of a free moving isolated individual.

A more objective method of splitting preening into different types may prove possible when data are obtained which allow preening bouts to be analysed in terms of their speed and the areas of the body with which they deal as well as their length. It may then be possible to test the hypotheses which have been proposed there to account for the temporal pattern of preening.

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THE TEMPORAL PATTERN OF FEEDING IN THE ZEBRA FINCH

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Abstract. Feeding in zebra finches occurs in clearly defined bouts, but strong individual differences have been found in the finer details of its pattern. Some birds showed a constant probability of starting feeding with passage of time between meals and a constant probability of stopping during a meal. In these cases meal length (number of pecks at seed) tended to correlate with the length of the preceding gap. By contrast, in most individuals both meals and gaps tended to be of a typical length, and in some of these autocorrelation showed feeding to follow a cycle approximately 24 to 30 min long. Meal length in most of these birds correlated strongly with the length of the succeeding gap. The individual differences found are discussed and hypotheses put forward for their causation.

The temporal pattern of feeding has probably received more exhaustive study than that of any other behaviour (e.g. le Magnen & Tallon 1966; Duncan et al. 1970). The reasons for this attention are not hard to seek. Firstly, by the use of Skinner boxes or other automatic recording equipment the incidence of feeding can be monitored over long periods of time without direct observation. Secondly, the fact that feeding serves to correct a physiological deficit suggests that its causation may be simpler and more easily analysed than would be that of, for instance, grooming or song. Thirdly, it is a more homogeneous category of behaviour than many others, again suggesting that underlying mechanisms may be easier to elucidate. Lastly, feeding tends in many animals to occur in fairly concentrated bouts or meals, thus making possible its analysis in terms of bouts and gaps rather than calling for more sophisticated treatment.

Despite this last point, workers differ markedly on the method used to define a bout and also on the definition arrived at even for the same species. Using rats, for example, le Magnen & Tallon (1966) chose a criterion of 40 min (gaps longer than this being taken as between meals), while Thomas & Mayer (1968) chose 20 min and Levitsky (1970) chose 10 min. In all these cases the same criterion was applied to each animal, a practice which ignores possible differences in the feeding pattern between individuals. The criteria of le Magnen & Tallon (1966) and Thomas & Mayer (1968) appear to have been arbitrarily selected; that of Levitsky (1970) was based on the examination of an interval histogram, but he doubled the time interval suggested by this 'to insure the inclusion of an entire meal'. It is possible to derive a criterion less arbitrary than these, and based more clearly on the structure of the behaviour itself, by examining the distribution of intervals between events plotted in the form of a log survivor function. This method has previously been used on feeding data by Wiepkema (1968) and will be used here as it is the most objective method currently available.

The work to be described in this paper forms part of a wider programme of research into the temporal pattern of various behaviours shown by isolated male zebra finches. In addition to the reasons given above for singling out feeding for more detailed study, it should be mentioned that previous work using an approximate measure of the amount of feeding suggested that it did not change with time of day. No significant difference was found in the number of 30-s periods in which feeding was recorded at four different times between 09.00 and 17.00 hours (Ollason & Slater 1973). If feeding does not differ markedly between times of day then it is reasonable to mass data from different times for statistical treatment, and more detailed examination becomes possible than would be the case with other behaviours. On the other hand, as will be seen, there are substantial differences between individuals in feeding behaviour making it necessary to keep the data for each bird separate throughout the analysis.

Methods

Nine adult male zebra finches (*Taeniopygia guttata*) were used for the recordings to be described, each being placed in the sound-proof chamber in which it was to be tested at least 3 days before recording began. Prior to this the birds had been kept in monosexual groups, but all of them had previous experience of isolation within sound-proof chambers and of feeding from hoppers. The cages used measured 61 × 37 × 28 cm, and each was provided with seed, water, sand and cuttlefish bone. The only source of seed was a tall hopper into the trough of which the bird could peck by leaning across from one of the perches. Small panican seed was used to ensure free flow from the hopper. A photocell placed on the far side of the trough from the only light supply present was used to record occasions when the bird pecked into the trough. The number of interruptions of the beam were added up by a Sodeco counter which printed out a running total every 20 s. The photocell was placed as low above the trough as possible so that individual pecks were scored, the raising of the head between pecks being sufficient to allow light to stimulate the photocell. It should be noted that the measure obtained by this method is one of feeding behaviour rather than of food intake, as some pecks into the trough may not result in food uptake, whereas others may lead to the bird obtaining more than one grain of seed. The number of pecks at food does not therefore provide a direct measure of food intake.

Each bird was scored for two consecutive days and the data from these were massed for statistical treatment. This was felt to be justified as in no bird did the number of bouts of feeding (as defined below) differ significantly between the two days ($\chi^2 < 1{\cdot}6$ in all cases). As lighting in the sound-proof chamber was switched on for 12 hr daily (07.00 to 19.00 hours), the analysis for each bird is based on 24 hr of data. In the case of some birds a further Sodeco counter was wired up to a microswitch under one of the three perches in the cage so that an approximate measure of locomotion was obtain concurrently with the data on feeding.

Non-stationarity due to differences between times of day is clearly a problem with this type of data. As a result not all the data could be used for analysis. Initially, however, it was decided to examine all the results from each individual to obtain a bout criterion for that bird, and later to see how times of day differed in the numbers and lengths of bouts as well as in the total number of pecks at food. Previous data had suggested that feeding occurs in very tightly clumped meals, so that it is unlikely that the bout criterion would be greatly affected by time of day.

Gaps between successive events of feeding were measured in multiples of 20 s as the number of intervals between print-outs in which no feeding was recorded. Although gaps shorter than 20 s could not be accurately measured, their number could be ascertained from the total number of pecks into the food trough recorded: if a bird took N pecks at food during the day, there were N-1 gaps between pecks. The distribution of gap lengths was then plotted in the form of a log survivor function (see Fig. 1 for three examples). With this type of plot the slope of the graph gives a measure of the probability of occurrence of an event at any given time interval after the last event. For behaviour patterns which are organized in bouts the slope is steep to begin with and changes fairly suddenly to become gradual. This point of switching is the most realistic point to choose as an interval for bout definition, the numerous intervals shorter than this being taken as within a bout and the less common longer ones as between bouts. The data for each bird were therefore plotted in this way and a bout criterion derived by inspection of the graph. Some degree of judgment is involved in this, particularly in the present instance where the method of data collection leads to a smoothing of the graph. This is because recorded gap lengths are shorter by a variable amount than the true breaks in feeding: thus a gap recorded as 20 s long could in fact be anything from 20 s to 60 s in length since it is not certain from the recording method at what point feeding occurred during the preceding and succeeding 20 s units. Nevertheless, this method is considerably less arbitrary than others in common use. Its application to various other behaviours will be examined in detail elsewhere (Slater in press).

Having reached a suitable criterion for bout definition, intervals without feeding longer than this, measured in 20-s units, were taken as gaps between bouts. Bout length was measured as the number of interruptions of the photocell beam between two such intervals, this being equivalent to the number of pecks at seed made during the course of a meal. References to gap length are therefore to the time elapsing between meals, whereas those to bout length are to the number of pecks making up a meal.

Results

The Bout Criteria Chosen

A different bout criterion was derived for each bird. Figure 1 shows three examples where the criteria taken were 60 s, 20 s and 80 s respectively, these being the stages at which the probability of feeding (slopes of the graphs) had fallen to a relatively constant level. For all nine birds the criteria chosen were: 20 s (four birds), 40 s (one bird), 60 s (one bird) and 80 s

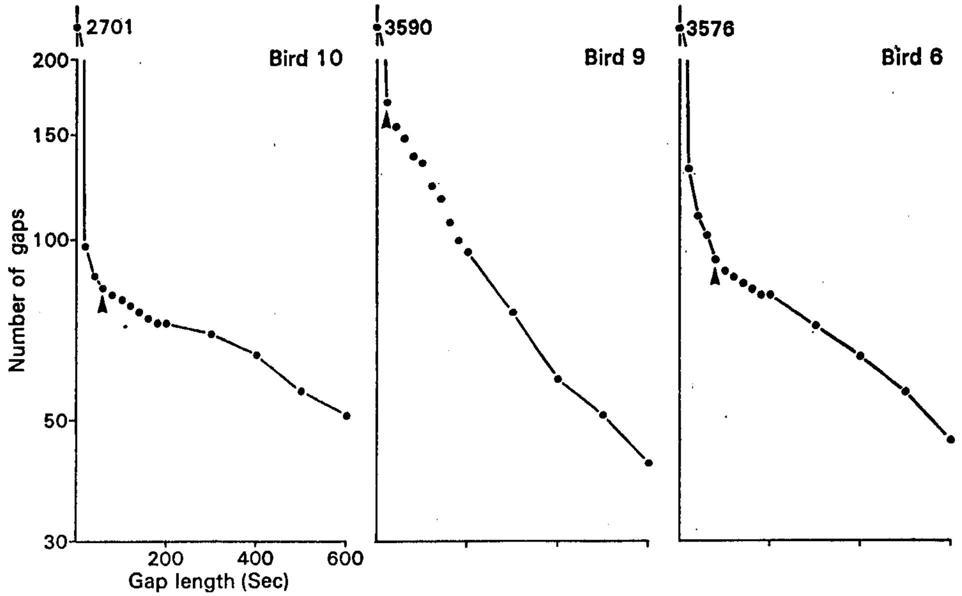

Fig. 1. Log survivor functions for intervals between pecks at food for three birds. Each point gives the number of intervals longer than the gap length shown on the abscissa. Arrows indicate the point chosen for bout definition for each bird.

(three birds). The criterion chosen for each bird is shown in Table II where the main results to be described are also summarized.

Changes With Time of Day

Daily changes in the number of pecks at food, bout length and the number of bouts of feeding were examined to see how reasonable it was to mass data from different times of day for further analysis. Figure 2 shows how these three measures were found to vary when assessed separately for each of the 12 hr of the day. As the results of Ollason & Slater (1973) had suggested, they change fairly slowly between 08.00 and 17.00 hours. Despite this the decline in the overall number of pecks and in the number of bouts per hour between these two times are both significant on a Friedman two-way analysis of variance ($P<0{\cdot}05$ and $P<0{\cdot}001$ respectively). The major changes take place, however, outside these limits. There are peaks in the number of pecks during the first hour and the second last hour of the day, but the temporal pattern underlying these is quite different. The peak between 07.00 and 08.00 hours results from many short bouts, while that at 17.00 to 18.00 hours is due to a few very long ones.

The general picture therefore is that the number of bouts per hour falls during the day, while the bout length rises. The number of pecks, which is the product of these two, shows peaks early and late in the day.

All further analysis will be restricted to the period between 08.00 and 17.00 hours because of the marked non-stationarities found by this analysis outside that period. As more minor trends were also apparent between 08.00 and 17.00 hours, this must be taken into account in interpreting the results from that period which are to be discussed.

The Distribution of Gap Lengths

If the probability of a new bout beginning remains constant with the passage of time since the last bout (i.e. bouts are statistically independent of each other) the slope of the log survivor function should be constant at intervals greater than the bout criterion. There are two major possible reasons why this may not occur. Firstly, the bout criterion may have been badly chosen so that there are rather too many short gaps between bouts. Secondly, the behaviour may tend to recur after a more or less fixed interval so that gaps tend to cluster around a particular length. The plots for birds 10 and 6 in Fig. 1 suggest that the latter may be the case as

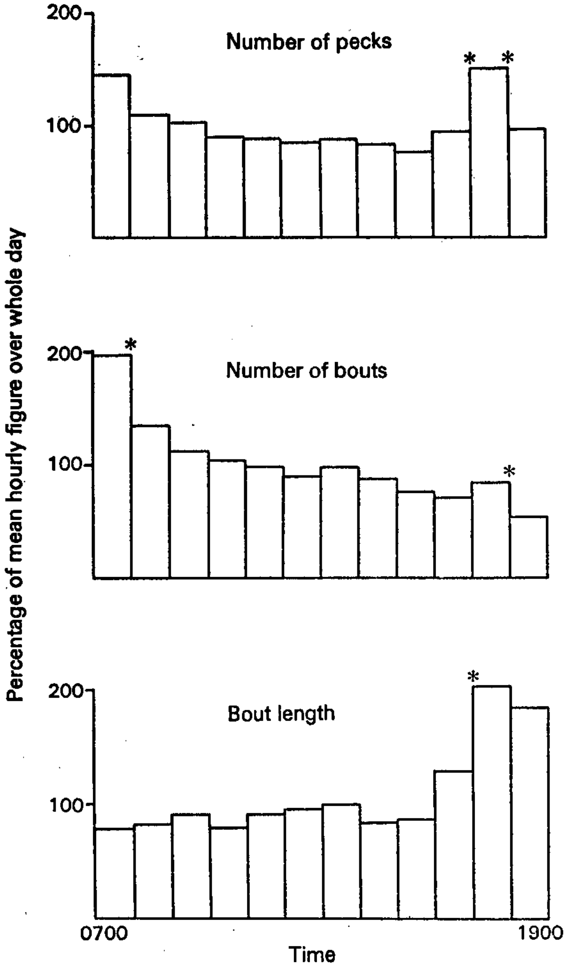

Fig. 2. Daily changes in the number of pecks at food, number of bouts of feeding and the mean length of feeding bouts. To allow for individual differences in overall number of pecks the figures for each bird were expressed as a percentage of the mean hourly value over the whole day for that bird. For each hour and each measure these figures were then averaged over all birds. Asterisks indicate significant differences between successive hours (two-tailed Wilcoxon matched-pairs test, $P<0{\cdot}05$).

their slopes increase with the passage of time between bouts (i.e. the probability of a new bout beginning becomes greater).

In order to test for effects such as these the distribution of all gap lengths between 08.00 and 17.00 hours was compared with a random model for each bird. As an example, the bout criterion chosen for bird 22 was 80 s. There were forty-eight gaps longer than this and their mean length was 1359·6 s. If gap length was randomly distributed it was calculated that one-quarter of these gaps (twelve in this case) should fall into each of the following brackets: 80 to 448, 448 to 966, 966 to 1852 and over 1852 s long. The number actually recorded as of these lengths were ten, six, twenty and twelve respectively. Comparing these figures with the expected gave a significant result ($\chi^2 = 8{\cdot}7$, $df = 3$, $P<0{\cdot}05$). In this bird there is thus a tendency for the gap length distribution to be non-random, with grouping around the third of the four time intervals indicating that the lengths of gaps between bouts tended to be similar. This bird can thus be said to have shown gaps between meals which were of typical length.

Several other birds gave similar results, with peaks in the third of the four brackets into which intervals between meals were split: bird 6 ($\chi^2 = 13{\cdot}3$, $P<0{\cdot}01$), bird 31 ($\chi^2 = 20{\cdot}3$, $P<0{\cdot}001$), bird 27 ($\chi^2 = 33{\cdot}4$, $P<0{\cdot}001$), bird 10 ($\chi^2 = 13{\cdot}6$, $P<0{\cdot}01$) and bird 30 ($\chi^2 = 14{\cdot}7$, $P<0{\cdot}01$). Of the other three birds two just failed to achieve significance because of peaks in the first of the four time intervals: bird 9 ($\chi^2 = 7{\cdot}8$) and bird 14 ($\chi^2 = 7{\cdot}6$). This might be taken as evidence that the bout criterion selected in these cases had been too short. The plot for bird 9 in Fig. 1 shows that gaps of between 20 and 400 s were indeed slightly more numerous than a random model would predict (the slope of the plot being steeper at this stage than subsequently). Nevertheless, the clearest switching point is at 20 s, the time interval taken for bout definition. In this bird, and in bird 14, feeding is less tightly clumped than in other individuals. Examination of the log survivor functions for these birds suggests, however, that in neither case would the choice of a different bout criterion have led to the discovery that gaps tended to be of a typical length.

The Distribution of Bout Lengths

As has been stated above, if the probability of starting feeding is constant the distribution of gap lengths plotted as a log survivor function should form a straight line. Likewise, if the probability of stopping feeding is constant regardless of the number of previous pecks within a bout the log survivor function of bout lengths should form a straight line. The same method as was used above for gap lengths can be used to test for a discrepancy between this hypothesis and the observed results. Three log survivor functions are shown in Fig. 3 and each is typical

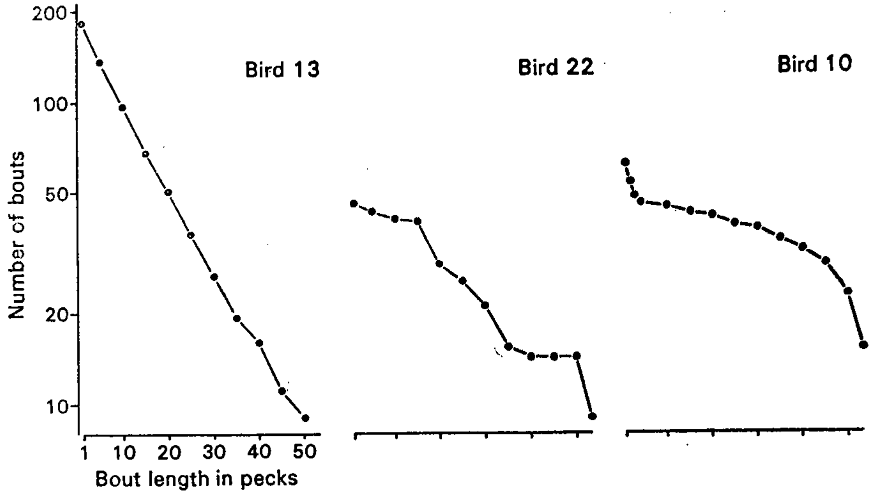

Fig. 3. Log survivor functions for bout lengths of three birds. Each point gives the number of bouts longer than the number of pecks shown on the abscissa.

of other birds as well as that illustrated. The three patterns are as follows:

(1) (Birds 9, 13, 14, 31). In these birds the probability of a bout ending remained almost constant and they thus yielded log survivor functions which were not significantly different from straight lines. The closest to significance were birds 9 ($\chi^2 = 7{\cdot}3$) and 31 ($\chi^2 = 6{\cdot}6$), and these should perhaps be regarded as intermediate between this category and the next.

(2) (Birds 22, 30). These birds gave convex log survivor functions indicating that the probability of a bout stopping increased as it became longer. Comparisons with a random model gave significant differences in both cases due to peaks in the third of the four brackets used (bird 30, $\chi^2 = 32{\cdot}5$, $P < 0{\cdot}001$; bird 22, $\chi^2 = 8{\cdot}8$, $P < 0{\cdot}05$).

(3) (Birds 6, 10, 27). In these cases the log survivor functions showed an initial peak indicating that there were many bouts of one or two events long. Comparison of bouts greater than this length with a random model showed that, like birds in the previous category, the probability of stopping increased with bout length. In all three cases the log survivor function for these longer bouts diverged very markedly from a straight line: bird 6 ($\chi^2 = 16{\cdot}4, P < 0{\cdot}001$), bird 10 ($\chi^2 = 38{\cdot}2$, $P < 0{\cdot}001$) and bird 27 ($\chi^2 = 62{\cdot}7$, $P < 0{\cdot}001$). The greatest difference was in bird 27 where, of thirty-five bouts greater than two events long, 8·75 were expected to fall into each of the following categories: 3 to 24, 25 to 55, 56 to 107 and more than 107 events long. The actual numbers were 1, 3, 29 and 2 respectively, indicating a very strong tendency for bouts, once they had reached three events in length, to continue until between 56 and 107 events had taken place.

In general, the same birds as showed typical gap lengths also tended to show typical bout lengths, although in three cases there was a surplus of very short bouts as well as long ones. Two of the three cases where gap length had been found to be random also showed random bout-length distribution.

Correlations Between Bouts and Gaps

For each bird the lengths of all bouts recorded between 08.00 and 17.00 hours were correlated with the lengths of the gaps before and after them. The results of this are presented in Table I. All but one of the correlation coefficients are positive, which is probably just a reflection of the gradual increase in both bout length and gap length during the day. The results highlight the strong differences between individuals, with five showing marked positive correlations between bout length and the length of the gap after, while two show almost equally marked correlations with the gap before. The strongest correlations with the gap after come from birds which showed typical gap lengths (31, 22, 27,

Table I. Correlation of Meal Size with Length of Surrounding Gaps

Bird number	N	Correlation with gap before	Correlation with gap after
13	185	+ 0·345‡	+ 0·101
14	88	+ 0·444‡	+ 0·121
9	126	+ 0·008	+ 0·219*
30	83	+ 0·203	+ 0·159
22	46	+ 0·171	+ 0·537‡
31	53	+ 0·195	+ 0·626‡
6	65	+ 0·247*	+ 0·646‡
27	41	+ 0·091	+ 0·476‡
10	61	— 0·008	+ 0·567‡

*$P<0·05$; ‡$P<0·001$ (Spearman rank correlation coefficient).

10, 6) and those with the gap before come from two birds which did not do so (13, 14).

Autocorrelation of Feeding

For six birds the analysis so far has indicated that gap lengths tend to cluster at around a particular length and for most of them bout length also tended to be typical. This suggests that feeding might take place, at least in these individuals, cyclically. To test for this possibility autocorrelations were carried out on the feeding data for each bird. Only the data for 08.00 to 14.00 hours were used for reasons which will be explained in the next section. The number of pecks at food in each 3-min period during that time was used as the basis for the calculation; as each bird was tested for 2 days this gave 240 time units. These were then autocorrelated by computer up to a lag of 72 min, using the Spearman rank correlation coefficient. Details of this technique will be found in Delius (1969).

Testing for the significance of such correlations is of doubtful value, especially in view of the trend in food intake during the day. Inspection of the results can, however, suggest possible cycle lengths. For clear evidence of a cycle the autocorrelation should peak at a lag equivalent to the length of that cycle and multiples thereof. This is the case in the four examples shown in Fig. 4: bird 27 (peaks at 30, 60, suggesting 30-min cycle); bird 31 (peaks at 21 to 27, 42 to 48, 69 to 72, suggesting 24 min cycle); bird 22 (peaks at 24 to 30, 45 to 48, 72, suggesting 24-min cycle); bird 10 (peaks at 24 to 27, 54 to 57, suggesting 27-min cycle). In all other cases, although occasional peaks were found, no clear evidence for cycles was obtained, though it is possible that their behaviour was influenced by two or more cycles superimposed on each other or by a single cycle of changing length, both of which influences would be difficult to detect with this method.

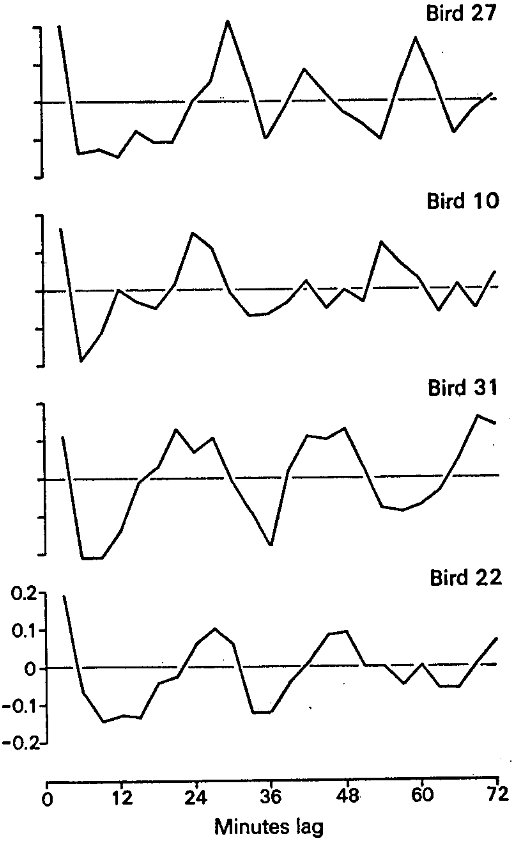

Fig. 4. Autocorrelations of feeding for four birds for lags of between 3 and 72 min (Spearman rank correlation coefficient).

Thus four of the birds which had been found to show typical gap lengths were also found to feed cyclically, with feeding tending to occur approximately every 24 to 30 min.

Cross-correlation Between Feeding and Locomotion

The possibility that some of the differences found in the temporal pattern of feeding might be related to the strong individual differences which exist in the amount of locomotion shown was next examined. Amongsg the seven individuals whose locomotion was monitored there was not even a suggestion that its level was related to the individual differences in the temporal pattern of feeding described earlier. For example, the most active individual (bird 10) and the least active individual (bird 6) are two which have been found to show very similar feeding patterns.

In an attempt to detect more subtle interactions between feeding and locomotion, the data used for autocorrelation in the last section were cross-correlated with locomotion data derived from the same time periods. The analysis was restricted to 08.00 to 14.00 hours because previous evidence suggested that locomotion is most constant during this period (Ollason & Slater 1973). To allow further for trends within the data the correlations were not carried out on the raw locomotion counts but on the discrepancy between each 3-min count and the mean of the eleven consecutive counts of which it was the sixth. This procedure serves to correct for major long-term fluctuations.

The results will only be mentioned briefly as they failed to reveal any consistent relationship with the individual differences in feeding found earlier. In all birds there was some tendency for feeding and locomotion not to occur in the same 3-min period. For two birds locomotion tended to occur 3 to 6 min after feeding (birds 6 and 9); for one bird the correlation peaked 3 to 6 min before feeding (bird 27); and for one bird it peaked 3 to 6 min before and 6 min after (bird 10). In two birds (30 and 13) no clear relationship between the two behaviours could be detected. In bird 31 peaks in the cross-correlation at 12, 36 and 57 min displacements in both directions reflected the 24-min cycle of feeding found in this bird and also suggested that peaks of locomotion occurred halfway between meals.

The interrelationship of feeding and locomotion is thus a complex one showing strong individual variations which cannot easily be tied in with those found in the temporal pattern of feeding.

Discussion

The results reported in this paper are summarized in Table II. They have revealed substantial variations between individual zebra finches in their temporal pattern of feeding which make it difficult to make any single generalization which would apply to all the individuals studied, apart from the comment that feeding occurs in bouts. The birds can, however, be split into two groups in each of which the individuals shared certain characteristics.

In one group of three birds (13, 14, 9) the

Table II. Summary of Results

Bird No.	Bout criterion (S)	Mean gap length (min)	Mean bout length (pecks)	Typical† gap length (*P* values)	Typical† bout length (*P* values)	Cycle length (min)	Correlation with gap before (*P* values)	Correlation with gap after (*P* values)
13	40	5·6	16·8	NS	NS	—	<0·001	NS
14	80	11·9	32·8	NS	NS	—	<0·001	NS
9	20	8·1	19·5	NS	NS	—	NS	<0·05
30	20	12·7	11·8	<0·01	<0·001	—	NS	NS
22	80	22·7	32·6	<0·05	<0·05	24	NS	<0·001
31	20	18·2	43·9	<0·001	NS	24	NS	<0·001
6	80	18·7*	41·6*	<0·01	<0·001*	—	<0·05	<0·001
27	20	29·0*	78·3*	<0·001	<0·001*	30	NS	<0·001
10	60	20·9*	45·3*	<0·01	<0·001*	27	NS	<0·001

*The calculations indicated were carried out after excluding the very short bouts of one and two pecks shown by these three birds.

†The expressions 'typical gap length' and 'typical bout length' are used to describe the phenomenon whereby the probability of a bout or gap stopping increases with its duration.

probability of starting to feed was constant with the passage of time between bouts, the probility of stopping feeding was constant regardless of the length of the bout and there was no evidence for cycles in their feeding. These birds took short meals rather often. Two of the three gave strong correlations between bout length and the length of the previous gap.

In the other six birds the longer a gap between bouts had continued, the more probable was the start of a new bout. In five of the six the cessation of a bout also became more probable the longer it had continued for, though in three of them this was only true after the bout length had exceeded two events. In these birds there were many very short bouts and many long ones with few of intermediate length. As might be expected when both bouts and gaps tended to be of typical length, four of these six birds showed evidence of feeding cyclically with a periodicity of approximately 24 to 30 min. The gap and bout lengths suggest that one feeding bout took place in each cycle and that, with the exception of bird 30, all these birds tended to take longer meals less often than those in the previous group. Also in contrast to the previous group, five of the six gave strong correlations between bout length and the succeeding gap.

The data used in this analysis, being gathered over a short period, cannot be used to decide whether the individual differences found are stable over time or whether a single animal may shift from one feeding pattern to another. Other results do, however, suggest that the pattern within an individual remains similar. Several of the birds in the second group described above (22, 27, 30, 31) were observed feeding for 3 hr some 18 months after the results reported here were obtained. While these later observations were too brief to allow detailed analysis, the impression was gained that the feeding pattern of each bird had changed little in the course of time. In particular, mean bout length, a measure which differs markedly between birds (see Table II), remained similar to its previous value in three of the birds (bird 27, 74·1; bird 30, 14·1; bird 22, 24·7). In bird 31 only seven bouts were recorded and their mean length was rather greater than before (73·3 pecks). This may, however, have resulted from the small number of bouts observed.

For several reasons some variation between individuals in the temporal pattern of feeding is perhaps to be expected, particularly in captivity. Firstly, in the wild, seed does not occur in easily accessible hoppers and considerable time may have to be spent foraging to obtain adequate nutrition. The pattern of feeding may therefore be moulded to a large extent by environmental constraints and any pattern intrinsic to the individual may seldom be expressed for natural selection to act on. Further, as long as the animal obtains sufficient food, the selection pressure to adopt one pattern of intake rather than another may be slight. Secondly, in captivity, relaxation of any selection pressure which does exist might allow various different patterns to arise. Lastly, in animals such as these which were reared in captivity, experimental differences might lead to the adoption of divergent patterns.

All of these factors might lead to variety, but they would not explain why particular constellations of characteristics tend to arise. It was at first thought that the different patterns of feeding might be related to the wide differences in locomotion reported elsewhere (Ollason & Slater 1973). Thus those birds which took frequent small meals might be the most active ones which therefore encountered the food hopper more often. No simple relationship between either the level or temporal pattern of locomotion and that of feeding could be found, however. Moreover, unpublished autocorrelation data suggests that cycles of locomotion, where these exist, tend to be around 45 min in length. This is rather longer than the cycles of feeding found here, again pointing to there being no simple interaction between the two behaviours.

From this discussion it seems unlikely that differences in feeding behaviour might depend on how often individuals encounter the food hopper. Given that the environment for all birds was the same, it is necessary therefore to postulate more complex mechanisms intrinsic to the individual. It is possible to develop an hypothesis which would account at least partly for the way in which the birds studied fall into two groups on the basis of the following assumptions about the short-term causation of feeding: (i) a certain time after feeding last occurred the animal has a food deficit sufficient to cause it to seek out a source of food and eat; (ii) before this stage if the animal encounters a source of food the combination of the appropriate stimulus and its minor food deficit may be sufficient to make it feed; (iii) animals differ in the probability of feeding being initiated in this last way; (iv) after feeding is initiated, animals eat approximately sufficient to remove their deficit.

As zebra finches are fairly active they will encounter the food hopper frequently but at variable intervals during movement round the cage. Animals which are particularly susceptible to the initiation of feeding by the sight of food might be expected to start feeding on these occasions. If they then eat approximately enough to make up their deficit, they will show a temporal pattern similar to that of the first group of birds discussed above: random bout and gap length and a tendency for bout length to correlate with the gap before rather than after.

In birds which were less susceptible to the initiation of feeding by external stimuli a more regular pattern of bouts and gaps of more or less fixed length would be expected with feeding starting each time the deficit reached a certain value. This would give a pattern similar to that of the second group of birds, although it would not explain either the very short bouts found in some birds or the strong correlation between bout length and succeeding gap found in most of them.

That the lengths of feeding bouts correlate more strongly with the gap after them than with the gap before has been reported also for rats (e.g. le Magnen & Tallon 1966) and for domestic hens (Duncan et al. 1970). It suggests that the timing of the start of a meal is more tightly controlled than its duration. Thus after a long meal a long gap tends to ensue, but the length of the meal following that long gap is harder to predict. In those three zebra finches which were found to show many meals of one or two events in length as well as long meals there seems to be a further reason for this correlation. These brief meals tended to occur shortly before the start of long bouts of feeding; thus long bouts were followed by long gaps and short bouts by short gaps. The causation of these short bouts requires further study, but one possibility is that they are initiated as suggested for birds in the first group (when the bird comes across food by chance) but that in this case feeding only starts when a certain deficit has been built up. This would not, however, explain why these bouts cease so soon and do not continue until the whole deficit has been removed. Another possibility is that the rate of feeding is not constant within bouts but builds up during them so that relatively longer gaps between pecks tend to be common at the start of a bout. The occasional gap in such a position which exceeded the bout criterion in length would give rise to a pattern such as is shown by these three birds (short bout–short gap–long bout–long gap). The records of rat feeding published by Thomas & Mayer (1968) indicate such a slow build-up in feeding rate at the start of a meal: had they chosen a shorter bout criterion they would probably have found that short bouts tended to occur a brief period before the start of longer ones. A phenomenon such as this seems therefore a feasible explanation for the existence of very short bouts of feeding in the three birds which showed this pattern. As Table II indicates, this did not, however, result from a shorter bout criterion having been selected for these birds than for the others.

Cycles of feeding behaviour have been described before by Richter (1927) for the rat, and briefly, by McFarland (1971), who found a Barbary dove to show a periodicity of about 25 min in its feeding. Baker (1953) subsequently failed to confirm Richter's finding, though an inspection of his published data suggests that he might have found cycles had more modern methods of analysis been available to him. Duncan et al. (1970) were also unable to detect cycles of feeding in the fowl. As they based this conclusion on autocorrelations of data massed in 20 min units, it is possible that cycles of the length reported here and by McFarland (1971) were present but remained undetected. Cyclical or periodic feeding thus remains a possibility in all these species, though the individual differences found here in the zebra finch, by Duncan et al. (1970) in the fowl and briefly mentioned as existing in the rat by le Magnen & Tallon (1966), caution against generalizing too readily either within or between species.

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2

TEMPORAL PATTERNING AND THE CAUSATION OF BIRD BEHAVIOUR

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INTRODUCTION

This chapter is concerned with the temporal organisation of behaviour and with quantitative methods for describing its fine structure. It will concentrate in particular on two concepts of behavioural organisation which are often mentioned, but rarely analysed in any detail: the idea that many behaviours occur in bouts and the idea that animals show short-term cycles of behaviour. Discussion of these will be illustrated largely by results obtained from work on adult male zebra finches which have been observed in isolation both from other birds and, as far as possible, from changing environmental stimuli (apart from a standard 12-h light—12-h dark lighting regime). This approach was adopted in the hope that the description of behaviour obtained would provide a base-line against which to compare behaviour in less constant conditions and a source of hypotheses about the mechanisms underlying the organisation of behaviour.

At first sight this subject may seem a curious one to find in a book of this sort, as neither neural nor endocrine mechanisms will be referred to directly. There are two reasons, however, why studies of temporal patterning are relevant to work at a more physiological level. The most obvious of these is that a detailed knowledge of the fine structure of behaviour poses questions about the way in which its organisation is achieved, the answers to many of which will ultimately lie in the study of nervous and hormonal mechanisms. A good understanding of the temporal pattern of behaviour thus helps to define more clearly the phenomena which need to be explained. The second contribution which this type of work can make is a methodological one. As more precise and quantitative methods for describing behaviour are developed, it will become possible to detect increasingly subtle departures from normality in animals subjected to neural and endocrine manipulations. Much of current experimental work on behaviour is concerned with detecting changes in the frequency of particular acts following treatments. Closer examination might reveal that an increased frequency of a behaviour resulted from the occurrence of more bouts of the normal length, or from the occurrence of the same number of bouts of a greater average length. In either case the likelihood of detecting such a change will be raised if the bout, as defined by the observer, is closely related to the actual switching on and off of the behaviour by the animal; how this may be achieved will be considered below. If a behaviour recurs cyclically, a treatment may also cause a change in its frequency by leading to an alteration in cycle length. The causal factors underlying cycles, or less regular fluctuations in the probability of a given behaviour pattern, may be specific or non-specific (Fentress, 1973). At one extreme they may affect that behaviour only, while at the other they may involve an arousal-like variable which affects the probability of many, or all, behaviours. Cycles approximating to both of these types seem to influence the behaviour of isolated zebra finches, and a preliminary examination of them will be presented later in this article. An understanding of features of behavioural organisation such as these should help in attempts to discover how experimental manipulations exert their effects.

To many people the most obvious and useful method for analysing the temporal pattern of behaviour is sequence analysis. This approach has been applied to the behaviour of zebra finches (Slater and Ollason, 1972), and its usefulness and limitations have been considered in detail elsewhere (Slater, 1973), so only a few words of caution will be mentioned here. A major difficulty involved in the analysis of sequences is that of non-stationarity: the tendency for the probability of occurrence of a behaviour to vary with time rather than to be simply dependent on the sequence of acts which preceded it. In behavioural terms, a major source of non-stationarity arises when the motivation of the animal shifts because internal and external causal factors change during the course of time. Non-stationarity, the bug-bear of the sequence analyst, is thus the bread and butter of anyone interested in motivation. As stationary sequences of behaviour in vertebrates are unusual it can be said, without much exaggeration, that behavioural problems become interesting when sequence analysis becomes impracticable. It is an aim of this article to explore ways of looking at behaviour where motivation is known to change, first in relation to individual behaviours and their distribution in time, and later in relation to the way in which behaviours are associated with each other.

THE BOUT ORGANISATION OF INDIVIDUAL BEHAVIOURS

Methods of bout definition

Many behaviour patterns are almost identical on separate occurrences and between individuals and, as they are of short duration and vary little in intensity, their distribution in time can be studied as if they were point events. For most behaviours an analysis of this sort reveals that events are not randomly distributed in time but tend to cluster or occur in bouts. Thus, if an animal has just scratched its head, taken a peck at food or flown from one perch to another, the most likely thing for it to do next is a repetition of the same behaviour. Reasons why this should be the case are not hard to find. In general, unless a behaviour is very effective at removing the causal factors which led to it, these are likely to persist and so cause further events. In the case of feeding, for example, a single peck at food will do little to remove a deficit and its influence will take time to operate. Furthermore, in this case, as in others, part of the bout organisation may stem from persistence of stimuli in the outside world. The bird which has just taken a peck at seed is likely to be still looking at the food dish, the appropriate stimulus for this, rather than any other, behaviour.

It is thus easy to see why behaviours should often take place in bouts. But how should one determine when one bout ends and a new one begins? Given that gaps between pecks at food are of variable duration and may or may not contain a variety of other behaviours, how should one decide which ones are within a bout of feeding and which are between bouts? An obvious, but unsatisfactory, solution to this problem is to say that a bout ends when the animal changes to doing something else. One reason why this gives a poor bout definition is that it depends to a large extent on what other categories of behaviour have been scored: if mandibulation of seed was one, then all successful pecks at food would occur in separate bouts. On the other hand, if only feeding and drinking were being studied (as by McFarland, 1970), some drinking would have to occur between them before two meals were regarded as separate. Another problem, which is apparent from the sequence analysis carried out on zebra finches (and from the work of Fentress (1972) on grooming in mice), is that a change in behaviour is often followed by a reversion to that shown previously, so that this cannot be regarded as having been totally switched off during the interruption. This is not just true amongst closely associated behaviours which may stimulate each other and so give rise to alternation. In the zebra finch, two behaviours which very seldom occur together in sequence are locomotion (Loco) and preening (Pr). In a sequence of nearly 9000 events of different types it was calculated from the frequencies of Loco—Pr and Pr—Loco that the triplet sequences Loco—Pr—Loco and Pr—Loco—Pr should have occurred six times and once respectively: the observed figures were 19 and 5. This surplus of observed over expected, which was also true of most of the other A—B—A type triplets studied, suggests that bouts which are defined as delimited by changes from and to other behaviour patterns are themselves clustered in time and not statistically independent of each other. For these reasons this is a poor way of defining bouts when studying the temporal pattern of individual behaviours.

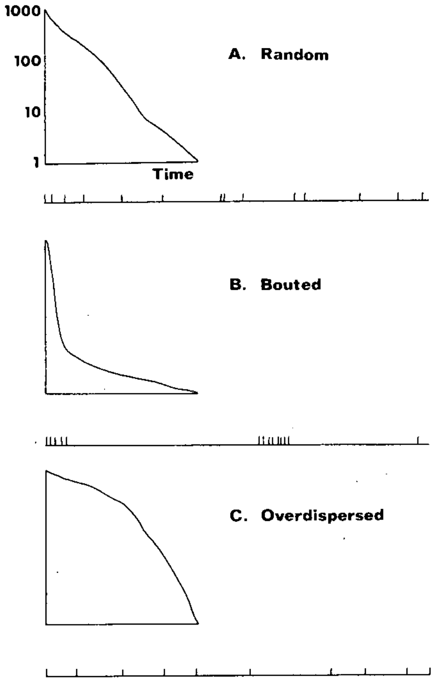

Fig. 1. The use of the log survivor function for plotting the distribution of intervals between events. In this type of plot, the log of the number of intervals greater than a particular length (ordinate) is plotted against that length (abscissa). This yields an approximately straight line if the events are randomly distributed (A); a concave plot if the events occur in bouts or clusters (B); and a convex plot if the events are overdispersed (C).

A more satisfactory way is to choose a time interval between events and define gaps shorter than this as within bouts and longer ones as between them. A useful way of choosing an interval appropriate to the way in which the behaviour itself is organised is derived from plotting the intervals between successive events of the same type in the form of a log survivor function (Fig. 1). If acts are randomly distributed in time the distribution of the intervals between them should follow a negative exponential. Plotted as a log survivor function this appears as a straight line, the slope of which is proportional to the probability of occurrence of an event with the passage of time since the last event. Where events are clustered, the slope is high to begin with and later drops, often to a fairly constant level, indicating that beyond that gap length the probability of a new event is low and relatively uninfluenced by the timing of the last. The point at which the probability becomes constant can be chosen with reasonable confidence as a suitable interval for bout definition. While this involves some degree of judgement, it is less arbitrary than other methods in common use. It may be made more accurate in the future by the application of line-fitting procedures which are currently being developed (Machlis, personal communication).

As can be seen from Fig. 2, the log survivor functions for most behaviours are concave and in some cases (*e.g.* preening, feeding and stretching in this bird) they appear appropriate for analysis in terms of bouts and gaps because the switch to a low probability is fairly abrupt, suggesting that this point is a significant one for the way in which the behaviour of this bird is organised. Other behaviours are less appropriate for analysis of this sort as the log survivor function tends to be smoother. In some of these cases the most economical description may be in terms of a renewal process (Heiligenberg, 1973); for song this is suggested by the fact that successive gaps between songs are, if anything, negatively correlated with each other. This is not compatible with a bout model which suggests an alternation between a high-probability state and a low-probability state each of which persists for some time. In other cases it has been suggested (Slater, 1974a) that more than one level of bout may exist, so that tightly-knit groups of acts may occur and these are assembled into more loosely-knit bouts; this too would lead to a rather smooth log survivor function.

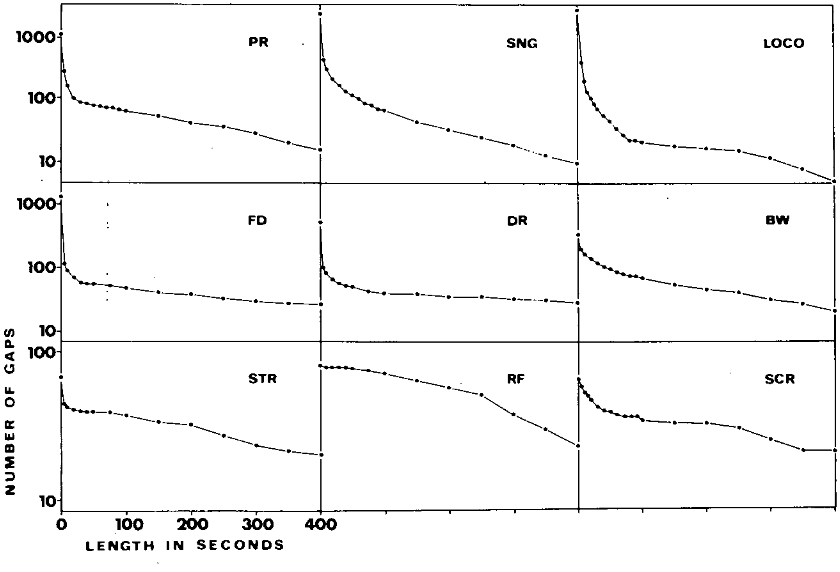

Fig. 2. Log survivor functions of the gaps between events for nine different behaviour patterns shown by one bird during 8 h of observation. All plots are up to a maximum of 400 sec, each point indicating the number of gaps recorded which were longer than the time shown on the abscissa. The abbreviations used are as follows: PR, preening; SNG, song; LOCO, locomotion; FD, feeding; DR, drinking; BW, bill-wiping; STR, stretching; RF, ruffling and SCR, scratching. Reprinted by permission of Slater (1974a).

The distribution of acts in time may also depart from randomness because they are overdispersed, the probability of a new event increasing with the passage of time since the last (Fig. 1). Ruffling in most birds shows this pattern (see Fig. 2). It is also a pattern which might be expected to occur in the distribution of intervals between bouts in those behaviours showing bouts. This is the equivalent of saying that one might expect the probability of a new bout beginning to increase with the passage of time since the last. This will occur where causal factors rise during non-performance and lead to the log survivor function curving downwards at long interval lengths.

Detailed analysis of feeding and preening

Once a behaviour has been split into bouts and the gaps between them, a number of ways of analysing the data further become possible. Detailed analysis has so far been restricted to feeding (Slater, 1974b) and preening (Slater, 1974a). The results obtained will be briefly summarised here to allow discussion of some interesting differences and similarities between these behaviour patterns, and of hypotheses about the organisation of behaviour which have been derived from the two studies.

Zebra finches eat in tight meals so that a bout criterion is not hard to derive from the log survivor function of intervals between pecks, though those chosen varied between 20 and 80 sec for the nine birds studied. Finer details of the temporal pattern of feeding show strong differences between birds, which are to some extent constant over time. This is shown in Table I where some of the results obtained by Slater (1974b) on five birds are compared with those of Holden (unpublished) who studied the same birds two years later without knowing which was which. Not only were bout

TABLE I

Bout criterion chosen and mean bout and gap lengths found for five birds, the feeding of which was recorded by two different observers two years apart

Bird number	Slater's results (July—November 1971)			Holden's results (October—November 1973)		
	Criterion (sec)	Mean gap (20-sec units)	Mean bout (pecks)	Criterion (sec)	Mean gap (20-sec units)	Mean bout (pecks)
9	20	24.3	19.5	20	33.3	26.1
31	20	54.6	43.9	40	57.3	47.2
14	80	35.7	32.8	60	60.6	35.0
30	20	38.1	11.8	20	39.9	21.2
6	80	56.1	41.6	60	75.5	50.1

lengths and gap lengths remarkably similar between the two studies, but it is gratifying to find that the two independent observers also chose rather similar bout criteria for each bird.

Despite the strong differences between individuals, Slater (1974b) found that his birds fell into two groups, within each of which feeding patterns were similar. In the smaller group the probability of a new meal starting did not increase with time since the last meal, nor did the probability of a meal ending change as it proceeded. There was no evidence for cycles in the feeding of these birds, and the number of pecks in a meal tended to correlate strongly with the length of the gap before it rather than with that after it. The simplest hypothesis to account for these results was that these birds fed sufficiently to make up their deficit whenever they came across food. By contrast, the majority of the birds conformed to another pattern. The longer it was since they last fed, the more likely were they to start feeding, and in most cases the probability of stopping feeding increased as a meal became longer. These birds thus tended to show meals of a rather constant length. In four cases feeding was also periodic, with a cycle length of 24—30 min. Meal length tended to correlate with that of the gap following rather than that before. Most of the results for these birds could be explained on the hypothesis that they went to the food hopper when they had accumulated a threshold deficit, rather than feeding when they happened to come across it during their movements round the cage.

Individual differences in the pattern of food intake are obvious to the observer watching isolated zebra finches and are also apparent in the distribution of gaps between pecks plotted as log survivor functions. It was clear from these that each bird should be assigned a bout criterion based on its own data rather than a general one being chosen for all birds. However, this leaves the possibility that some of the other differences found may stem from the fact that different criteria were used for different individuals. Slater (1974b) could find no evidence that the two different patterns of feeding mentioned above were related to the bout criteria which the birds showing them had been given. More recently the same data have been partially analysed using five different bout criteria for each bird: 20, 40, 60, 80 and 100 sec. The results of this did not suggest that the feeding pattern of any bird would have appeared to be markedly different from that originally found had it been assigned another criterion.

A more interesting result came when correlations were carried out between bout length and the gaps before and after it for each of the five different bout criteria. These were examined to see which bout criterion gave the most significant correlation. There were 18 cases (gap before and gap after for each of nine birds) and in nine of these the most significant result was at the criterion originally chosen. By chance this should have been true in less than four cases ($\chi^2 = 10.4, P < 0.01$). This highlights the point that, if the criterion is carefully chosen so that it is closely related to the temporal structure of the behaviour, the chance of detecting organisation during subsequent analysis is maximised. With arbitrarily chosen criteria, or a common criterion for all birds, fewer of these correlations would have been detected, not because they were not there, but because the criterion used was inappropriate to the animal in question.

In contrast to the feeding behaviour of most birds, the analysis of preening showed few individual differences and a surprising lack of temporal organisation (Slater, 1974a). As with feeding, each bird was given a different bout criterion depending on the form of its log survivor function. These criteria varied from 25 to 70 sec amongst the ten birds studied. In no bird was the probability of preening starting found to change with the passage of time since the last bout, and only a negligible number of correlations between bout lengths and those of the gaps surrounding them were found to be significant. It is thus very hard to predict from its previous behaviour when a bird will start preening. The organisation of bout lengths was more striking, with a surplus of very short and very long bouts compared with the numbers predicted by simple mathematical models. The simplest such model, the geometric distribution, which assumes that the probability of a further event is independent of the number of previous events within a bout, gave a very poor fit to the data. The logarithmic distribution, in which the probability of continuing increases as the bout becomes longer, gave a better fit but still consistently underestimated the number of bouts of one and two events compared with that observed.

Perhaps the simplest hypothesis to account for this finding is the suggestion that when preening bouts start they are very likely to stop within one or two events but, if they get beyond this stage, their probability of continuing increases in a rather complicated manner. According to this hypothesis, long and short bouts would be similar in causation, so that it is reasonable to mass them for analysis. Short bouts are simply potential long bouts which, for some reason, stop early. An alternative hypothesis, which deserves further study, is that long and short bouts differ from each other in causation and that the apparently complex bout organisation results from massing together two phenomena which should be kept separate. There is some evidence in favour of this latter explanation: short bouts are significantly more likely to be preceded by locomotion than are long ones and the movements comprising them also give the impression of being more hurried than are those at the beginning of long bouts. These differences in form and context suggest that a causal difference may exist between long and short bouts so that, while each may have a comparatively simple bout length distribution, when they are massed the resultant distribution is a complicated one. The curious finding that the probability of preening does not increase with the passage of time since it last occurred, and that bout and gap lengths are not correlated with each other, could also be accounted for more easily if two disparate phenomena had been lumped together under the single heading of ‘preening’. The possibility of such a causal difference between long and short bouts of preening will be discussed further below.

Discussion

It is hoped that the above section will have illustrated the usefulness of analysing the temporal pattern of individual behaviours, particularly in terms of bouts and the gaps between them in cases where this is appropriate. Many of the methods used could be easily, and usefully, applied to detecting differences between experimental and control groups of animals. An advantage which such studies would have over those discussed here is that looking for differences between two groups of animals is much more simply carried out than is testing a single group against random models of one sort or another. Now, however, we will go a little further towards considering the hypotheses for causation which can be derived from studies of the sort described above.

From the detailed analyses of feeding and preening, and work on other behaviours which has been referred to more briefly, it is clear that behaviour patterns differ from each other in some of the basic features of their temporal organisation. Why should this be the case? One consideration which is likely to be of major importance is the extent to which internal and external causal factors affect them and how these act. The term 'causal factor' is an unsatisfactory one to use in any explanatory sense, for it can embrace such a multitude of different things and is usually just a cloak for ignorance. But, by subdividing the blanket term, one can see that different behaviours are affected by different general types of causal factor. For example, solitary song in birds, of the sort shown by isolated zebra finches, is spontaneous in the sense that it does not require any specific external stimulus for its elicitation. While its frequency may vary with external factors such as levels of light and noise, it is primarily internally motivated; hormones clearly play a part here, but its short-term temporal pattern is probably largely a neural phenomenon (Lemon and Chatfield, 1973). The temporal pattern of feeding is also obviously influenced strongly by internal factors, but it differs from song in that it requires an appropriate external stimulus. This is an added complication, for an animal whose deficit is not sufficient to make it seek out food may, nevertheless, feed when it comes across it. A further situation is illustrated by grooming movements for not only does external stimulation appear to have an important part to play in eliciting these (Andrew, 1956), but the animal also carries the appropriate stimuli around with it.

The extent to which different behaviours are affected by internal and external causal factors, and the mode of operation of these, may thus account for the differences which are found in their temporal patterns. It has also been suggested here, however, that the same behaviour may have different causation in one situation from that in another. The two different patterns of feeding found were most easily explained on the hypothesis that one group of birds were induced to feed largely by the external situation (*i.e.* when they came across food), whereas the other fed in a more regular manner, suggesting that they were induced to feed largely by their internal state (*i.e.* when they had built up a certain deficit). Some birds of the latter group, as well as taking regular long meals, sometimes took a few brief pecks at food when they passed the food hopper during their movements round the cage. It seems likely that these meals were caused largely by the sudden appearance of the appropriate external stimulus, as has been suggested for the majority of meals in birds of the first group. The possibility that short meals are differently motivated from long ones has also been raised by Duncan *et al.* (1970) in their study of the feeding of domestic hens in Skinner boxes. During part of their analysis they ignored meals consisting of a single reinforcement on the grounds that these were likely to be 'motivated by factors other than hunger'.

In the case of preening, the surplus of very short and very long bouts compared with the numbers predicted by simple mathematical models suggested that long and short bouts might differ from each other in causation. The hurriedness of short bouts and their association with locomotion, the random distribution of gap lengths and the lack of correlation between bout and gap lengths all fitted in with this hypothesis. Slater (1974a) suggested that such a difference might occur if short bouts dealt with specific sources of irritation which might arise at any time, whereas long bouts resulted either from generalised irritation, perhaps building up slowly between them, or from a central programme. Short bouts in this case would be expected to deal more often with those areas of the body most prone to being dishevelled by other activities, while long bouts would cover all areas. According to this hypothesis short bouts occur when causal factors for preening suddenly rise so that the behaviour takes place briefly, the source of irritation is removed and the previous behaviour can continue. This hypothesis, therefore, proposes that ongoing behaviour is temporarily inhibited and then disinhibited by preening. It is, therefore, the opposite of the disinhibition hypothesis usually proposed to account for the occurrence of displacement activities (Andrew, 1956; van Iersel and Bol, 1958; McFarland, 1966). It is worth considering this alternative possibility because these short bouts do have certain characteristics in common with behaviours normally classed as displacement activities. The two features of displacement behaviour which survive from those given by Tinbergen (1952) are its hurriedness and its appearance out of context; if these are used to define it, then the short bouts of preening described here clearly fall under the displacement umbrella.

The disinhibition hypothesis, as set out by McFarland (1966), suggests that the conflict or thwarting, thought to underlie displacement, leads to a switch in attention to peripheral stimuli so that subsidiary behaviour is disinhibited. More recently he has suggested that disinhibition may be an important mechanism of switching between acts in normal sequences of behaviour (McFarland, 1969). In zebra finches, isolated from all other individuals, it seems unlikely that short preening bouts are associated with conflict or thwarting, though it is not in general beyond the ingenuity of ethologists to postulate a conflict of one sort or another in any situation where one seems to be required! Nevertheless, it could be that causal factors for the ongoing behaviour are lowered for a time for some other reason, so allowing preening as the second in priority act to appear briefly. The dominant behaviour would thus disinhibit and then reinhibit preening according to the general mechanism proposed by McFarland (1969). There are two objections to this. First, it is difficult to accommodate the hurriedness of the disinhibited behaviour into such a model (Duncan and Wood-Gush, 1972). Second, preening and locomotion normally occur in very different behavioural contexts (hence the idea that preening during locomotion is out of context) so that preening would be unlikely to be the second in priority act during periods of locomotion.

While a decision between these two models must await experimental evidence, it is important to bear in mind that disinhibition is not the only mechanism whereby short bouts of behaviour may appear out of context. In the present situation the inhibition hypothesis appears more likely and it is probable that it is appropriate in some cases of displacement also. In the displacement preening of terns, studied by van Iersel and Bol (1958), for example, the main behaviour pattern shown was head-shaking and, as this frequently followed displays involving pronounced head movements, it would seem more parsimonious to suggest that it was induced by these (its causal factors rising to inhibit them) than to postulate an internal conflict.

A further feature of the proposals being made here for the causation of short bouts of preening and that of the two feeding patterns found is the idea that the same behaviour may, on different occasions, be differently motivated. This idea has not of recent years been a popular one and, once again, views of the causation of displacement activities provide an interesting example. The conventional view has, in this case, moved from one extreme to another. Tinbergen (1951) saw displacement behaviour and its normal example as totally different in causation. Later, it was discovered that external stimuli appropriate to the normal behaviour also affected displacement (van Iersel and Bol, 1958; Sevenster, 1961). The disinhibition hypothesis was born and with it the idea that displacement activities were the same as normal behaviour but switched on in a different way. While the latter is clearly a more realistic view, it may be too simple. The proposal being made here is that if the occurrence of a behaviour depends to some extent on both internal and external factors, or both central and peripheral ones, it may appear on some occasions when one group is high and the other low and on others in the reverse situation. It is misleading in cases like this to suggest that the causation is always the same. The neatest demonstration of a system like this in operation is that by Baerends *et al.* (1955) on courtship in the guppy. They found that three different displays would be shown by males of high internal motivation (as assessed by the extent of their colour patterns) to small females, but an increase in the size of the female was necessary to elicit them from males of lower motivation. Thus a variety of mixes of internal and external factors could lead to the behaviour being shown.

To discuss ideas such as these in relation to purely descriptive work on the behaviour of zebra finches may seem unduly speculative, as all of them will need experimental work before they can be tested. However, one of the main aims of the descriptive project was to provide hypotheses about the causation of the organisation which was discovered; it is hoped that this discussion has illustrated how this has been realised.

SHORT-TERM CYCLES OF BEHAVIOUR

The phenomenon

It will be clear from the results presented so far that the probabilities of different behaviour patterns change with time, and that in some cases these changes are ordered enough to allow some prediction as to when the behaviour will next occur. But analysis in terms of bouts and gaps is not easily applied to all behaviour patterns and, even where it is appropriate, it does not provide a complete picture of the organisation in time of the behaviour being studied. One feature which may be missed is any tendency for the probability of a behaviour to change in a cyclical manner, although this can be detected from bout and gap analysis if there is usually only a single bout per cycle. Nevertheless, methods of looking for cycles provide a useful additional tool in the search for regularities in the organisation of behaviour.

That there are cycles in animal behaviour has been recognised for a long time and there are, of course, extensive studies on daily cycles, breeding cycles and annual cycles (Sollberger, 1965). The existence of cycles of less than a day has sometimes been referred to in passing (*e.g.* Crook, 1961; Rowell, 1961; in birds), but there have been few attempts at detailed study beyond those of Richter (1927) and Wells (1951). One problem in making such an attempt is that, while the rotation of the earth provides both an entraining stimulus and a selective advantage for cycles of behaviour 24 h long, short-term cycles would not in general be subject to such external constraints. Variability, both between animals and with time, is therefore to be expected.

The idea that cycles might occur in the behaviour of zebra finches came originally from the results of sequence analysis (Slater and Ollason, 1972). These showed that the animals fluctuate between periods of high activity, during which ingestion takes place, and low activity, which is associated with preening and drowsiness. Song tends to occur on the borderline between the two. In order to test whether such fluctuations were regular enough to be termed cycles, it was necessary to obtain long records and these were only practicable with two behaviours which could be recorded automatically: feeding and locomotion. As has already been mentioned, feeding in some zebra finches was found to be periodic, tending to occur every 24—30 min. The results of the locomotion analysis will be presented below, as well as those of some preliminary experiments aimed at finding out the extent to which other behaviours show cycles and, if they do so, how their cycles fit in with one another. From the theoretical point of view this last aspect is an important one. At one extreme all behaviours might show the same cycle length, so that the animal went through a set sequence of activities once in each cycle, suggesting that they were influenced by a single non-specific variable. At the other, each behaviour might have a cycle length of its own, suggesting that specific factors were more important, although there would obviously be some interactions between behaviours because many of them cannot occur at the same time as each other. If cycles are found in a number of different behaviour patterns, the extent to which they are of similar length and can be teased apart from each other experimentally will provide a useful means of assessing the importance of non-specific variables in the causation of behaviour. Such variables have often been postulated, under such names as arousal, activation and responsiveness (Andrew, 1974). While their reality is not easy to either confirm or disprove, the effort is worthwhile, for the existence of any such variable would obviously have an important influence both on the organisation in time of individual behaviours and on their associations with one another.

Cycles of locomotion

The data used to look for cycles of locomotion took the form of counts of the number of perch changes (gauged by microswitches under the perches) during each 3-min unit of the 12-h day. The data obtained were analysed using autocorrelation. With this technique the same data are placed in two columns and correlated with each other with progressively larger lags introduced between the figures in one column and those in the other. Before a lag is introduced the correlation coefficient obtained is +1.0 because the two sets of data are identical and each figure sits opposite itself. As progressively larger lags are used the value of the correlation coefficient falls but, if a cycle is present, it rises to peak again at a lag equivalent to the cycle length. This is because at this lag the peaks present in one set of data have been moved forward by one cycle so that they lie opposite the previous peak in the other set. While this technique is a useful way of detecting cycles, it involves some difficulties. First, the lag used should not exceed 10% of the observation period (Weiss *et al.*, 1966), which limits the length of the cycle which can be detected and often precludes the discovery of a second peak at twice the cycle length, which is otherwise a useful confirmation that the cycle found is a real one. Second, because the successive figures which are correlated are not independent of each other, there are difficulties in statistical interpretation (Sollberger, 1965). Third, it is affected by long-term trends in the data which tend to lead to high correlations at short lags and low ones at long lags regardless of whether a cycle is present or not. In the case of locomotion this last point is a difficult one because the behaviour shows a strong daily cycle, with a great deal of activity in the morning and little in the afternoon (Ollason and Slater, 1973). In the results to be presented, the effects of this were minimised by correlating not the raw data, but the difference between each figure and the mean of the 21 consecutive figures of which it was the eleventh.

A pilot study was first carried out on nine birds, with correlations being calculated for all lags between 3 and 45 min. As expected the results showed considerable individual variation, with some birds providing no evidence for cycles, while in others the main peak in the autocorrelation plot varied from 12 to 45 min. In those birds showing a peak at short lags subsidiary peaks were found at multiples of that lag. As several of the birds in this pilot study showed pronounced peaks close to the maximum lag which was used, more systematic data were later collected from 14 individuals using lags of up to 1 h. The results are summarised in Fig. 3, and suggest a tendency amongst these birds to show cycles of locomotion approximately 45 min in duration.

These results should be regarded as preliminary, and a more detailed study is planned to see whether cycle length in the same individual varies with time of day and over the course of several days and to see also how it relates to the overall activity level of the individual. Nevertheless, at this stage one can conclude that zebra finches show short-term fluctuations in locomotion and that in some birds these changes are regular enough to be termed cycles. While individual variation is great, the cycles found are most commonly around 45 min long.

The relationship of other behaviours to changes in locomotion

Slater (1974b) was unable to find any consistent relationship between locomotion and feeding by cross-correlating between them. This is in line with the fact that the commonest cycle length found for locomotion, 45 min, is longer than those found for feeding. These two behaviours, therefore, appear relatively independent of each other in their temporal patterns.

The main problem in detecting how other behaviour patterns fit in with the fluctuations in locomotion is that these fluctuations are so different between birds. This prompted some pilot experiments in which attempts were made to induce different animals to show cycles of the same length by subjecting them to a cyclical input from the outside world. In the first such attempt, a tape-recording was played to isolated birds on two consecutive

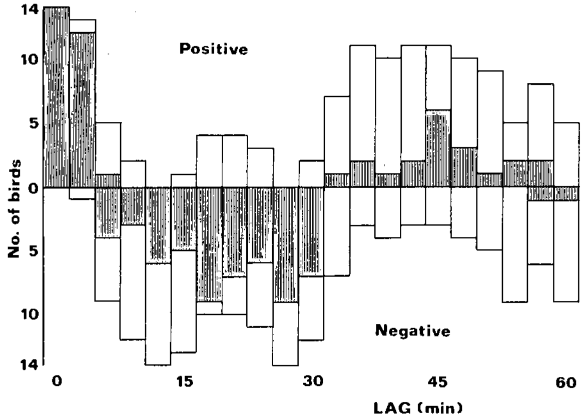

Fig. 3. Summary of the autocorrelation results for locomotion recorded from 14 birds for one day each. The open columns indicate the number of birds showing positive and negative correlations at each lag. The shaded columns indicate the number in which the correlation found was significant ($P < 0.05$, using the parametric method described by Weiss *et al.*, 1966).

days for 6 h. In each 19.5-min period there were 9.5 min of silence followed by a period of 10 min during which a brief tone was played at a rate which rose from 1/10 sec to 8/10 sec and then fell off to 1 again. Each of six birds was watched through three of these cycles on each day and the presence or absence of a number of behaviour patterns in every 15-sec period was recorded.

Fig. 4 shows the results for the four birds which were influenced by the input; as far as could be seen the other two ignored it. The birds tended to be active when the tones were on and preening and song, if they changed at all, tended to occur when the tones were off. The results on preening, however, should not be stressed on the basis of only two hours of observation, as they depend a great deal on whether or not a long bout occurred. The feeding results were very varied; one bird tended to feed as locomotion was rising, one as it was falling, one as it was rising and as it was falling, and one at any point during it. This confirms the point made earlier and by Slater (1974b) that, although feeding does not occur when a bird is inactive, its relationship with locomotion is a loose one.

Three of the birds which were tested in this way were, on the following two days, tested for locomotion for 6 h, with the tape-recorder being played on the first but not on the second day. The autocorrelations obtained are shown in Fig. 5. Bird 6 showed a weak 15—18-min cycle without the tones, but a clear 18—21-min one with them. In the other two birds the main cycle of locomotion was at about twice the length of the tone cycle whether or not the tones were switched on, though in bird 14 there was a suggestion of

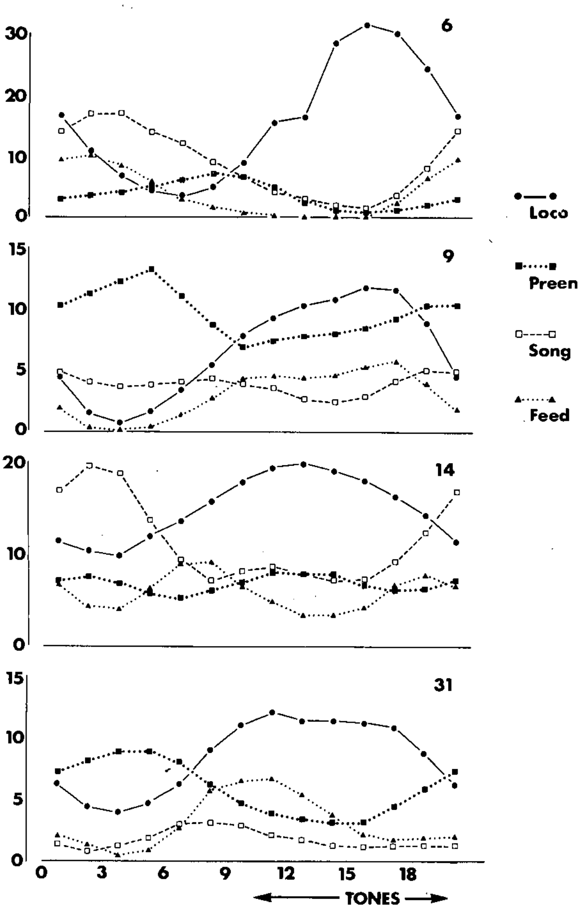

Fig. 4. The distribution of four behaviour patterns as shown by four birds during a 19.5-min tone cycle (described in the text). Each bird was observed for six cycles and the presence or absence of a behaviour pattern was noted in every 15-sec time unit. The results were summed over 1.5-min periods, thus giving a maximum score of 36. The figures plotted have been smoothed to remove minor fluctuations. (This involved adding to each figure, 2/3 of each of those immediately before and after it and 1/3 of those two before and two after it, then dividing this sum by 3.) The plots for each individual are labelled with its code number.

a weak 18—21-min component coming in when the tones were present. Unfortunately the amount of observational data on these two birds is insufficient to allow analysis of the results presented in Fig. 4 on the assumption that they were showing a 39-min cycle rather than 19.5-min one. Presumably the quite marked changes in locomotion which they show in Fig. 4 are because this behaviour peaked at the end of every second tone cycle.

In summary, one, and probably two, birds synchronised their locomotion

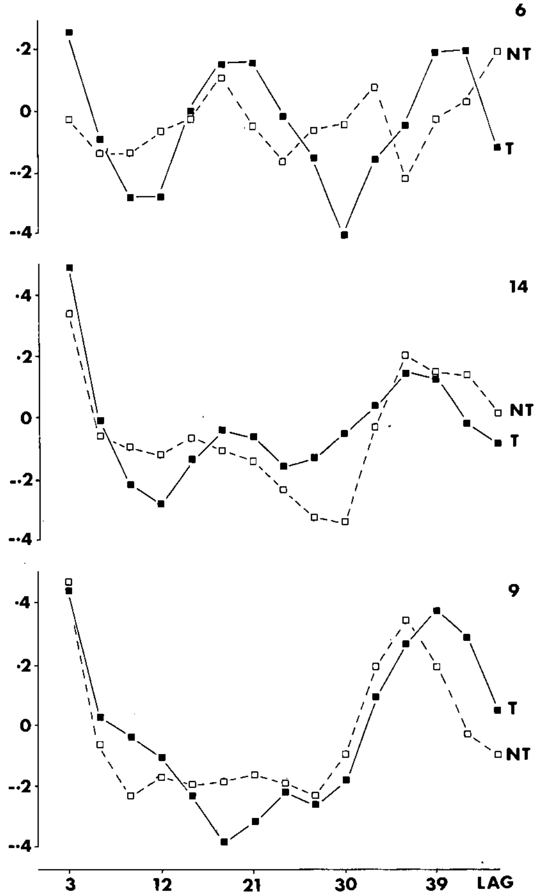

Fig. 5. Autocorrelations of locomotion with lags up to 45 min for three of the birds shown in Fig. 4, based on 6 h data with the tones being played (T) and 6 h on the following day without the tones (NT).

with the cyclical input, two birds showed cycles of twice the length of the tone cycle, and two birds appeared to ignore it altogether. That these experiments were not more successful may have been partly due to the choice of a rather short cycle length and partly due to the choice of stimulus. They did, however, suggest that cycles of external stimulation may synchronise and standardise in length the cycles of locomotion shown by zebra finches as long as their length is not too different from that of the cycle normally shown by the individual.

More systematic experiments have now been started using cycles of varying light intensity. Three birds have so far been tested and their results are shown in Fig. 6. All of these had been kept for 3 months on a 12-h day

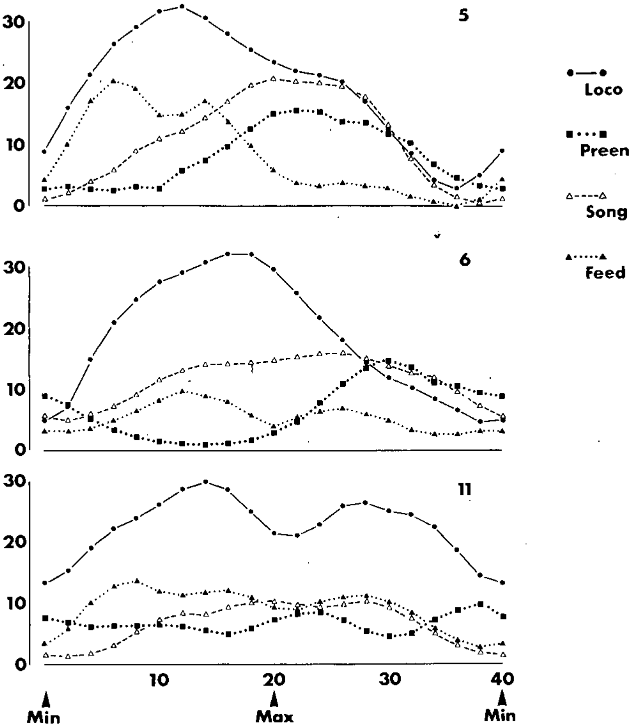

Fig. 6. The distribution of four behaviour patterns as shown by three birds during a 40-min light cycle (described in the text). Each bird was observed for ten cycles and the presence or absence of a behaviour pattern was noted in every 30-sec time unit. The results were summed over 2-min periods, giving a maximum possible score of 40, and smoothed using the procedure described in the legend to Fig. 4.

during which the light level in their cages rose in a linear manner from about 3 lux to about 52 lux and then fell again on a 40-min cycle repeated 18 times during the day. The low point of the light cycle was adequate for them to be observed on closed circuit television without special equipment, and birds were several times seen to fly around at this point indicating that they were not being forced into inactivity. The data for each bird in Fig. 6 are based on ten 40-min watches carried out, as nearly as possible, on consecutive days at the same time.

The behaviour of these birds was strikingly predictable from day to day. Bird 5 provides a good example. It was invariably inactive when the light intensity was at its low point but would quickly start to move around the cage, taking a long meal within a few minutes and, on some occasions, a shorter meal a little while later. Despite the fact that the data are smoothed, two peaks of feeding show up in Fig. 6 indicating that the timing of these meals was very consistent. The bird would remain active throughout the first half of the cycle, but as its activity began to decline it showed increasing amounts of singing and then preening. This preening continued when it became inactive about 10 min before the end of the cycle; for the last few minutes of the cycle it sat drowsily and showed none of the four behaviours plotted in Fig. 6 (the rise seen in locomotion and feeding at the end of the cycle results from the smoothing procedure which is described in the legend to Fig. 4). Bird 6 shows a similar general pattern, with locomotion and feeding being followed by song, then preening and then inactivity, except that the feeding is more spread out in this bird. Interestingly, this bird also followed the 20-min cycle used in the last experiment very closely (see Fig. 5). Bird 11 is more problematic, with a trough in locomotion and a slight peak of preening in the middle of the cycle as well as at the end. Its behaviour was much less well synchronised with the imposed cycle than was that of the other two: although it was usually inactive when the lights were low, it sometimes started to move about at once when they began to rise and on other occasions remained still for over 10 min. Nevertheless, there is a suggestion from the data that it was fitting approximately two behavioural cycles into one of the cycles of light intensity; this is interesting in view of the fact that, when its locomotion had been studied 2 years earlier, it had been found to show an 18-min cycle.

Discussion

The results reported in this section are largely preliminary and, as such, based on rather few birds. But they do seem to point to short-term cycles as an important and neglected influence on animal behaviour. Both of the experiments carried out so far suggest that birds can be induced to synchronise their locomotion cycles with those of imposed stimuli unless the period of these diverges too strongly from that which they normally show. Some birds show one cycle of behaviour for every two imposed cycles, and in one case there was a suggestion that the bird showed two cycles within each imposed one. One bird which was used in both experiments synchronised its behaviour with both the 20-min and the 40-min stimulus cycles.

The long-term aim of these studies is to try to tease apart the causal factors affecting different behaviours using cycles of different stimuli and lengths. If it proves possible to synchronise different behaviours with different imposed cycle lengths, this will provide evidence that the cyclical factors affecting the different behaviours are separate from one another. The clearest evidence that this can be achieved comes from data on the interrelation between locomotion and feeding. Present evidence suggests that these two behaviours are controlled by cycles of different lengths which are only loosely coupled to one another. While feeding occurs mainly during brief breaks in locomotion, it may occur at any stage during a period of activity and there are strong individual differences in the time of its occurrence in relation to the activity cycle. An additional piece of evidence comes from a pilot experiment in which six birds were put on a regime in which the lights in their cages were off for 5 min and on, at a constant level, for 25 min in each half-hour. This synchronised feeding which tended to occur in the first 5 min after the lights came on ($\chi_r^2 = 11.1, P < 0.05$, using a Friedman test between the five successive 5-min blocks when the lights were on). No significant effects were discovered in seven other behaviour patterns examined, including locomotion.

In contrast to feeding, some other behaviours do seem to fit into the cycles of locomotion at specific points. Both sequence analysis on birds in constant conditions (Slater and Ollason, 1972), and the results of birds which synchronised well with imposed cycles (bird 6 in Fig. 4; birds 5 and 6 in Fig. 6) suggest that this is true of song, preening and resting. It is possible that the oscillations in these behaviours are separate but synchronised so that further experiments will show that they can be dissociated from each other. An alternative, and at present more likely, hypothesis is that the probability of each of them is affected by the value of a single underlying variable. Although this might be called arousal, this word has many meanings: of these, that to which the variable proposed here would be most akin would be that termed activation by Andrew (1974). On this model locomotion would be most prevalent when the variable was high, song when it was rather lower, preening when lower still and resting at the bottom of the continuum.

A merit of this activation model is that it fits not only data on short-term cycles but also that on daily changes in behaviour as well (Ollason and Slater, 1973). Zebra finches are considerably more active in the morning than in the afternoon. Not surprisingly, sitting still, both alert and drowsily, rises during the course of the day, and there is also a slight increase in preening. Song falls with locomotion. These changes can be accounted for by assuming activation to be lower in the afternoon than in the morning; thus behaviours high on the continuum decrease and those low down increase. As before, feeding fails to fit into the model as its level was found to remain fairly constant during the period of the day in which the other behaviours were changing most rapidly.

If an activation model is to fit the facts already known about the temporal pattern of zebra finch behaviour, the variable underlying it must have certain characteristics. Its effects on behaviour must be to set probabilities rather than to determine which act should occur. Zebra finches do not go through a fixed sequence from locomotion to song to preening to rest, and there is considerable temporal overlap between these categories. It is possible for a bird which is moving round the cage to suddenly stop and rest or preen; likewise a resting bird may suddenly sing or move off. These types of sequence are, however, unusual. More common are alternations between adjacent behaviours on the postulated continuum: locomotion with song, song with preening and preening with resting. The level of the variable is thus seen as making certain behaviours more likely than others, rather than dictating exactly which should be shown. More precise determination of which behaviours are shown when, will, of course, depend on factors specific to them as well as on activation level.

A second point is that activation level need not vary in a cyclical manner. It would be hard to justify postulating this type of influence were it not for the fact that some birds show cycles of behaviour. Nevertheless, activation may be an important factor in the behaviour of other individuals, but one which varies in a non-cyclical manner, making it more difficult to detect. Finally, it should be mentioned that even in those birds which do show cycles, activation cannot be thought of as varying sinusoidally. The decline from locomotion, through song and preening, to resting is a slow process but the change from resting to locomotion tends to take place rather abruptly, with little, if any, song and preening in between. This can be seen clearly in the plots shown in Fig. 6. The level of a single variable underlying these changes in behaviour would thus have to follow a saw-tooth pattern, rather like a relaxation oscillation, running slowly down and then resetting rapidly.

There have been many attempts to explain changes in behaviour in terms of a single arousal-like variable, and in some cases efforts have been made to relate this to measures of neurophysiological arousal, but often without much success (Hinde, 1970; Andrew, 1974). The present results do no more than suggest the existence of such a variable but, if this can be confirmed, it will be an important task to discover its neural or endocrine basis and how this influences the behaviour patterns which are affected by it.

CONCLUSION

The work discussed in this article has been largely descriptive. While this approach may raise only a limited number of possibilities for the causation of the patterning of behaviour discovered, it is difficult to choose between these without more extensive experimental work. It is, nonetheless, certain at this stage that many different mechanisms underlie the temporal pattern of behaviour so that no single analysis can hope to elucidate all of them. At the simplest, one behaviour pattern may stimulate another in a more or less reflex-like manner; for example, it is presumably for this reason that bill-wiping follows drinking in zebra finches. But in most of the cases which have been discussed in this paper the mechanisms involved are more complicated, with each behaviour being influenced by a number of factors, both internal and external, specific and non-specific, which change with time and as a result of feedback from performance. These causal factors must, presumably, combine to give the behaviour some rating, which must be compared with those for all other behaviours before a decision is taken as to which act will occur. How all this is done is a dauntingly complex problem. Behavioural work can define it, and perhaps scratch the surface of it, but its solution lies not only inside the animal but also a good distance in the future.

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DOES ACTIVATION INFLUENCE SHORT-TERM CHANGES IN ZEBRA FINCH BEHAVIOUR?

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Abstract. Zebra finches show short-term fluctuations between activity and inactivity, with feeding associated primarily with the former and grooming with the latter, while song tends to occur on the transition between the two. Experiments were carried out to test the hypothesis that these relationships between behaviour patterns stem from fluctuations in a single underlying variable, termed activation, the level of which alters the probability of different acts. In some individuals it proved possible to synchronize fluctuations in locomotion with short-term cycles of light intensity and in most cases the relationships of other behaviours to these cycles followed the predicted pattern. However, the fact that cycles in one behaviour were not necessarily accompanied by cycles in others, and that a bird whihc synchronized its locomotion with all four of the cycle lengths used showed variable relationships between behaviours, both argued against this hypothesis. It is suggested that rest precludes the occurrence of other behaviour patterns and that the relationships between these arise because they occur in order of priority when rest terminates.

Introduction

Andrew (1975) has reviewed the evidence that general variables, often loosely termed 'arousal', play a role in the organization of behaviour. He differentiates between two main classes of model used to explain such influences. 'Responsiveness' models postulate that all behaviours, with the obvious exception of sleep, become more likely as the variable rises. The findings of Lat (1965) and Brady (1975), amongst others, are most easily explained on such a model. On the other hand, 'activation' models are based on the idea that different behaviour patterns tend to appear at different levels of the variable (Moruzzi 1969). On this model, certain behaviours, such as locomotion and aggression, are seen as occurring when activation is high, while others, like sleep or grooming, are associated with low levels of activation. Such a system might account, for example, for the common observation that grooming tends to occur in association with sleep (e.g. Delius 1967). This paper is concerned with testing the hypothesis, based on previous observational work, that certain of the associations between behaviour patterns in isolated zebra finches may be acounted for by this latter type of model.

The notion that activation might be involved in the organization of zebra finch behaviour is based on a number of lines of evidence. Sequence analysis of the behaviour of isolated males indicated that the birds tend to fluctuate between activity, with which ingestion is associated, and inactivity, which typically involves grooming in the active morning hours when the recordings were made. Song tends to occur on the transition between the two, and it is rare for locomotion and preening to succeed each other directly (Slater & Ollason 1972). The impression was gained during these observations that the birds tended to move slowly from periods of intense activity, through a phase during which song and locomotion alternated, into a phase of song and preening, followed by uninterrupted preening and finally (particularly later in the day) rest. The change from rest to locomotion was, by contrast, more abrupt, with little if any preening and song in between (Slater 1975). Feeding tends to be loosely associated with the active phase, though its exact relationship to locomotion varies considerably between individuals (Slater 1974). These qualitative impressions, together with the results of sequence analysis, suggest a model in which activation fluctuates during the course of several minutes and affects the probability of various actions in such a way that locomotion and feeding occur mainly at high levels, song rather lower, preening at lower levels still and rest at the bottom of the continuum. Note that activation is seen here as affecting probabilities, rather than dictating which behaviour is shown; the exact act which appears at any given moment will clearly depend on a number of other, more specific, causal factors.

Another form of analysis, the results of which tie in with the activation model, is correlation between the frequencies of different behaviours

Table I. Correlations Between Pairs of Behaviours in Different Birds and Their Relationship to Levels of Locomotion (5-min Time Units; $N = 96$ in All Cases). Figures in Bold Type: $P < 0{\cdot}01$. Spearman Rank Correlation Coefficient

Bird No.	Locomotion (counts/min)	Correlations between					
		Loco/pr	Loco/sng	Pr/sng	Loco/fd	Pr/fd	Sng/fd
9	26·9	− **0·754**	− **0·539**	+ **0·299**	+ 0·072	− **0·323**	− 0·044
2	22·2	− **0·337**	− 0·189	+ 0·143	− 0·174	− 0·048	− 0·166
6	19·7	− **0·321**	− **0·307**	+ **0·587**	− **0·299**	+ 0·006	+ 0·044
25	11·8	− **0·627**	− 0·174	+ 0·041	− 0·119	− 0·190	+ 0·165
28	9·3	− **0·598**	− **0·352**	+ **0·293**	− 0·009	− **0·359**	− 0·025
13	8·9	− **0·481**	+ **0·283**	+ 0·015	+ 0·215	− 0·194	+ **0·270**
11	7·2	− **0·539**	+ 0·151	− 0·031	− 0·003	− 0·196	+ **0·309**
22	6·9	− 0·174	+ **0·453**	− 0·109	+ 0·262	− 0·103	+ 0·039
5	6·7	− **0·655**	+ 0·130	− **0·275**	+ **0·543**	− **0·453**	+ **0·338**
12	1·9	+ 0·032	+ **0·549**	+ 0·132	+ **0·505**	− 0·044	+ **0·325**

in 5-min time units. This was carried out on data collected during eight 1-hr observation periods on each of 10 birds, all the observations being made in the late morning, as were those for sequence analysis. The correlations between locomotion, song, feeding and preening are shown in Table I. The correlation values depend strongly on the level of locomotion of each bird, which shows great variation. In a highly inactive bird, such as bird 12, most behaviours are positively correlated with each other for the simple reason that there are many 5-min units in which none of them appear. In the most active birds, shown at the top of the table, locomotion tends to be negatively related to other behaviours as most of the time units contain it alone. Looking at all the birds in the table, it is clear that locomotion and feeding tend not to be associated with preening regardless of how active an individual is. Feeding and song tend to have similar relationships: they are associated with each other in all but the most active individuals, and they are both associated with locomotion in less active birds. In more active birds song moves to being associated with preening. These results are compatible with the model of activation outlined above: locomotion and feeding near the top (clearly not associated with preening); song at an intermediate position (associated with preening in highly active birds and with locomotion and feeding in less active ones); preening low down (tending not to be correlated with other behaviours except for song in more active individuals).

A different line of evidence comes from observations on daily cycles (Ollason & Slater 1973). Locomotion declines during the day and the amount of time spent resting increases. Song declines with locomotion and preening shows a slight tendency to rise: recent unpublished evidence also suggests that preening occurs frequently during the night, when birds are otherwise totally inactive. All these changes could be accounted for if activation is very low at night and lower in the afternoon than in the morning. Feeding is less satisfactorily accommodated as its level (measured either as number of pecks or as number of 30-s intervals in which it occurs) remains constant through the main part of the day, though the number of meals does decline. Other evidence also makes it doubtful whether feeding can be fitted neatly into an activation model: its relationship with locomotion varies greatly between individuals (Slater 1974) and cycles of feeding, when present, tend to be shorter than those most often found in locomotion (Slater 1975). It seems unreasonable, however, to discard the model purely on these grounds, as its pattern may simply indicate that the occurrence of feeding is more dependent on specific causal factors than is that of the other behaviours under consideration.

We have carried out a great deal of work on the problem of whether the short-term fluctuations in behaviour found by transition analysis are of a cyclical nature and, in cases where they appear to be so, have attempted to discover the periodicity of these cycles. This has involved the automatic recording of locomotion, followed by autocorrelation and power-spectrum analysis. The results show considerable variation, both within and between individuals, with the dominant cycle present in the data varying from 15 min to over 1 hr in length. The commonest cycle length found was around 40 min. In some individuals the cyclic nature of changes in locomotion is clear, while in others apparent cycles in the data may be artefacts of the methods used. Such effects may arise for three main reasons: (i) Non-normality in the data. This makes autocorrelation difficult to apply and interpret. Lack of normality is usual in behavioural data when put into a form suitable for autocorrelation, because many time units tend to contain no events, while organization into bouts means that others contain a large number. (ii) Serial correlation. Again, because of bout organization, successive time units tend to be strongly serially correlated. This may, on its own, lead to apparent cycles in series of otherwise random numbers (Clifton & Slater, unpublished). For example, autocorrelation was carried out on a series of 240 1s and 0s, the only constraint on which was that the probability of switching from 1 to 0 or from 0 to 1 was 0·2, while that of staying in the same mode was 0·8. Clear evidence of cycles was obtained on some runs because, by chance, two series of 1s occurred in close proximity and thus, when the appropriate lag was introduced, these were correlated with each other to give a high coefficient. Where serial correlation is high, it is thus necessary to have a long data series to avoid the appearance of such artefacts. (iii) Daily cycles. Short-term changes in behaviour tend to be superimposed on strong daily cycles or trends, and this is certainly the case with zebra finches. Efforts to remove daily trends also tend to introduce spurious cycles. This is well documented where simple running averages are used (the Slutsky-Yule effect), but we have also found the more complex running averages recommended by Kendall (1973) to have this effect, probably because the data to which they were applied were non-normal.

Because of these difficulties, we prefer, at this stage, to refer to the short-term changes in behaviour which we have found as fluctuations, even though they are regular enough to be termed cycles in some individuals (see Slater 1975).

The experiments to be reported here were aimed at examining more closely the interrelationships between locomotion, feeding, song, preening and rest in zebra finches and, in particular, at testing the activation hypothesis. The fact that zebra finches show short-term cycles or fluctuations in locomotion was taken as a starting point. Pilot studies suggested that these changes could be synchronized in some cases with short-term cycles of either sound or light intensity (Slater 1975). The present experiments use the latter technique, but avoiding light levels which would be so low as to force the bird into inactivity. By studying animals in a situation where regular cycles of locomotion occur, it is possible to see how other behaviour patterns fit in with the changing levels of locomotion. By varying the cycle length, it is also possible to see whether all behaviour patterns tend to cycle together but out of phase with each other, as would be predicted by the activation model, or whether their relationships can be modified, as would occur if they depended on independent oscillators. Activation would predict that, where an animal is showing cycles in one behaviour, it should show cycles of the same length in others. It would also predict that the phase relations between different behaviour patterns should remain similar over a variety of different cycle lengths. The results of the experiments will be analysed to assess the extent to which these predictions are realized. Emphasis throughout the paper will be placed on those birds in which changes in behaviour were synchronized with the external cycles, as it is only from these that any firm conclusions can be drawn.

Methods

The subjects were 10 adult male zebra finches kept in two groups of five each in a separate sound-proof chamber. The lights in these, and in the sound-proof chambers used for isolation and observation, were switched on from 05.00 to 17.00 hours G.M.T. daily, with the experimental light fluctuations superimposed upon this. Before testing on a particular light regime, each bird was kept on that regime for at least 5 weeks, the last of which was spent in isolation. It was then placed in another chamber for a further week during which observations were carried out on several successive days between 10.30 and 12.30 hours G.M.T. for a total of 360 or 400 min. The exact schedule of observa-

Table II. Schedule of Observations Used on Each of the 10 Birds Tested

Test	Cycle length (min)	Cycles watched per day	Days watched	Total cycles watched	Total min watched
1	40	2	5	10	400
2	60	1	6	6	360
3	20	4	5	20	400
4	30	2	6	12	360

tions for each of the four light cycles used is shown in Table II.

In each experimental situation the light within the chambers rose and fell on a linear ramp between a low point of approximately 3 lx and a high point of approximately 52 lx on a short-term cycle which was repeated throughout the 12-hr day. The first low point was synchronized with the time when the lights came on. Four different short-term cycles were used in the following order: 40 min, 60 min, 20 min, 30 min. Shortage of chambers made it necessary to test all birds in this order rather than in a balanced design.

The same maximum and minimum light intensities were used on each cycle length but the rate of change of light intensity varied between them. The light cycles were generated using potentiometers driven by reversing motors. In each case the cycle length obtained was slightly in excess of that planned (maximum 1·5 min on 60-min cycle); for the purpose of analysis the excess period at the end of each cycle (as the light approached its low point) was ignored.

Observations were carried out using closed-circuit television with a camera sensitive to low light intensities; the level of light at the low point of the cycles used was chosen such that the bird could still be clearly seen. The only behaviour which may have been missed on some occasions during the few minutes surrounding this point was preening, some elements of which involve little movement. Care was taken only to score this behaviour when it was clearly present and, despite this possible source of error, it tended to occur mainly at low light intensities, so that the effect is primarily to lower the height of peaks in occurrence rather than to lead to spurious troughs.

Check sheets were used to record observations, each cycle being split into the appropriate number of 30-s intervals, in which different behaviours were simply recorded as present or absent. Fifteen types of behaviour were scored, but this paper is concerned with only five of them: locomotion (movements of more than approximately 3 cm), song, feeding, preening (bill to feather grooming movements) and resting (the absence of all other recorded behaviour patterns from a complete 30-s unit: in effect the bird sits with only minor head movements. This category includes sleep).

The extent to which particular birds followed an imposed cycle was assessed by splitting each cycle into five equal time units and testing whether the number of 30-s periods in which a behaviour occurred differed between these using a Friedman two-way analysis of variance for each bird. Although more cycles were watched on some regimes (Table II), all these tests were based on the first 360 min of data collected from each bird. For example, on the 30-min cycle, the Friedman tests were carried out using 5 columns (five 6-min periods) and 12 rows (the 12 cycles watched). This was done in each bird for each behaviour pattern. The value of χ_r^2 obtained indicated whether the level of the behaviour under consideration differed significantly between stages of the light cycle. Where such an effect was found, the exact relationship between the light cycle and changes in behaviour was examined by plotting the data. This also made it possible to detect cases where a significant result stemmed from more complex fluctuations than a single behavioural cycle per light cycle.

To show finer details, the figures have been prepared using units which are smaller than those employed for statistical testing, but again constant in proportion to the cycle length, in this case one-twentieth (i.e. 1-min units for 20-min cycle; 1·5-min units for 30-min cycle, etc.). Minor fluctuations between successive points have been removed by a smoothing procedure. This involved adding to each figure two-thirds of each of those immediately before and after it and one-third of those two before and two after it, then dividing this sum by 3. This is done purely for illustrative purposes and, in addition to ironing out minor fluctuations, has the effect of lowering peaks and raising troughs as compared with those in the original data.

Results

Synchrony of Locomotion with Imposed Cycles

Table III gives the results of the Friedman tests used to decide whether changes in locomotion were synchronized with the four different light-cycles. With the exception of bird 5, which will be discussed later, no bird followed all four cycles to a marked degree, though all but two birds showed significant synchrony on at least one of them. In those cases where more than one cycle length was adhered to, the cycles followed tended to be of similar duration (i.e. birds 33, 35 and 37 all followed the 30- and 40-min cycles but not the other two), suggesting that individuals can be entrained by a particular cycle length but will not follow one which diverges too strongly from it. In bird 36, however, this was not the case. It showed strong synchrony with the 30-min cycle (see Fig. 2) and weak synchrony with the 60-min cycle, but none on 40 min. As Fig. 1 shows, the distribution of all five behaviour patterns analysed was bimodal for this bird on the 60-min cycle and, although its level of locomotion was low at this cycle length, the results were sufficiently consistent between the six observation periods to give a significant result on the test used. This does not stem from the bird showing a 60-min cycle, but from a tendency to show two cycles within the 60-min period. Bird 33 was another bird with this tendency (see Fig. 1), but its distribution of locomotion was not similar enough between observation periods to give a significant result on the Friedman test.

As well as the possibility that a bird may show two cycles of locomotion within a light cycle, there exists the possibility that a bird may show one cycle of locomotion for every two light cycles. Thus a bird might show a 40-min cycle on the 20-min regime, becoming inactive at every second low point. This was suspected of occurring in some cases, and was reported for synchrony with sound cycles by Slater (1975), but testing for it is not possible with the methods of data collection used in the present experiments.

The lowest light intensity used in these experiments still allowed the birds to see and move around the cage, as many did when their behaviour was not synchronized with the light cycle. A stronger effect on locomotion would undoubtedly have been obtained had the lighting fallen to a lower level than this. This procedure was avoided as it was felt that enforced inactivity at regular intervals would be likely to have widespread disruptive effects on the organization of behaviour.

Relationships of Other Behaviours to Locomotion

Of the four different light cycles used, the 30 min was that followed by most individuals (Table III). Figure 2 gives the results of three birds which followed this cycle particularly clearly. Their results are very similar, all showing a peak in resting shortly after the low point of the light cycle, and thereafter successive peaks in locomotion (with which feeding tends to be associated), then song and then preening. This is much in line with the sort of result expected from the activation model proposed earlier, with the sequence rest–locomotion and feeding–

Table III. Results of Friedman Tests Used to Decide Whether Locomotion in Each of 10 Birds was Synchronized with Four Different Short-term Light Cycles. Values of χ^2_r, all with Four Degrees of Freedom, are Given in the Body of the Table

Bird No.	Short-term cycle length (min)			
	20	30	40	60
11	2·1	1·5	4·3	14·1**
5	40·7***	26·1***	24·7***	13·4**
42	8·3	27·7***	1·9	2·1
40	1·0	14·9**	4·1	7·7
38	7·8	5·5	4·9	3·0
37	8·9	27·3***	10·2*	5·6
36	9·1	18·8***	7·0	12·4*
35	4·1	10·0*	10·9*	6·2
34	0·3	5·7	8·8	3·9
33	5·6	9·5*	12·1*	7·4

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

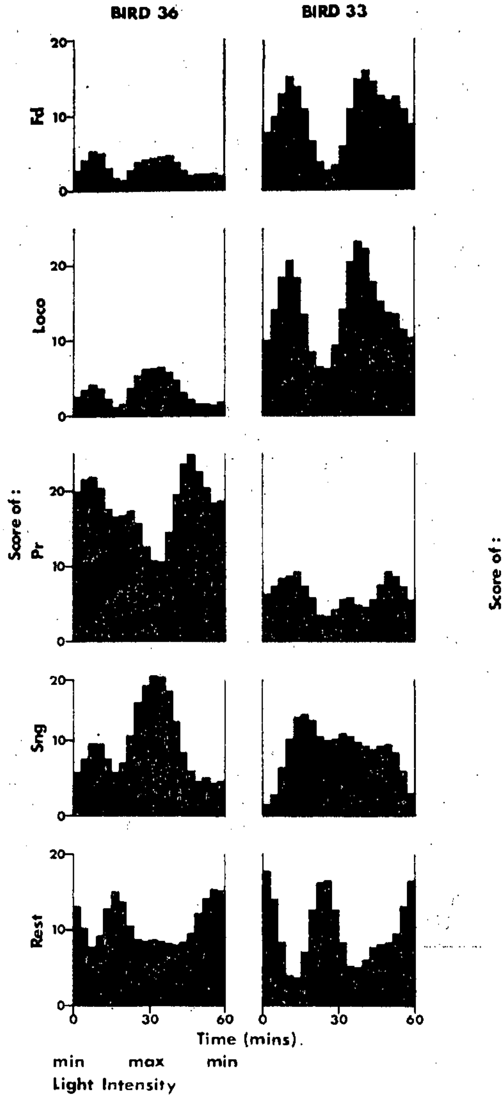

Fig. 1. Changing levels of five different behaviour patterns over a 60-min light cycle for two birds. The score for each behaviour pattern is the total number of 30-s periods within a time unit during which the behaviour was observed, summed over the six 60-min cycles watched and smoothed. Each time unit is one-twentieth of the cycle length in this and the other figures. The behaviour patterns included are as follows: Feeding (Fd); Locomotion (Loco); Preening (Pr); Song (Sng); Resting (Rest).

song–preening–rest emerging here as it had done from the observational data on which the model was based.

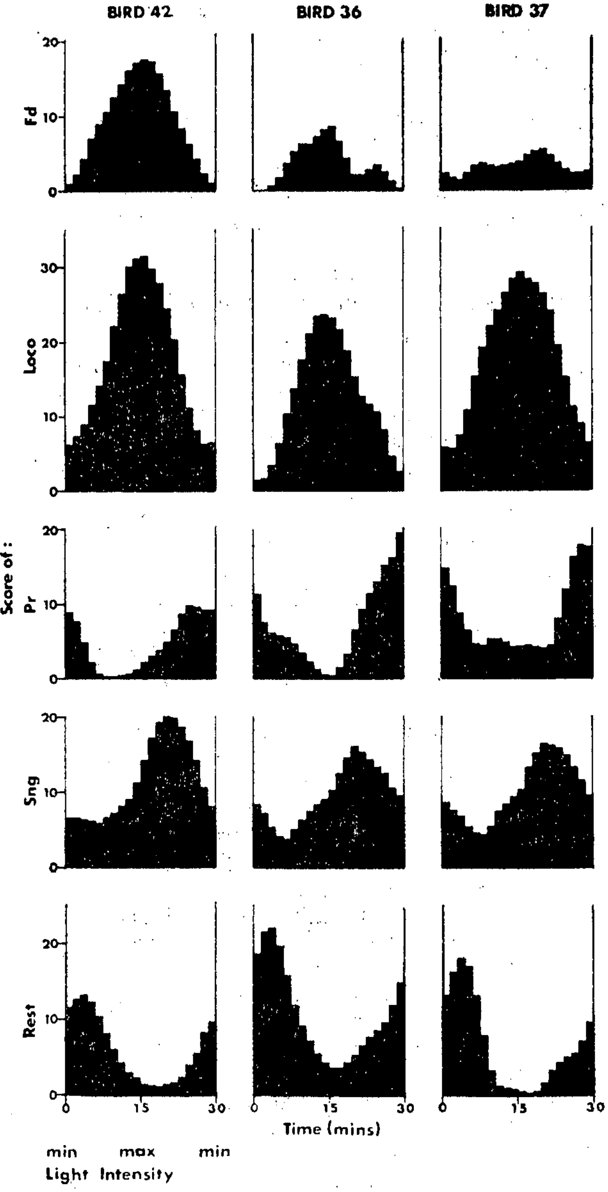

Fig. 2. Changing levels of five different behaviour patterns over a 30-min light cycle for three birds. For further details see legend to Fig. 1.

Can the Relationships Between Behaviour Patterns be Modified?

If activation is a strong influence on the probability of several behaviours, and the light cycles are affecting activation rather than these behaviour patterns directly, then the extent to

Table IV. Results of Friedman tests Used to Decide Whether Changes in Four Different Behaviour Patterns were Synchronized with the 30-min Light Cycle. Values of χ^2_r, all with Four Degrees of Freedom, are Given in the Body of the Table

Behaviour pattern	Bird No.									
	11	5	42	40	38	37	36	35	34	33
Preening	9·2	0·9	20·3***	2·0	3·2	16·7**	9·0	4·1	18·3**	4·3
Locomotion	1·5	26·1***	27·7***	14·9**	5·5	27·3***	18·8***	10·0*	5·7	9·5*
Song	11·6*	20·7***	9·5*	13·4**	2·6	10·4*	14·7**	7·6	3·1	13·8**
Feeding	2·5	7·7	26·8***	9·2	7·2	2·8	12·8*	8·5	7·7	7·3

(***$P < 0{\cdot}001$; **$P < 0{\cdot}01$; *$P < 0{\cdot}05$).

which the different patterns show cycles would be expected to be similar. If, however, behaviour patterns are separately affected, one may show cycles of the same length as the light cycle while others do not do so.

Whether or not a particular behaviour pattern follows a particular light cycle can be assessed by the Friedman test, and the results of this for four behaviour patterns on the 30-min cycle are given in Table IV. Resting is not included here because it can only occur in time units not occupied by other types of behaviour. In practice, locomotion is often recorded in nearly all the time units in which resting does not take place, so that if cycles occur in one of these behaviours they will do so in the other purely by exclusion.

As Table IV shows, some birds (e.g. 35 and 38) do not follow the 30-min cycle very clearly for any of the behaviours considered, but it is not true to say that those which follow the cycle well for one type of behaviour also do so for others. For example, bird 5 showed strong cycles for locomotion and song, but was the weakest for preening. Two methods were used to see if there was any tendency for different behaviour patterns to show a similar degree of cycling: the Friedman tests on sums of squares and the Friedman tests on coefficients of variation.

Friedman tests on sums of squares. The sums of squares on which the χ^2_r values shown in Table IV were based provide a measure of how cyclical each bird was for each behaviour pattern. A minimum sum of squares of 6480 is obtained when the behaviour pattern is equally distributed across the five times units: the more cyclical the behaviour, the greater the value obtained exceeds this figure. As the χ^2_r values shown in Table IV are simply a linear transform of these sums of squares, they also provide a measure of how cyclical the behaviour was. They were therefore ranked along rows and a Friedman test carried out to see whether an effect of the light cycle on one behaviour tended to be associated with one on others. The same procedure was adopted for each of the other cycle lengths used. The result was just significant for the 20-min cycle ($\chi^2_r = 17{\cdot}56$, $df = 9$, $P < 0{\cdot}05$) but not significant for any of the other cycle lengths.

Friedman tests on coefficients of variation. This method was also based on a Friedman test across birds for each cycle length using the same four behaviour patterns as shown in Table IV. In this case, however, the measure used for each behviour in each bird was a coefficient of variation (Standard deviation × 100/Mean). This was again based on each cycle length being split up into five units. Taking the locomotion of bird 33 on the 20-min cycle as an example, 20 cycles were watched, giving a total of 160 ½-min units in each 4-min subdivision of the cycle. Locomotion was recorded in 60, 53, 62, 88 and 72 of these respectively, giving mean = 67.0, standard deviation = 13·6 and coefficient of variation = 20·2. The higher the coefficient, the greater the variation in the level of that behaviour pattern between different stages of the cycle. This method gives a rather different ranking of birds from the last, because it does not take into account whether or not a particular bird is consistent between observation periods in following a given cycle length; it is based on its overall result. Like the last method, however, it failed to produce striking evidence that different types of behaviour cycle to the same degree as each other. The only significant result was that for the 60-min cycle ($\chi^2_r = 19{\cdot}58$, $df = 9$, $P < 0{\cdot}05$), though that for the 40-min cycle was just short of being so.

This evidence is against activation being an important variable in the organization of these cycles, for clearly one behaviour may show cycles synchronous with the imposed light cycles while others do not do so. The mild tendency in some birds for different behaviours to show the same degree of cyclicity can probably be accounted for by exclusion, a very active bird, for example, tending to show other behaviour patterns primarily in periods when it is not flying around.

Further evidence against the activation model comes from examination of the results of bird 5, the bird in which locomotion showed a significant tendency to cycle on all four light regimes. These results are shown in Fig. 3.

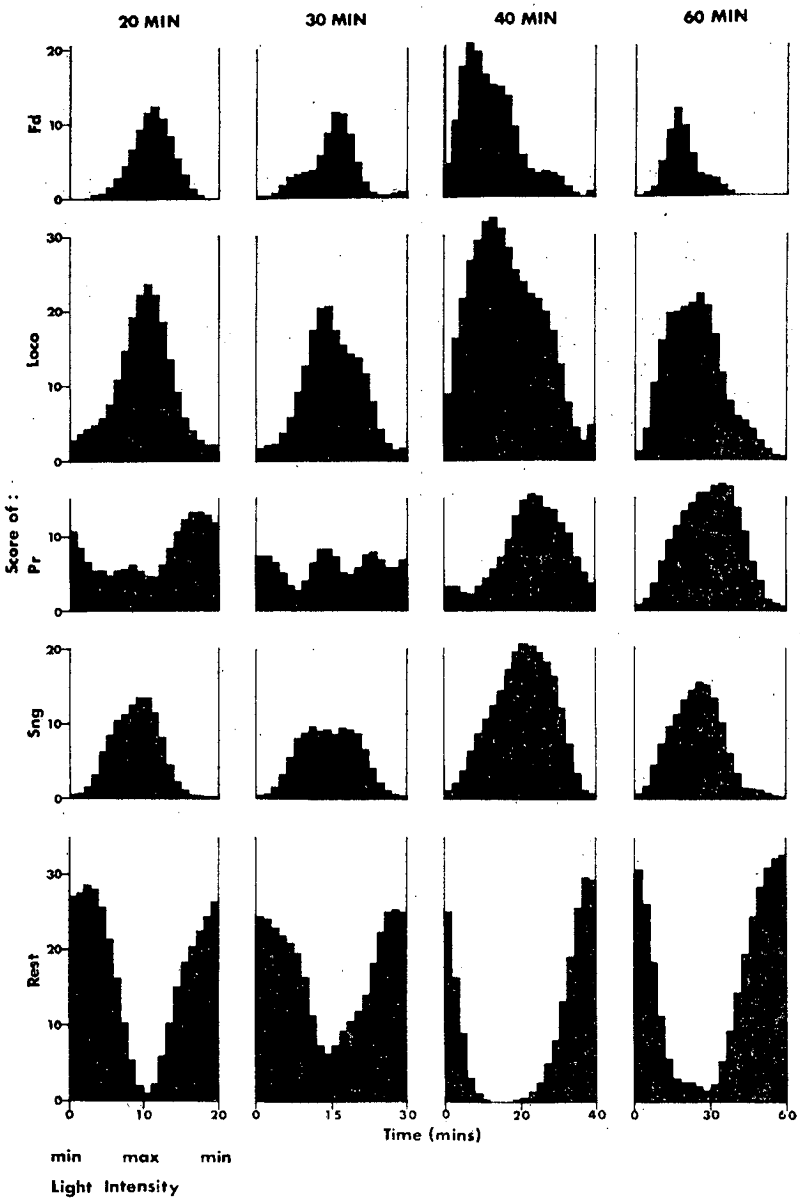

Fig. 3. Changing levels of five different behaviour patterns in bird 5 on four different light cycles: (a) 20 min; (b) 30 min; (c) 40 min; (d) 60 min. For further details see legend to Fig. 1.

The sequence rest–locomotion–song–preen–rest is apparent on the two longer cycle lengths, but on the shorter cycle lengths song tends to occur earlier and feeding later in relation to locomotion, while preening ceases to show clear evidence of cycling. Closer examination suggests that song tends to occur mainly at a particular phase of the cycle, while other behaviour patterns occur primarily at a particular time after the start of the cycle. Thus on all cycle lengths the peak of song is reached at around the middle of the cycle. The peak of locomotion moves nearer to the beginning of the cycle on longer cycle lengths, so that the relationship between locomotion and song differs between the regimes. This is even more strongly noticeable in the case of feeding, which moves forward markedly on longer cycles: its peak occurs after that of locomotion on short cycles (20 or 30 min) but before it on longer ones. This is, however, only a shift in relation to the phase of the cycle: in contrast to song, feeding peaks at approximately the same time (10 to 15 min) after the low point on each cycle length. Finally, resting, though always occurring mainly when the lights are low, tends to be primarily after the lowest light intensity on short cycles and before it on long ones. As the distribution of resting tends to be a mirror image of that of locomotion, it is not surprising that the earlier occurrence of one of these behaviours is accompanied by that of the other.

One of the original intentions of using several different lengths of light cycle in these experiments was to see whether the temporal relationships between behaviour patterns remained the same on different cycle lengths (as the activation model would predict) or whether these relationships could be modified (as would be likely if cyclical changes depended on different mechanisms for each type of behaviour). Although bird 5 was the only animal the locomotion of which followed all the light regimes, its data clearly indicate that the phase relations between behaviour patterns can be altered in this way.

Discussion

The results presented in this paper demonstrate that it is possible to standardize the length of short-term fluctuations between locomotion and rest in zebra finches by means of short-term light cycles. Pilot studies had suggested that the behaviour of most birds might be modifiable in this way (Slater 1975): these experiments have shown that birds vary greatly in their flexibility in this respect. Two showed no evidence of following any of the cycles used, some followed one or two cycle lengths but not others, and only one bird was flexible enough to follow all cycle lengths (Table III). From this it seems likely that most birds will only synchronize their periods of locomotion and resting with an imposed cycle when it does not diverge too greatly in period from the rhythmicity which they would normally show. This is also suggested by the fact that birds which did follow more than one cycle length tended to follow two of similar duration. While there is considerable variation in the results, the 30-min cycle was that most commonly adhered to.

In those cases where changes in locomotion showed the same period as the light cycle, the peak in locomotion occurred at around the peak in light intensity, while that in resting tended to be at, or a little after, the low point of the light cycle. In cases where locomotion was strongly cyclical ($P < 0{\cdot}01$) the sequence rest–locomotion and feeding–song–preening–rest was observed in most instances (Fig. 2, Fig. 3, lower plots): this is the same sequence as had been noted in unconstrained animals and had led to the activation hypothesis. This sequence of peaks in occurrence could be accounted for if activation level set the probabilities of different behaviours, and if it declined slowly during the course of several minutes and then reset rapidly to a high level.

The experimental results did not, however, lend support to such a model. If cyclical changes in activation are responsible for the appearance of cycles in several different behaviours, then all of them would be expected to show cycles when activation was synchronized with a light cycle, and none of them when it was not. The results showed only a weak tendency in this direction and there were some striking exceptions where one behaviour pattern showed strong cycles, while another was unaffected by the light regime. Such a result could be as easily accounted for by interactions between behaviour patterns, such as high levels of one being incompatible with the performance of others. Only a strong tendency for different types of behaviour to show cycles of the same period, but out of phase with each other, could be taken as evidence for activation, and this was not present.

The results of bird 5, the locomotion of which showed cycles on all light regimes, also suggested that activation was unimportant, as the timing of other behaviours in relation to locomotion and resting varied with the length of the light cycle. It appears from this that each behaviour pattern was being influenced independently by the light regime and that this led to modifications of the sequence in which they occurred. While it could be argued that an influence of activation exists, but is overriden by these direct effects, the fact that the sequence can be changed easily with a mild stimulus argues against any such effect of activation being an important one.

Although short-term relationships between behaviour patterns have not been examined before in this way, there is a parallel between the results reported here and those of Aschoff on circadian rhythms in man. Humans kept under continuous illumination (Aschoff, Gerecke & Wever 1967) or on light regimes diverging from the normal 24-hr period (Aschoff, Pöppel & Wever 1969) sometimes show activity rhythms and rhythms of body temperature which differ in period. This argues against the idea that these different rhythms are under the control of a single 'clock', in the same way that the flexibility in relationships between behaviour patterns which was found here is incompatible with a single underlying variable having an important influence on all of them.

If activation is not an important variable in the organization of these short-term changes in behaviour, alternative possibilities must be explored. Certain of the relationships between behaviours may be explained in terms of changing responsiveness. In the tsetse fly, Brady (1975) postulated the existence of a variable of this sort, which he called central excitability, to account for parallel in-phase circadian changes in a number of responses. High responsiveness could account for the association between feeding and locomotion in zebra finches, and for the earlier finding (Slater & Ollason 1972) that other behaviour patterns which involve responding to external stimuli, such as drinking and pecking at parts of the cage, are also associated with locomotion. However, testing for this would have to involve a wider range of experimental stituations, for these associations could equally result from the fact that an active animal comes across the appropriate stimuli for these behaviours more frequently.

As with the results of the present study, some of the responses examined by Brady (1975) were out of phase with the others, and he suggested two reasons why this might be the case. One possibility was that certain responses were promoted by low arousal, in which case one would expect them to occur 180° out of phase with the others. This could account for the relationship between flight and rest in tsetse flies and that between locomotion and rest in zebra finches, though it is unnecessary to invoke a general variable to explain the temporal relation between two behaviour patterns such as these which are clearly mutually incompatible. Given that both locomotion and resting tend to occur in bouts several minutes long, and tend to exclude each other, such an inverse relationship is to be expected.

Brady's other suggestion was that 'there is a hierarchy of responses where "strong" activities with high thresholds occur only at high arousal states, and then inhibit the "weaker", low threshold ones already occurring'. This is similar to the model of activation which was proposed here and could, like it, account for a variety of different phase relationships between behaviours. But the fact that the degree of cyclicity and phase relations between locomotion, song, preening and rest varied considerably under the experimental treatments used here also make this explanation an unlikely one to account for the normal sequencing of these behaviours.

An alternative explanation, which is at present being examined, is that no such general variable exists, but that the observed sequence of behaviours between locomotion and rest results from competition between behavioural systems which differ in priority. This could account for the observation that periods of rest tend to be followed by locomotion and feeding, then song, then preening and finally rest again if, for example, rest or sleep precludes the occurrence of other types of behaviours, causal factors for which build up at different rates. If rest periods are other than very brief, this will lead to a fixed order of priorities when they terminate, and the behaviour patterns will then be performed in that order, leading to an organized sequence. Such an hypothesis is attractive for a number of reasons. First, being based on simple competition between behaviours, it would account for the ease with which their temporal patterns may be dissociated from one another. Second, if causal factors for locomotion and feeding build up rapidly during non-performance, those for song more slowly and those for preening slowest, it predicts the occurrence of these behaviour patterns in that order. A difficulty with the activation hypothesis is the prediction that, if song and preening occur between locomotion and rest, they should also take place as activation rises from low to high levels. To account for their rarity in this position (see Fig. 2) it is necessary to assume that activation rises more rapidly than it falls. A third attraction is that a model based on competition is more easily tested than is one based on a single intervening variable, and such tests are currently under way.

The hypothesis put forward here, that the regular occurrence of one behaviour pattern leads to a fixed ordering of others, suggests a similarity between the present findings and those of Staddon (1972; Staddon & Ayres 1975). He has found that regular food delivery, at intervals of 12 s in pigeons and 30 s in rats, leads to stereotyped sequences of behaviour between feeding bouts when the animal has become accustomed to the procedure. While this phenomenon follows a very different time course, and the animals are being forced to feed briefly and at very short intervals, some of the principles of organization which emerge may also be applicable to behaviour in a less constrained situation. The idea of making the temporal pattern of one type of behaviour fixed, and then examining the way in which others fit in with it, promises to be a useful way of studying the causal basis of associations between behaviour patterns.

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A SIMPLE MODEL FOR COMPETITION BETWEEN BEHAVIOUR PATTERNS

by

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(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

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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 of varying priority. Efforts to test this possibility have proved difficult because of the highly varied reactions of birds to stimuli which interrupt their behaviour. This was one reason why the simulations described in this paper were initiated, the aim being to discover the sort of structure which might emerge when a number of different behaviour patterns competed for a single output pathway.

The exact model used was based on the observation that some behaviour patterns in zebra finches occur in bouts which tend to be of a typical length and at intervals which are also more or less regular. This suggests a cyclical underlying process. The simplest model to account for this is one in which the level of causal factors for a particular act oscillates between start and stop thresholds, falling during performance and rising during non-performance. Models of this sort are commonly used by those interested in feeding behaviour (*e.g.*, BOOTH & TOATES, 1974; GEERTSEMA & REDDINGIUS, 1974) as a possible mechanism underlying meals and the gaps between them. Such models, dealing as they do with only one behaviour pattern, can of course become very sophisticated, introducing many parameters, variables and nonlinearities based on physiological and behavioural data in an effort to achieve a realistic simulation. The model used here does not involve such complications because it has a less ambitious aim: to take a first step towards understanding the influence which different behavioural systems may have on one another when they are forced to compete for expression. It is therefore essential to keep the individual systems simple so that their output in the absence of competition can be easily understood and compared with that which occurs when competition is introduced. The earlier model with which it has most similarity in aim is that described by LUDLOW (1976), although it was developed independently and has a quite different structure. LUDLOW was interested in simulating the interactions between different behavioural systems in aphids. His model was based on each activity having an underlying centre which was excited by internal and external factors and had inhibitory connections with all other centres, the strength of the inhibition on it depending on the degree to which they were excited. The activity which was performed was that controlled by the centre with the highest output; this dominant centre fatigued when active, so that its inhibition on other centres declined until eventually one of them became dominant. This model is therefore quite different in construction from one involving start and stop thresholds, such as that explored here, but it has the similar aim of attempting to shed light on the interactions between systems. Another feature which it has in common with the present model is that its output is surprisingly complicated.

Computer simulation is a useful source of hypotheses about behaviour, and is ideally suited for studying the competition between several acts for expression. The model described here is a very simple one, the assumptions and parameters of which were kept to a minimum, even though this means that its output lacks many of the features of real behaviour. It is, however, instructive to see just what features do emerge from a simple model for several reasons. First, it may indicate what additional or different assumptions would be required to achieve a more realistic model of behaviour. Second, as is the case here, it may transpire that aspects of the organisation of behaviour, previously thought to require complex assumptions, may emerge without them. Third, features of the output may provide hypotheses for testing against the behaviour of animals, the results of which testing will in turn reflect on the validity of the assumptions. Thus the combination of simulation and experiment may lead to models which are increasingly sophisticated and realistic.

II. THE MODEL

The model was endowed with six behaviour patterns, only one of which could be performed at any time. Five of these competed for the output and the sixth was a residual category, shown when none of the others were being performed. Each of the competing behaviours had a level which moved down when it was being performed and up when it was not. These levels were initially set at between 1 and 0, and 1 was labelled as the "start threshold" and 0 as the "stop threshold". Figure 1 shows how the level of a single behaviour pattern would have changed had it not been in competition with any other for performance. During non-performance it rises till the start threshold is reached, it then falls as it is performed until it reaches the stop threshold. It thus takes place in bouts of fixed length at fixed intervals.

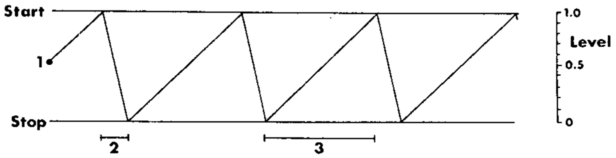

Fig. 1. Diagram illustrating how the level of a single behaviour pattern would oscillate between the start and stop thresholds if it did not have to compete with other acts. In the simulations, three parameters were set for each behaviour pattern: (1) Starting level; (2) Performance time; (3) Recovery time. The cycle length referred to in the text is the sum of performance time and recovery time.

Three parameters were set for each of these five competing behaviour patterns:

1. *Starting level.* Each behaviour was given a different starting level, though all were between 1 and 0. The levels were arbitrarily chosen and checks were made to ensure that they did not influence the output. Because all these levels at the outset were beneath the start threshold, the residual category was performed until one of them had climbed to that threshold.
2. *Performance time.* This sets the number of time units in each cycle for which the behaviour pattern would be performed if uninfluenced by others. This quantity determines the rate at which the level declines from 1 to 0 during performance.
3. *Recovery time.* This is the time taken for the level of a behaviour pattern to recover from 0 to 1. It thus determines the rate of recovery during non-performance. The addition of recovery time and performance time gives the *cycle length* which each behaviour pattern would show if uninterrupted by others. For many of the results to be discussed cycle length is a more useful measure than recovery time.

The performance and recovery times used in the initial simulations were chosen with various features of zebra finch behaviour in mind. The time units used, though arbitrary, were regarded as being seconds (and will be referred to as such) so that reasonable parameters for feeding would be cycle length 1,800 and performance time 105, giving a recovery time of 1,695. Behaviour pattern 4 (BP4) was endowed with these characteristics. In line with the pattern of ruffling in zebra finches, it was determined that BP5 should occupy a single time unit about once every 5 min. It was given a performance time of less than 1 (0.9) to ensure that its level fell from above the start threshold to beneath the stop threshold in the single unit for which it was performed. Its cycle length was set at 300 but, because of the low level to which it fell on performance, its realised cycle length was 333 seconds (300/0.9). The other three competing acts were loosely based on the locomotion (BP1), song (BP2) and preening (BP3) of zebra finches. A realistic performance time could be set for these on the basis of the time per hour for which they are normally shown, but cycle length had to be chosen more arbitrarily: the figures selected initially are shown in Table 1. These figures were such that, in this first set of simulations, the five competing acts occupied, on average, 2,461 time units in every 3,600 (68.3% of the time). The remaining time units were occupied by the residual category (BP6). As Table 1 shows, the numbers assigned to the five competing acts were such as to place them in order of diminishing performance time or percentage time performed, BP1 occupying the most time and BP5 the least.

Each simulation lasted 36,900 times units. The first 900 were discarded as likely to be strongly influenced by the starting levels chosen. In each time unit the computer selected the behaviour pattern to be shown, lowered its level and raised that of the others, and then passed to the next time unit. The behaviour to be performed was, quite simply, that which had the highest level, except that a bout could not be initiated unless the level was above the start threshold. Once initiated, the bout continued until either the level for that act had fallen below the stop threshold or that of another act had risen above the start threshold. If, as could happen in some later simulations, the level of more than one behaviour pattern was above the start threshold, that with the highest level was selected to be performed.

Each simulation was split into two sections of 18,000 time units for which separate print-outs were obtained. This enabled a check to be made that the output was stationary. The basic analyses provided by the print-outs were:

(i) A transition matrix showing the first order sequences with which acts followed each other.
(ii) Plots of bout lengths and gap lengths for each behaviour pattern in the form of log survivor functions. Bout and gap lengths should follow a negative exponential distribution if the probability of terminating remains constant. Plotted as a log survivor function such a distribution gives a straight line, so that bout and gap length distributions plotted in this way can be easily compared with this expectation.
(iii) A statistical test (Kolmogorov-Smirnov one-sample test) to check whether the bout and gap lengths departed significantly from the expected negative exponential distribution.
(iv) Pearson correlation coefficients for the relationship between the lengths of bouts and those of the gaps before and after them.
(v) An intensity function plot to indicate the extent to which each behaviour pattern tended to occur cyclically. For this treatment the data were condensed by massing the output for each set of 60 time units (the plots can therefore be regarded as dealing with 1 minute intervals rather than 1 second intervals). The function is prepared by looking at each time unit (minute) in which the behaviour pattern took place and plotting the frequency with which it also took place in the series of 60 time units thereafter. This leads to a peak at a particular lag if the pattern tends to recur at that interval (see DELIUS, 1969).

This paper will describe three sets of simulations. First, those carried out with the cycle lengths and performance times given in Table 1. Second, simulations in which performance times were either raised or lowered so that competition was intensified or weakened. Third, a set in which performance times and cycle lengths were varied.

III. SOME BASIC FEATURES OF THE OUTPUT

The sort of output provided by the model will be illustrated using simulations with the parameters shown in Table 1. One simulation was run with each of the starting levels given in the table and, as the output from each simulation was split in two, this gave results separately for each of six periods of 18,000 time units. The results of these were very similar to each other suggesting, first, that the starting levels chosen did not materially affect the output and, second, that the output was stationary, the first half of each simulation giving similar results to the second. Various features of the output can therefore be considered with reference to all of these simulations.

TABLE 1

Parameters used for the first set of simulations

Behaviour pattern	1	2	3	4	5	6
Performance time	700	360	300	105	1	—
Recovery time	1100	2040	3300	1695	332	—
Cycle length	1800	2400	3600	1800	333	—
% time performed	38.9	15.0	8.3	5.8	0.3	31.7
Starting (i)	0.75	0.85	0.90	0.80	0.95	
levels (ii)	0.95	0.85	0.80	0.90	0.75	
used (iii)	0.50	0.30	0.20	0.40	0.10	

(1) Sequences.

Table 2 gives a transition matrix from the massed results of these simulations showing the number of times that each behaviour pattern followed each other one. It is clear from this that the patterns do not succeed each other randomly but that certain sequences are more frequent than expected by chance. As the only influence that the patterns have on each other is a competitive one, this may seem surprising. However, some of the relationships are easily explained. The most obvious feature is that BP5 is nearly always succeeded by BP6. This is because the performance time of BP5 is only 1 second. It can only start when it reaches the start threshold and always ceases 1 second later. This means that it will give way to the residual category unless one of the other patterns has crossed the start threshold during that second. BP4 can also be followed by BP6. Again, BP4 has a low performance time, so that it can sometimes be completed before it is interrupted by another act crossing the start threshold, and in this case it gives way to BP6.

This simulation gives rise to sequences of patterns which diverge markedly

TABLE 2

Matrix of transitions between the six behaviour patterns massed from the three runs of the first simulation

		Following behaviour pattern					
		1	2	3	4	5	6
Preceding behaviour pattern	1	—	63 (34.6)	51 (32.3)	84 (58.2)	168 (114.8)	0 (126.1)
	2	54 (34.0)	— —	15 (8.0)	9 (14.4)	38 (28.4)	0 (31.2)
	3	38 (30.9)	7 (7.8)	— —	13 (13.1)	25 (25.8)	25 (28.4)
	4	87 (58.6)	15 (14.8)	13 (13.1)	— —	75 (49.0)	0 (53.8)
	5	1 (114.5)	2 (28.9)	1 (27.0)	0 (48.5)	— —	320 (105.1)
	6	185 (126.3)	31 (31.8)	31 (29.7)	82 (53.5)	18 (105.6)	— —

(Expected values in brackets are based on the assumption of statistical independence).

from independence. Further, in some of these cases the sequences found are strongly asymmetrical: for example, BP5 → BP6 occurs much more than BP6 → BP5, which might be taken as evidence that the first behaviour pattern in some sense causes the second. The only sense in which this is true here is a disinhibitory one: BP5 tends to interrupt other acts and lead to BP6 by disinhibiting it. The non-randomness of the transition matrix is not, however, solely due to the influence of BP5. The matrix resulting from a simulation in which this pattern was omitted also gave rise to divergent observed and expected figures ($\chi^2 = 40.59$, 11 d.f., $p<.001$).

(2) Bout organisation.

Were it not for competition, each behaviour pattern considered here would occur for a fixed period at regular intervals, but once competition is introduced the patterns tend to be interrupted before completion. Log survivor functions for five of the patterns are given in the second column of Fig. 2 (the results elsewhere in this figure will be referred to later). Of the competing patterns BP2 and BP3 come closest to following a negative exponential distribution, their plots being approximately straight. Only in the cases of BP4 and BP5 did bouts occur of the full length set by the performance time. The typical bout length of these acts arises because their performance times

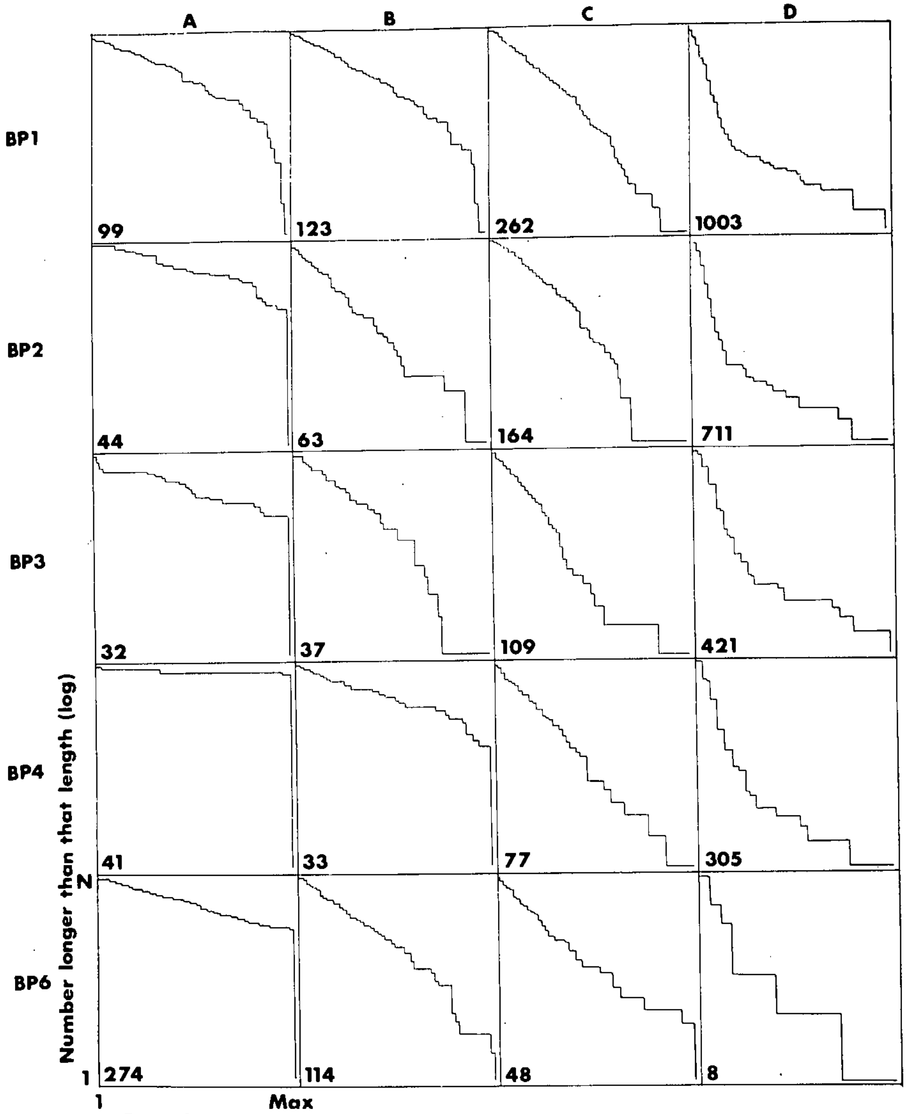

Fig. 2. Log survivor functions of bout length distributions shown by five behaviour patterns in simulations involving four different degrees of competition. These are: A. relaxed competition (plots based on a run of 72,000 time units); B. original level of competition (36,000 time units); C. increased competition (18,000 time units); D. intense competition (9,000 time units). The simulations were run for different numbers of time units to obtain adequate numbers of bouts for plotting. BP5 is not included as its bouts were always one time unit in length. The scales vary between the plots: in each case the ordinate extends from 1 to N and the abscissa from 1 to the maximum bout length recorded. The plots thus all start in the upper left corner and finish in the lower right, differences between them being in the route taken between these points. The number of bouts (N) on which each plot is based is given in the lower left corner of each box.

were shorter than those of other acts and they were therefore more likely to fall to the stop threshold without interruption. In BP5 all bouts were of 1 second duration, and 8 out of the 33 bouts of BP4 shown in Fig. 2 were 106 seconds long, so giving its log survivor function a convex form. The plot for BP1 also shows a tendency to be convex, but this is not because its level fell to the stop threshold giving many bouts of the performance time set. It seems to arise because its bouts are terminated prematurely by BP5 and, as this act occurs regularly, they cannot achieve a length greater than the interval between two acts of BP5.

The form of the distribution of gaps between bouts was the same as that for bouts for all the five competing behaviour patterns: all gaps for BP5 were 332-333 seconds long, gaps between bouts of BP4 clustered at around 1711-1712 seconds, while the gaps between bouts of the other patterns were more nearly negative exponential in distribution. This identical bout and gap organisation occurs simply because the time taken for an interrupted act to return to the start threshold once more is entirely dependent on the level beneath the start threshold from which recovery starts. For all the competing patterns the correlation between bout length and that of the gap after is therefore a perfect one (see Table 3). On the other hand, the correlation between bouts and the gaps before them is low, as the length of the preceding gap can give no prediction of how long the next bout will go on before it is interrupted.

TABLE 3

Correlation coefficients for the relationship between bout lengths and the lengths of the gaps before and after them for the behaviour patterns in the first simulation

Behaviour pattern	Correlation with gap before	Correlation with gap after
1	—.18 to +.25	1.0
2	—.16 to +.23	1.0
3	—.47 to +.17	1.0
4	—.30 to +.31	1.0
6	+.14 to +.35	—.77 to —.49

BP5 is excluded as all bouts of it were the same length, as were the gaps between them. The figures given are the extreme values from six different runs.

Considering just these competing patterns, the conclusion is clear. The shorter the performance time allotted to an act, the more likely is its regular pattern of occurrence to show through in the competitive situation. Those patterns with longer performance times either show no tendency for bouts or gaps to be of a typical length (BP2 and BP3), or show a tendency towards a typical length which differs from the performance time set and is determined by their interaction with other behaviour patterns (BP1).

The organisation of BP6 differs from that of the others, as one might expect given that its pattern is determined purely by exclusion. Its bout lengths are randomly distributed (see Fig. 2), but the gaps between bouts tend to be of typical length, around 250-330 seconds long. As with BP1, this feature stems from interaction with BP5. Acts of BP5 occur at regular 332 second intervals and are nearly always followed by a bout of BP6. Brief bouts of BP6 therefore tend to be followed by gaps of rather less than this duration, and gaps longer than 332 seconds occur rarely. This constraint on the occurrence of BP6 also means that longer bouts of it are followed by shorter gaps, giving the negative correlation with following gap shown in Table 3. On the other hand, unlike the competing patterns, this behaviour tends to show a positive correlation with gap before. This result is probably to be expected for a residual category excluded by other patterns all showing correlations between bout length and the gap after, for gaps between bouts of BP6 are made up of bouts of the other patterns. This is obvious in the simpler situation of two competing acts: gaps in one are bouts of the other, so that the same result is obtained by correlating one with preceding gap as would be if the other was correlated with following gap.

(3) Cycles.

All the behaviour patterns, with the exception of BP6, would show cycles of occurrence were it not for competition, the cycle length being determined by that initially set. The sample intensity functions shown in Fig. 3 indicate that BP4 and BP5 do show such cycles, of 30 minutes and 5-6 minutes respectively, as might have been expected from the fact that they showed typical bout and gap lengths. BP6 also shows a 5-6 minute cycle, due to its almost invariable occurrence after BP5.

The plots for the other three behaviour patterns give no evidence of cycles of the specified length. For BP2 and BP3, peaks in the intensity functions, where present, tended to be in different places in each of the simulations, and a peak at one lag was not necessarily accompanied by peaks at multiples of that lag. There is thus no evidence to suggest that the simulations led to consistent cycles in those behaviour patterns. However, in BP1, the six runs consistently produced peaks at 11, 22 and 33 minutes: these data have been massed and are plotted in Fig. 4. The fact that this cycle length is exactly twice that of BP5 suggests a reason for it. BP1 frequently follows BP6, which in turn occurs after BP5 (see Table 2). If the bout of BP1, once started, continues until it is interrupted by the next event of BP5, it will have lasted about 250 seconds. It will then take about 400 seconds to recover from the level it has reached (see Table 1), so that it will show a cycle of about 11 minutes. This pattern is partly set by the pattern of occurrence of BP5 and partly by the relationship between performance time and recovery time in BP1, which is such that gaps are rather longer than the bouts which precede them. A bout of this act therefore takes place in every second interval between events of BP5, giving a cycle length very different from that set.

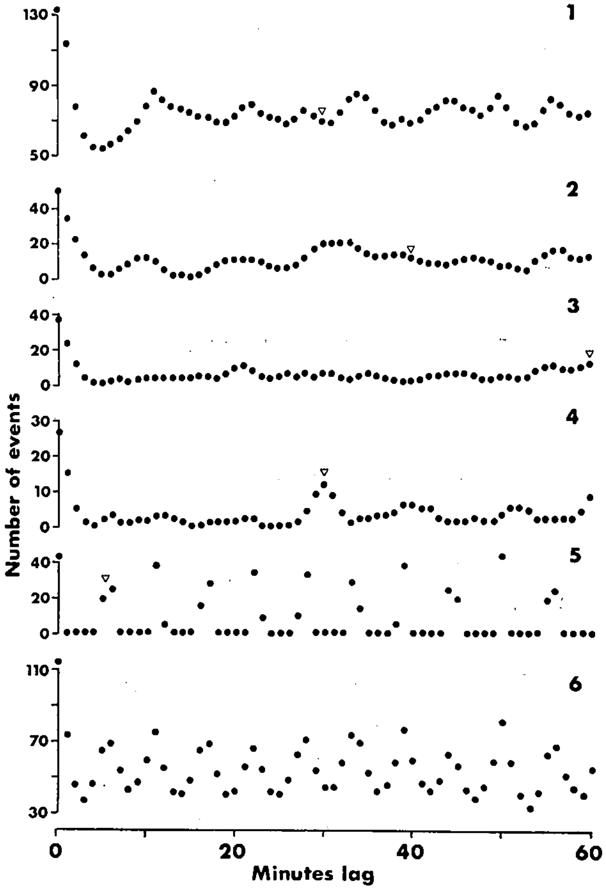

Fig. 3. Intensity functions for the six different behaviour patterns, labelled 1-6, based on one run of 18,000 time units. Pointers indicate the cycle length which each was given: peaks in the plots should appear at this lag and multiples of it if the output also showed this cycle length.

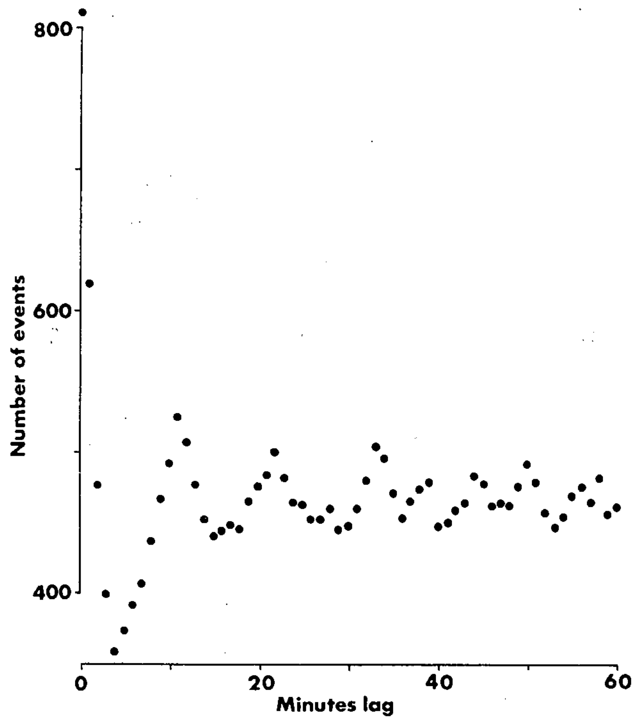

Fig. 4. Intensity function for BP1 based on data from three full simulations with different starting levels (108,000 time units).

(4) Conclusion.

Although some features of these simulations were only to be expected from the rules used to determine transitions (*e.g.* the correlation between bout lengths and the gaps following them), the output showed greater complexity than was anticipated. Despite the fact that the competition between different acts was not great, the competing acts being performed for a total of only 41 minutes in each hour, the organisation which resulted showed that they had a strong impact on each other. In particular, the interruptive influence of BP5, which had a very short cycle length and performance time, had a marked effect on the temporal patterning of the other acts. A comparison between features of the output of the model and the behaviour of zebra finches will be made in the discussion.

IV. THE EFFECT OF VARYING THE AMOUNT OF COMPETITION

As mentioned above, competition was not strong in the initial simulations and the residual category was therefore shown for quite long periods of time. To assess the effect which varying the degree of competition would have, three other simulations were run, using the same cycle lengths as before but different performance times. As Table 4 shows these were varied in the same proportion for BP1, BP2, BP3 and BP4, while the very low performance time of BP5 remained unaltered. The variations were designed so that, in each series of 3,600 time units, the competing acts would occupy about 1,232 (34.2% of the time), 3,411 (94.8%) and 3,600 (100%) in the three different simulations. In the first and second of these the competition is thus relaxed and increased respectively; in the third it is very strong. The most interesting aspects of the results of each will be discussed in turn: log survivor functions for the bout length distributions found in each case are shown in Fig. 2 alongside those obtained in the original simulations.

TABLE 4

Parameters used for simulations in which competition was varied

Behaviour pattern		1	2	3	4	5	6
Starting level		0.95	0.85	0.80	0.90	0.75	—
Cycle length		1800	2400	3600	1800	333	—
Performance times	(1)	350	180	150	50	1	
	(2)	971	500	416	146	1	
	(3)	1023	529	440	155	1	
% time performed	(1)	19.4	7.5	4.2	2.7	0.3	65.9
	(2)	53.9	20.8	11.6	8.1	0.3	5.3
	(3)	56.8	22.0	12.2	8.6	0.3	0.0

Note: The starting levels and cycle lengths used were the same for all three simulations, but the performance times were varied to give (1) Relaxed competition, (2) Increased competition and (3) Intense competition compared with that involved in the first simulation (see Table 1). Recovery times are not shown: these are simply the difference between cycle length and performance time.

(1) Relaxed competition.

The effect of this is to give fewer, longer bouts for all acts except BP5 and BP6. BP5 occurs as single events with the same frequency as before. BP6 shows more bouts which are of longer mean length than before. It also shows typical bout lengths, many of its bouts being 332 seconds long, indicating that it often occupied the whole interval between two events of BP5. These bouts cause the sharp drop at the end of the log survivor function for it in Fig. 2. The other acts also show typical bout length, in BP1 with its long performance time, this is due to interruption by BP5 as before; in the other cases it is because bouts of the full performance time set could often occur without interruption.

As before, BP4 and BP5 showed clear cycles of the length fed in. There was also a suggestion of a 60 minute cycle in BP3, but neither BP1 nor BP2 showed clear cycles, the competition being sufficient to override these. The 5 minute cycle previously found in BP6 was no longer present, this pattern occurring more frequently than before and not simply when disinhibited by BP5.

(2) Increased competition.

This led to many more bouts of BP1, BP2, BP3 and BP4 (see column 3 of Fig. 2). In none of them were bout lengths or gap lengths typical, nor did any of them show cycles. The greater competition than was present in the original simulations had thus removed the tendency for BP4 to show cycles and bouts and gaps of typical length. As in the original simulations, BP6 showed cycles 5-6 minutes long, with bout lengths randomly distributed but typical gap lengths. The lengths of bouts did not, however, correlate negatively with the following gap as they had done previously. This is probably because BP6 was not always shown immediately after BP5: on about 10% of occasions the level of another pattern rose above the start threshold during the single time unit for which BP5 was performed. Hence the gaps after bouts of BP6 were in some cases greater than 332 seconds long.

(3) Intense competition.

In this situation the levels of all the competing behaviour patterns rise slowly to the start threshold and then oscillate about it, switching rapidly from one to another. The log survivor functions are concave (Fig. 2) because the output is non-stationary, with some longer bouts at the start of the simulation, but only short bouts thereafter. The simulation was only run for 9,000 time units, but the number of bouts obtained was still very much larger than the figures for earlier simulations for BP1-BP4. The competition was such that BP6 was virtually absent, except for very occasional brief bouts following BP5. Only BP5 continues to show a cycle, and the other patterns do not show typical bout or typical gap lengths either, though bout lengths continue to be perfectly correlated with the lengths of the gaps after them. The only situation in which these correlations cease to be perfect is where the computer has more to do than time allows (*i.e.*, where the competing acts are set to occupy more than 3,600 units in each 3,600). In this case more than one pattern can be above the start threshold at the same time, and the fixed relationship between bouts and the gaps which follow them no longer holds.

V. VARIATION OF CYCLE LENGTHS AND PERFORMANCE TIMES

In the original simulations the five competing acts were given cycle lengths of 1,800, 2,400, 3,600, 1,800 and 300 seconds and were performed for 38.9%, 15.0%, 8.3%, 5.8% and 0.3% of their cycle lengths respectively. Under the conditions of competition used, the only ones which showed typical bout and gap lengths and the same cycle length as fed in were BP4 and BP5. To clarify the reasons for this, three further simulations were run. These

TABLE 5

The results of simulations in which performance times and cycle lengths were varied

Behaviour pattern	1	2	3	4	5	6
Starting level (all simulations)	0.75	0.85	0.90	0.80	0.95	
1.						
Cycle length	2400	300	1800	3600	3600	
Performance time	936	45	144	209	12	
% time	39	15	8	5.8	0.3	32
Typical bout length?	—	+	+	—	+	
Cycles?	—	+	+	+	+	
2.						
Cycle length	3600	1800	300	2400	2400	
Performance time	1400	270	24	140	8	
% time	39	15	8	5.8	0.3	32
Typical bout length?	—	—	+	—	+	
Cycles?	—	—	+	—	+	
3.						
Cycle length	300	3600	2400	300	1800	
Performance time	118	540	192	17	6	
% time	39	15	8	5.8	0.3	32
Typical bout length?	+	—	—	+	+	
Cycles?	+	—	—	+	+	

The parameters used in each of the three simulations are shown. The symbols indicate whether or not these resulted in typical bout lengths or cycles of the length set by the input.

used the same cycle lengths and degree of competition as yielded by the figures in Table 1, but varied the performance times systematically so that all the above percentages were tried for each cycle length. The parameters used and whether these resulted in typical bout lengths or cycles of the expected length are summarised in Table 5.

This table confirms that typical bout lengths and cycles of the length fed in occur when the performance time of a behaviour pattern in each cycle is brief. They will thus appear if cycle length is long only if performance time is a low percentage of it (0.3% and, in some cases, 5.8%); they invariably appeared when cycle length was short (300 units). Clearly, behaviour patterns which are only shown briefly in each cycle, regardless of the cycle length or time per hour for which they are shown, are the ones whose intrinsic pattern will show through. They are less likely to be interrupted during performance by other behaviour patterns, simply because their performance time is low. With low cycle lengths performance time is bound to be low but, in addition, as the influence of BP5 on the results of all the previous simulations shows, patterns with very short cycle lengths are those most likely to interrupt others and impose their own organisation on them. The form of the output thus depends on both the performance times and cycle lengths used, as well as the degree of competition.

VI. DISCUSSION

In this section I shall summarise the behaviour of the model, make comparisons with that of the zebra finches on which it was based and suggest lessons which may be learnt from it.

The main features of the output of this simple model are as follows:

(i) Competition between acts for a single output pathway can generate a first-order matrix of transitions between them which is non-random. Some types of transition are more common than would be expected by chance in both directions (A→B and B→A, *e.g.* 1→4 and 4→1 in Table 2); in other cases the transition is very much more common in one direction than in the other (*e.g.*, 5→6 in Table 2).

(ii) For competing behaviour patterns the form of the distribution of bout lengths was the same as that of gap lengths (the shape of the plots for BP1-BP4 in Fig. 2 would be identical if these were for gaps rather than bouts). This shape is convex where the competition is not strong, both bouts and gaps tending to be of a typical length. As competition becomes stronger, mean bout length and mean gap length become shorter and these lengths tend to follow a negative exponential distribution. Concave distribution occurs only where competition is extreme, and then only because non-stationarity has been introduced.

(iii) Unless competition is so strong that more than one behaviour pattern can be above the start threshold at the same time, bout lengths of the competing acts show a perfect correlation with the lengths of the gaps which follow them. In the case of the residual category the correlation is greater between bout length and preceding gap.

(iv) Bouts and gaps of typical length and cycles of the length with which a behaviour pattern was endowed occur most when competition is not strong. They are most frequently found in behaviour patterns in which performance time is shortest in each cycle. They do not depend on cycle length or the time per hour for which the pattern is set to be performed. In some circumstances behaviour patterns may show cycles which are not of the preset length (*e.g.*, BP6 in Fig. 3; BP1 in Fig. 4). These cycles arise through the interactions between behaviour patterns and, in particular, the interruptive influence of patterns with short cycle lengths.

Some features of this output are reminiscent of aspects of zebra finch behaviour and may indicate that competition alone can account for these, although of course the way in which competition occurs in animals is unlikely to be the same as that incorporated in the model. The following similarities are worth noting:

(i) In zebra finches, as in other species which have been examined, behaviour patterns do not follow each other at random. The fact that this is also true of the output of the model cautions against assuming that statistical dependencies in a transition matrix indicate causal dependencies between the acts included in it. The discrepancy between the observed and expected figures in Table 2 is largely, though not entirely, due to the influence of BP5. This pattern was modelled on ruffling in zebra finches and it is interesting to note that, like BP5, ruffling is a pattern which tends to be followed by a different act from that which preceded it.

(ii) The two patterns which most often show cycles in zebra finch behaviour are feeding and ruffling, and this is also true of the two patterns which were given their characteristics in the simulations (BP4 and BP5). The fact that cycles were not so often found in song, locomotion and preening in zebra finches, as is true of BP1, BP2 and BP3, may be simply because these types of behaviour have longer intrinsic cycle lengths and that competition stops these from being discovered in the behaviour of the animals.

(iii) Zebra finches spend longer periods resting in the afternoon than in the morning, a situation likely to be equivalent to the relaxation of competition between other behaviour patterns. Bouts of feeding have been found to be longer in the afternoons (SLATER, 1974a), and this fits in with what simulation involving little competition would predict.

(iv) As mentioned earlier, bouts of song in zebra finches tend to correlate with the lengths of the gaps which precede them: if the model of competition proposed here is a realistic one, this might suggest that song is more like the residual category than one of the competing acts (see correlations in Table 3). This would fit in with the argument presented by SLATER & OLLASON (1972) that song is produced largely when gaps in other behaviour allow it.

There are, of course, many facets of zebra finch behaviour which the model does not mimic, and it was not set up with the idea that it should resemble finches in detail. Perhaps the most obvious discrepancy is in the form of the gap and bout length distributions found. Unless competition was relaxed, the model generated distributions which were close to negative exponential, as one would expect if bouts and gaps showed a constant probability of terminating. Unlike this, the feeding and preening of zebra finches tend to show a surplus of short bouts and short gaps, so that the log survivor functions of bout and gap lengths are concave in form. Thus, though bout and gap length distributions are similar in form to each other in both cases, in real behaviour the probability of continuing rises as length increases, whereas in the simulations it tends to remain constant. This discrepancy might arise because of any one of a number of factors which may affect real behaviour, yet of which no account is taken in the simulations. Some of these possibilities are as follows:

(i) Positive and negative feedback. The levels of the competing acts in the simulations rise and fall linearly between the start and stop thresholds. Nothing equivalent to positive feedback occurs and negative feedback has no influence until it switches in abruptly at the stop threshold. This is unlikely to be realistic. The first few acts of a particular type may have a positive feedback effect so that bouts are more likely to terminate early than they are after this has come into operation (WIEPKEMA, 1971). Negative feedback influences probably become progressively stronger as the length of a bout increases. The exact relationship between these positive and negative influences is likely to have a complex effect on the probability of a bout terminating: to incorporate this in the simulations would involve making the level of each act change in an equally complex manner rather than linearly.

(ii) External influences. The probability of a particular behaviour pattern may be greatly affected by the presence or absence of appropriate external stimuli. The simulations take no account of this, the probability of each of the stimulated acts depending simply on the rules of competition and on its level, as determined by its past history.

(iii) Interactions between acts. The probability of one behaviour pattern may be influenced by the performance of another. No such effects are involved in the simulations, except for the disinhibitory influence which acts with short performance times have on BP6.

(iv) Fluctuation in levels. In the simulations the levels change according to set rules and are precisely measured. A more noisy pattern with superimposed random fluctuations might be more realistic.

Any of the above influences might lead to complex changes in the level of the causal factors for different acts and might, for example, lead to two patterns being of very high priority simultaneously. If competition such as that postulated here then determines which is shown, the two would tend to alternate with each other rapidly (as happens in the simulations when two patterns are at or above the start threshold). This would lead to the occurrence of many short bouts when they were competing strongly, the competition dying away as their levels fell beneath the start threshold. Changing levels of competition, which could arise from the above influences, might therefore lead to two features which are typical of zebra finch behaviour but not of the output of these simulations: a surplus of short bouts and rapid alternation between pairs of behaviour patterns.

The extent to which this model bears any relation to real behaviour must rest on observations and experiments in the future as well as on its ability, or lack of it, to generate output similar to the known behaviour of animals. It makes a number of predictions which require testing. For example, if competition is relaxed, bout lengths and gap lengths tend to become typical and cycles are more likely to be found. Bouts also tend to be longer, though there are fewer of them. Collection of data from animals which are not pressed for time, as for example zebra finches watched late in the day, would indicate the extent to which these predictions are realised for different patterns of behaviour. By contrast, when competition is increased, the model predicts the occurrence of many short and rapidly alternating bouts of different behaviour patterns. Again, this prediction may be tested by observing animals which have been deprived of the possibility of performing different acts.

Whether or not a more sophisticated model based on the present one would produce behaviour similar to that of a real animal is, at this stage, a matter for speculation. The two most important conclusions from these simulations lie in directions only loosely related to their realism. First, the model shows how competition, even when not intense, could modify the pattern of occurrence of a particular act to the extent that any rules intrinsic to it are difficult to discover. Second, the model demonstrates that the simulation of behaviour, based on a few simple rules, may generate surprisingly complex output. This may give reason to hope that the complexity of animal behaviour may also be attributable to relatively simple rules and that further study will bring the most important of these to light.

SUMMARY

This paper explores the properties of a simple model for the interactions between a number of behaviour patterns competing for a single output pathway. In the model, the level of causal factors for each of five competing acts oscillates between start and stop thresholds, rising during non-performance and falling during performance. A sixth, residual, category is shown when none of the other behaviour patterns has been initiated by its level reaching the start threshold. The characteristics of each of the competing acts were chosen, as far as possible, to be similar to those of behaviour patterns previously studied in zebra finches.

Were it not for competition, each of the competing acts would have shown cycles in its occurrence with bouts of fixed length taking place at fixed intervals. Competition led several of them to show no cycle in occurrence and to have bout lengths which followed a random, negative exponential, distribution. Only acts with low intrinsic bout lengths exhibited their natural patterns under conditions of competition, the extent to which they did so depending on the degree of competition. As competition became stronger, bout and gap lengths became shorter and, with intense competition, the output was non-stationary. The influence of competition was, however, more than a disruptive one: under some circumstances behaviour patterns showed clear cycles of a different length from those with which they had been endowed, and the matrix of first-order transitions between acts also diverged from randomness.

The output of the simulations is discussed in relation to the behaviour of zebra finches and several points of similarity are noted. For example, feeding and ruffling in the finches, like the two simulated acts based on their characteristics, are the behaviours most likely to show a regular pattern of occurrence. Failure to find this in the other patterns of zebra finch behaviour may be because competition hides their intrinsic pattern rather than because they are not scheduled to occur regularly. While the model used is a very simple one, and there are many ways in which it is unrealistic, it demonstrates the marked influence which competition can have on the output of individual systems, so making it hard to discover any pattern intrinsic to those systems. Simple as it is, the model leads to a complex output and a number of testable predictions: it highlights the point that complexity is bound to arise when several acts compete for expression regardless of how simple are the mechanisms underlying each individual behaviour pattern.

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ZUSAMMENFASSUNG

Diese Arbeit untersucht die Eigenschaften eines einfachen Modells zur Feststellung der Wechselwirkung zwischen einer Anzahl von Verhaltensmustern, die miteinander für einen Ausgang konkurrieren. In dem Modell schwankt das Niveau der Kausalfaktoren für jede der fünf konkurrierenden Handlungen zwischen Schwellen, die Anfang und Ende bestimmen; es erhöht sich während des Ausbleibens und fällt während der Ausführung der Handlung. Eine sechste Restkategorie gilt für alle Fälle, in denen keine andere Verhaltensweise ausgelöst wird. Die Eigenschaften der konkurrierenden Grössen des Modells wurden gemäss der Verhaltensmuster, die bei Zebrafinken beobachtet wurden, ausgewählt, und sind diesen so weit wie möglich ähnlich.

Wäre es nicht ein Wettbewerb, so würde jede der konkurrierenden Handlungen zyklisch in Gestalt von regelmässig auftretenden Stössen bestimmter Länge ausgelöst worden sein. Die Konkurrenz führte dazu, dass sich bei einigen kein Zyklus im Auftreten zeigte und dass die Länge der Stösse von zufälliger (negativ exponentieller) Ausdehnung war. Nur Handlungen mit kürzerer Eigenperiodizität wiesen ihre natürlichen Muster unter Konkurrenzbedingungen auf, wobei das Ausmass vom Grad der Konkurrenz abhing. Sobald sich der Wettbewerb verstärkte, wurden Stösse und Zwischenräume kürzer, und bei intensivem Wettbewerb waren die Ergebnisse veränderlich. Der Einfluss des Wettbewerbs erwies sich jedoch als nicht nur zerstörend: Unter einigen Bedingungen zeigten die Verhaltensmuster zyklische Neubildungen, die sich zeitlich ganz klar von den gegebenen Zyklen unterschieden, und die Matrix der Übergangszeit zwischen den Handlungen erwies sich ebenfalls als nicht zufällig. Die Ergebnisse des Modells wurden bezüglich des Verhaltens der Zebrafinken untersucht, und verschiedene Ähnlichkeiten konnten festgestellt werden. Zum Beispiel sind die Futteraufnahme und das Aufplustern der Zebrafinken Verhaltensweisen, wie die beiden simulierten Handlungen die auf den Charakteristiken basieren, die am wahrscheinlichsten ein regelmässiges Auftretensmuster zeigen. Das Fehlen eines Musters bei anderen Verhaltensweisen der Zebrafinken rührt wahrscheinlich davon her, dass ein Wettbewerb eher die Eigenperiodiziteit verbirgt, als dass kein regelmässiges Muster unterliegen würde. Obwohl das angewandte Modell einfach und in vieler Hinsicht unrealistisch ist, veranschaulicht es doch deutlich die

Beeinflussung, die der Wettbewerb auf die Handlungen bestimmter Systeme ausüben kann, derart, dass die ursprünglichen Muster, die diesen Systemen eigen sind, schwer festzustellen sind. So einfach wie das Modell ist, führt es doch zu einer komplexen Ausgangsgrösse sowie zu einer Anzahl von prüffähigen Voraussagen: Es veranschaulicht, dass Schwierigkeiten auftauchen, wenn verschiedene Handlungen sich bemühen Ausdruck zu finden; ungeachtet der Tatsache, dass der Mechanismus der jedem einzelnen Verhaltensmuster unterliegt, recht einfach ist.

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ZUSAMMENFASSUNG

Eine ausführliche Untersuchung der Gesangsarten von männlichen Buchfinken wurde auf den Orkney Inseln vorgenommen. Nur ungefähr 50 Buchfink-Paare nisten dort. Diese kommen überwiegend in drei Waldgebieten vor, und nur vereinzelte Buchfink-Paare wurden in einer Anzahl von anderen Plätzen beobachtet. Tonaufnahmen von 41 individuellen Vögeln zeigen, daß der Gesang dieser Vögel ganz deutlich charakteristische Merkmale aufweist, und 16 verschiedene Gesangsarten wurden entdeckt. Einige Gesangsarten waren einem einzigen Individuum eigen, während andere Arten im Repertoire vieler Vögel vorkamen. Die meisten Gesangsarten waren auffallend häufiger in einem bestimmten Waldgebiet anzutreffen als in den anderen. Die auffallendste Abweichung innerhalb einer Gesangsart bestand in einer vielzähligen Wiederholung von Silben in einem Satz. Dies variierte bezeichnenderweise zwischen individuellen Vögeln, jedoch nicht zwischen verschiedenen Waldgebieten; die Variation innerhalb eines Individuums war ebenfalls bemerkenswert.

Die zwischen den Gesangsarten angestellten Vergleiche deuten darauf hin, wie diese im Laufe der Evolution abgewichen sind. Die wesentlichsten Veränderungen scheinen durch geringe Modifikation der Silben aufgetreten zu sein, durch Änderungen bei der Wiederholung von Silben, durch Hinzufügung oder Auslassung von Teilen und durch Neukombination von Gesangsteilen, die von anderen Gesangsarten herrühren. Ergebnisse von der Veränderlichkeit und Verbreitung der Gesangsarten sprechen gegen die Auffassung, daß diese Vogelart während ihrer Evolution einen Gesang lernt, um dem Individuum zu ermöglichen, Informationen über seine Identität, über die örtliche Lage oder über die Verwandtschaftsgruppe, zu der es gehört, weiterzugeben. Es wird stattdessen angenommen, daß das Erlernen einer Gesangsart als ein Mittel zur Erreichung einer komplexen vokalen Leistung entstanden ist, und daß die Verbreitung von Gesangsarten teilweise auf Fehler beim Imitieren des Gesangs zurückzuführen ist, und teilweise darauf, daß sich einige Individuen weiter verbreiten als andere, nachdem sie ihren Gesang gelernt haben.

made for the existence of song repertoires, and these will be discussed in more detail in relation to chaffinch song repertoires in a later paper (Slater & Ince, in prep.).

SUMMARY

A detailed study has been made of the song types of male chaffinches in the Orkney Islands. Only about 50 pairs of chaffinches nest there and these are mainly concentrated in three woods, with isolated pairs in a number of other places. Recordings of 41 individuals showed that songs fell clearly into distinct types, 16 of which were discovered. Some song types were peculiar to a single individual, while others occurred in the repertoires of many birds. Most were markedly more common in one wood than in others. The most noticeable variation within a song type was in the number of repetitions of syllables in a phrase. This varied significantly between individuals, though not between different woods; variation within an individual was also great.

Comparisons between song types suggested ways in which these had diverged during the course of cultural evolution. The main changes seem to have occurred by minor modification of syllables, by changes in the number of repetitions of syllables, by the addition or omission of sections and by the recombination of sections from different song types. Evidence from the variability and distribution of song types argues against song learning in this species having evolved because it enables individuals to transmit information about their identity or about the locality or kinship group to which they belong. Instead it is suggested that song learning arose as a means of achieving a complex vocal output and that the distribution of song types arises partly because mistakes are sometimes made in copying and partly because some individuals disperse more widely than others after song learning.

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boundaries. Another possibility is that the variability of song which arises through learning could give a measure of genetic relationship if song types are passed culturally from fathers to sons, more divergence being found between less closely related individuals. Whether such transmission does occur in chaffinches is not yet known, but the available information suggests that song could not provide an unambiguous measure of kinship because the random way in which song types are assorted between repertoires indicates that young birds learn songs from more than one individual.

Although these explanations seem implausible when viewed in relation to the current pattern of song learning in the chaffinch it is possible that one or other of them was responsible for its origins earlier in evolution even if not important at the present time. A further possibility is that song learning evolved simply because it was the most rapid and easily achieved means of obtaining song complexity in those species where this was selected for. Many bird species have very large repertoires and, in at least some of these, increased repertoire size as such seems to have been selected for through sexual selection (*e.g.* CATCHPOLE, 1977), a process likely to favour improvisation and imitation. But even in species like the chaffinch, where repertoires are small, song is a complex vocalisation with detailed structure and precise timing. Learning has a role in the development of such songs also and only amongst the simplest of vocalisations have examples been found where normal ontogeny can occur without copying (NOTTEBOHM, 1970; KROODSMA, 1977). That songs which are relatively long, diverse or detailed tend to be learnt need not imply that learning is a prerequisite if a complex output is to be achieved, but this may be the case.

Once song learning exists, for whatever reason, geographical variation and variation between individuals in a small area are almost certain to arise. This may, in turn, lead to it being advantageous for individuals to have more than one song type. That copying is normally very precise and that song falls into distinct types rather than being continuously variable, suggests that it benefits individuals to be able to match one another's output. Chaffinches certainly countersing with similar song types where possible (HINDE, 1958; SLATER, personal observation). If song development was under tight genetic control, all individuals within a population would have similar song types and thus matching would always be possible. But, given the existence of cultural transmission and the divergence that this leads to, the ability to match an intruder or neighbour with a single song type is less likely. Individuals with more than one song type will then have a greater chance of being able to match the song or songs of an intruder and thus achieve any benefits which this gives. This is, however, only one of many suggestions which have been quency of song types varying between areas but with no clear dialect boundaries. He argues, as we have done, that this results because birds learn their songs early in life and usually return to breed in their natal area, but that song types are introduced from one area to another by occasional individuals which disperse more widely.

The speed at which song types change remains a matter for speculation, although we have found marked differences in the song types recorded in a wood in Sussex on two occasions 17 years apart (INCE, SLATER & WEISMANN, in prep.). The evidence from other birds suggests that species differ strongly in this characteristic. Thus SNOW (1968) could detect no change in song types over a period of three years in the little hermit hummingbird (*Phaethornis longuemareus*), while THOMPSON (1970) found the same period to be sufficient for all song types to differ from those previously found in a population of indigo buntings (*Passerina cyanea*). The basic elements comprising the song types had become reassorted between them. The rate of change is likely to depend on how restricted the learning period is and also on whether birds use one or a number of individuals as models from which to copy. If one individual is usually used, then progressive changes might be expected from one cultural generation to another. If, however, a bird copies a particular song type from two or three other individuals which possess it, then the process would tend to be more conservative, with individual idiosyncracies less likely to pass from one animal to another. To some extent this may depend on the availability of models; common song types may be more conservative than rare ones. Chaffinches with repertoires certainly learn their different song types from more than one individual, for song types are randomly distributed between repertoires rather than being passed on in combinations as would be expected if a single model was used (SLATER & INCE, in prep.). It is not known whether learning of a single song type also involves copying from the output of more than one individual.

The above points all concern the effects of cultural transmission rather than its causes. Several reasons which might be proposed for the existence of song learning seem unlikely to apply to chaffinches on the basis of our results. The fact that the copying process is usually very faithful, together with the finding that variations in a particular song type are as marked within animals as they are between them, argues against learning having been selected for because it leads to songs which are individually identifiable. Song is also unlikely to give a clear indication of the population or area from which an individual comes because several song types exist in each locality, some possessed by some individuals and some by others, and because song types vary in how widespread they are without clearly defined dialect distinct song types in different places being linked by a series of intermediates between them (BORROR & GUNN, 1965; SHIOVITZ & THOMPSON, 1970). The results from Orkney, supplemented by those we have obtained in a large wood in Sussex, suggest that neither of these patterns is true of chaffinches, although gradual change might be apparent over greater distances. In both of these areas the frequencies of particular song types change from one place to another but without sharp discontinuities which would enable one to define dialect boundaries. The word dialect is also inappropriate because even the commonest song type in a small area does not occur in the repertoires of more than 65% of individuals (see Table 1).

Some ways in which song may change during the course of cultural evolution have come to light as a result of comparisons between the different song types within the Orkney population and between the ways in which different individuals may render the same song type. The most marked variations occur in the trill and several of the song types found had near-identical end phrases. This is the opposite of the conclusion reached by MARLER (1952), who considered the end phrase to be most variable. This difference probably stems from the fact that his analysis was carried out by ear: it is not easy to detect differences in the trill without sonagraphic analysis, whereas end phrases, where they do differ, often sound quite distinct from each other.

The most detailed previous studies of how song may change during the course of cultural evolution have been those by JENKINS (1978) on the saddleback (*Philesternus carunculatus*), by LEMON (1975) on the cardinal (*Richmondena cardinalis*) and by BAPTISTA (1975) on the white-crowned sparrow (*Zonotrichia leucophrys*). JENKINS followed the same population over several years and was able to observe cultural changes actually occurring. He concluded that 'new song forms have been shown to arise variously by change of pitch of a note, repetition of a note, the elision of a note and the combination of parts of other existing songs'. The changes which he found were thus very similar to those suggested here. On the other hand, some of the types of change described by LEMON and BAPTISTA do not appear to take place in chaffinches on the basis of the present study. Thus no examples have been found here of the copying of other species or of reordering of phrases within songs: where two song types share a phrase it tends to occur in a similar position in each. The chaffinch apears to be a species in which conformity is relatively high, song types usually changing rather little in their transmission from one individual to another and differences building up slowly. The pattern of distribution of song types seems similar to that which LEMON (1975) described in cardinals, with the frehas similarities to other song types, but this section is distinctly different. Although it may have been invented by a single bird, it is also possible that it was copied from a song type as yet unrecorded or that it evolved over several generations from, for example, T2 of song type H, with which it shows slight similarities.

Despite these changes which may take place and lead to the creation of new song types, there is no doubt that the copying process is normally very accurate. Song types B and C, for instance, are common at both Balfour and Finstown suggesting that they were not first introduced from one wood to the other in the recent past. That the form of each of these song types has remained the same in these two places suggests that a song can be passed down through several cultural generations without major alteration.

4. DISCUSSION

The results obtained in this study point to a considerable degree of complexity in the song types in chaffinches and in their distribution, even within a small area. It had originally been anticipated that each wood might have a dialect of its own, or that the same song types might be found throughout the area. The situation found is to some extent intermediate between these possibilities, with some song types more or less restricted to a particular wood while others are common in more than one wood. Several types were peculiar to only one individual, so that the total number found was large. Two main factors seem to be responsible for this distribution of song types. First, the woods are not totally isolated from one another, so that songs learnt in one wood may subsequently be sung in another. Second, a close comparison of the song types found suggests a number of ways in which these may have changed during cultural evolution. While the similarities amongst individuals singing the same song type indicate that precise copying is the norm, differences both within and between song types point to the sorts of changes which can occur and how these may lead to new types. With little movement of birds between woods after their song types are learnt, a type introduced from one wood into another may evolve to be separate over several generations in much the same way as geographical isolation encourages speciation in animals but with far greater rapidity.

Studies of other bird species in which song shows geographical variation suggest that this variation does not always follow the same pattern. In some species, nesting in more continuous habitat than the birds studied here, sharp geographical boundaries can be drawn between song types, so that clear dialect areas may be discerned (*e.g.* NOTTEBOHM, 1969; GRIMES, 1974). Another possibility is that change with distance is a gradual process, two

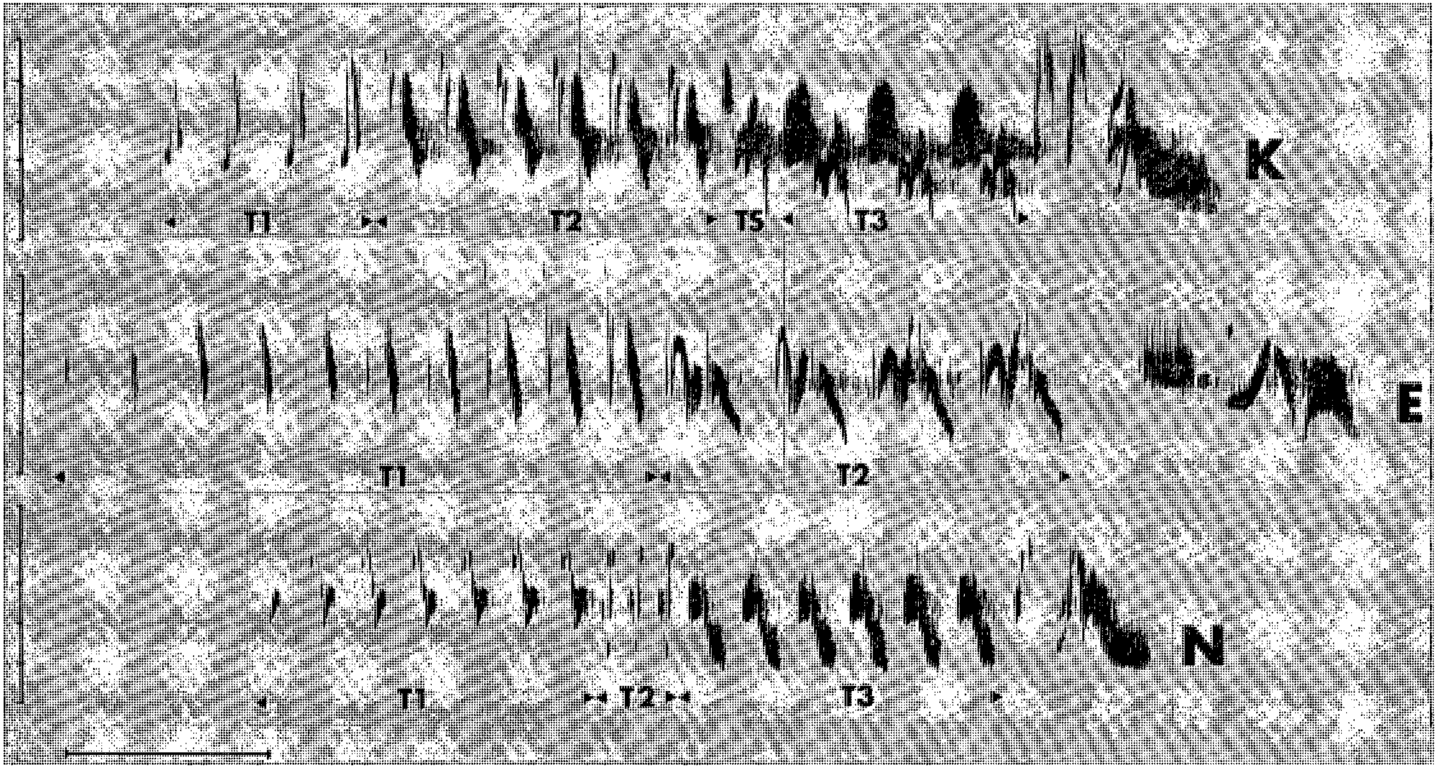


Fig. 6. Sonagrams of song types K, E and N. For further details see legend to Fig. 2.

section of the trill just before the end phrase (T2) again consists of syllables like those in the same position in type D (T3) and type G (T4). The similarity with type G goes further, however, for T1 syllables are alike in the two types and the transitional syllable between T1 and T2 in type J is clearly the same as the latter part of the T2 syllables in type G. Type J is thus a simpler version of type G with the central section missing. It is therefore probable that one of these evolved from the other.

These similarities between song types, and others which are less obvious, suggests a number of ways in which types have diverged during the course of cultural evolution. These may be summarised as follows:

1. *Minor modification of syllables.*

The distinction between types C and Y, and types B and M, is based mainly on changes of this sort.

2. *Changes in the number of repetitions of syllables.*

The similar syllables comprising T3 in types C, M and H are repeated more frequently than is usual in the same section of B. The differences here are, however, simply more marked than those which can be observed within a song type.

3. *Addition or omission of sections.*

The main distinction between types G and J is that a central section, present in G, is absent in J. The omission of a section may, of course, arise through the accumulation of quantitative changes such as those mentioned in the previous category, the number of syllables in a section being cut down until it reaches zero.

4. *Recombining of sections from different song types.*

T1 of song types X and Y is clearly of the C type, while both these songs have end phrases more akin to that of B or H. A more convincing example is from song type K (see Fig. 6) which includes syllables similar to those found in four other song types, which do not have syllable types in common with each other: T2 is like T1 of type E, T3 is like T2 of J (Fig. 5), T4 is like T3 of B (Fig. 4) and the end phrase is like that of N.

5. *Incorporation of sections of novel form?*

The extent to which individual chaffinches can introduce major innovations must remain in doubt, although the song types found include possible cases of this. Section T2 of song type X is an example: the rest of this song

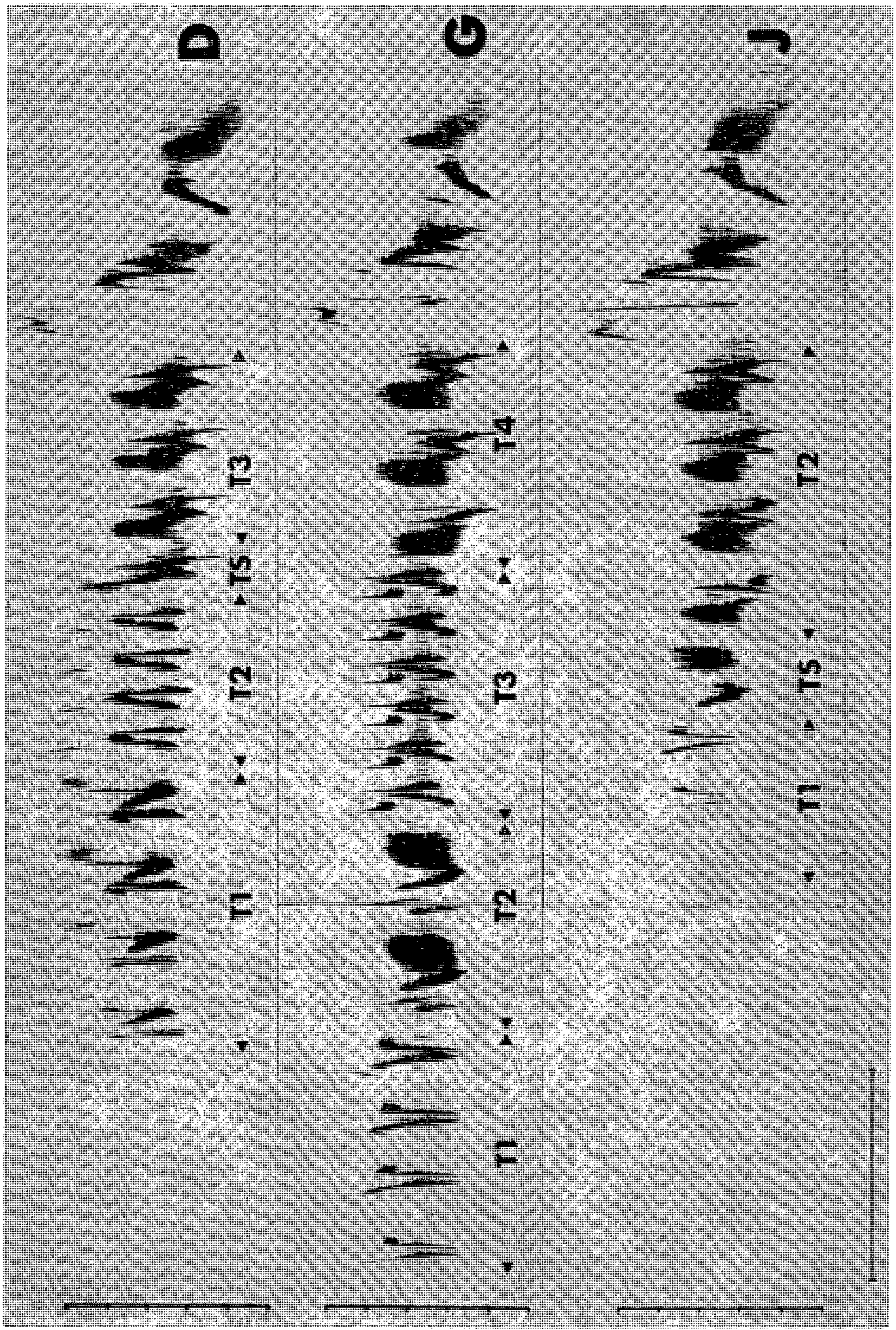


Fig. 5. Sonagrams of song types D, G and J to illustrate the features which they have in common. Fur further details see legend to Fig. 2.

differs from those in T1 and T2 it is therefore more correctly classified as a transitional one. Differences in detail may also be seen in the T2 sections of these songs, but the main difference to the ear is that M usually has more syllables in T3 than does B. Song type M most often has 3-5 syllables in this section while B usually has only 2. It is worth noting that the bird with B which diverges most strongly from this norm, usually producing 3-4 syllables in T3, was recorded at Trumland, in the only area where M is found (see Table 1). This suggests that song type B was introduced into that area by a bird with a longer than usual T3 section, or that it evolved to achieve one after introduction, and that song type M became separated from B when this had happened. Although these two song types are as similar as any pair discovered, and we are unable to separate them reliably by ear, there is no doubt that they should be regarded as distinct because the differences in form between them are consistent. Furthermore, one bird was found to have both of them in its repertoire suggesting that differences as slight as these can be separated by the birds themselves.

A second sub-group consists of types C, X and Y. C and Y have trill portions which differ only in very small details. The most distinctive feature of C, that the pitch rises and falls sharply at the end of the first half of the end phrase, is however not present in Y. Although the difference between these two types looks slight on the sonagrams, it is sufficient to give a difference in quality which was immediately recognisable in the field on the first occasion that song type Y was heard. It seems certain that these two types arose by divergence from a common original: as only one bird has been found to produce type Y, it is possible that miscopying by that bird was responsible for the innovation. Song type X is more different from C, although again the syllables in T1 of the two types are nearly identical. The syllables in T2 of type X are, however, quite different, while both T3 and the end phrase resemble type B songs more closely; in particular the flourish lacks the frequency peak found in C. Here then it appears that elements from different song types and, in the case of T2, a syllable structure not found otherwise, have been combined to give a new song type. Once again, as only one individual with type X has been discovered, it is possible that the song type was first produced by that bird.

ii) Song types D, G and J (Fig. 5).

These song types have the same complex end phrase and also share other elements in the song. Type G is the longest, having four sections in the trill. The form of T3 and T4 here is very like that of T2 and T3 in song type D. The main divergence is, therefore, in the first part of the song. In song type J the trill has only two sections with a transitional syllable between them. The

Although the differences between individuals were significant, there was also considerable variance amongst renderings by the same individual, as Table 2 indicates. This within-individual component accounted for 45.5% of the total variance in the data for section T2. The overlap in the distributions for different birds suggests that this measure, the number of syllables in a phrase, is unlikely on its own to provide a useful cue for individual identification. In rare instances it may do so, as for example in the case of one bird at Finstown which consistently sang this song type with three syllables in section T3, while others in that neighbourhood almost invariably produced only two. In other cases individual identity could not be so easily gleaned from a single feature although it could be by a combination of characteristics such as the number of elements in each of several sections, the position of the singing bird, the song type or types which it produced and the number of one type which it produced in a series before switching to another. All of these characteristics are more or less variable between individuals and, as they could be used in combination by the human observer to identify singing birds by ear, it seems likely that they are also used by chaffinches as a means of individual identification.

Variation between song types.

The accumulation of small differences within a song type may lead, during the course of time, to types different enough to be classified as separate. If new song types arise in this way, then it should be possible to identify similarities between some of the types in a population suggesting that they were derived from a common original. The procedure is analogous to the reconstruction of the course of genetic evolution by comparing closely related species.

Comparison between some of the songs shown in Figs 4-6 supports this idea, it being particularly noticeable that the end phrases of some of the song types are closely similar. These fall into two groups.

i) Song types B, C, H, M, X and Y (Fig. 4).

All these types have an end phrase consisting of two parts, the first rising in frequency, the second falling. In each of these songs the section of the trill immediately prior to the end phrase (T3 in all cases) is also similar: the syllables are brief and rapidly repeated, rising and then falling over a wide frequency range. This group of songs may be further divided, however, according to differences in the earlier components of the trill. Types B and M are nearly identical, but the noisy final component of each syllable in T1 is of higher frequency in M (4-5 kHz) than in B (3-4 kHz), except for the last syllable of T1 in M where it is of lower frequency. As this syllable

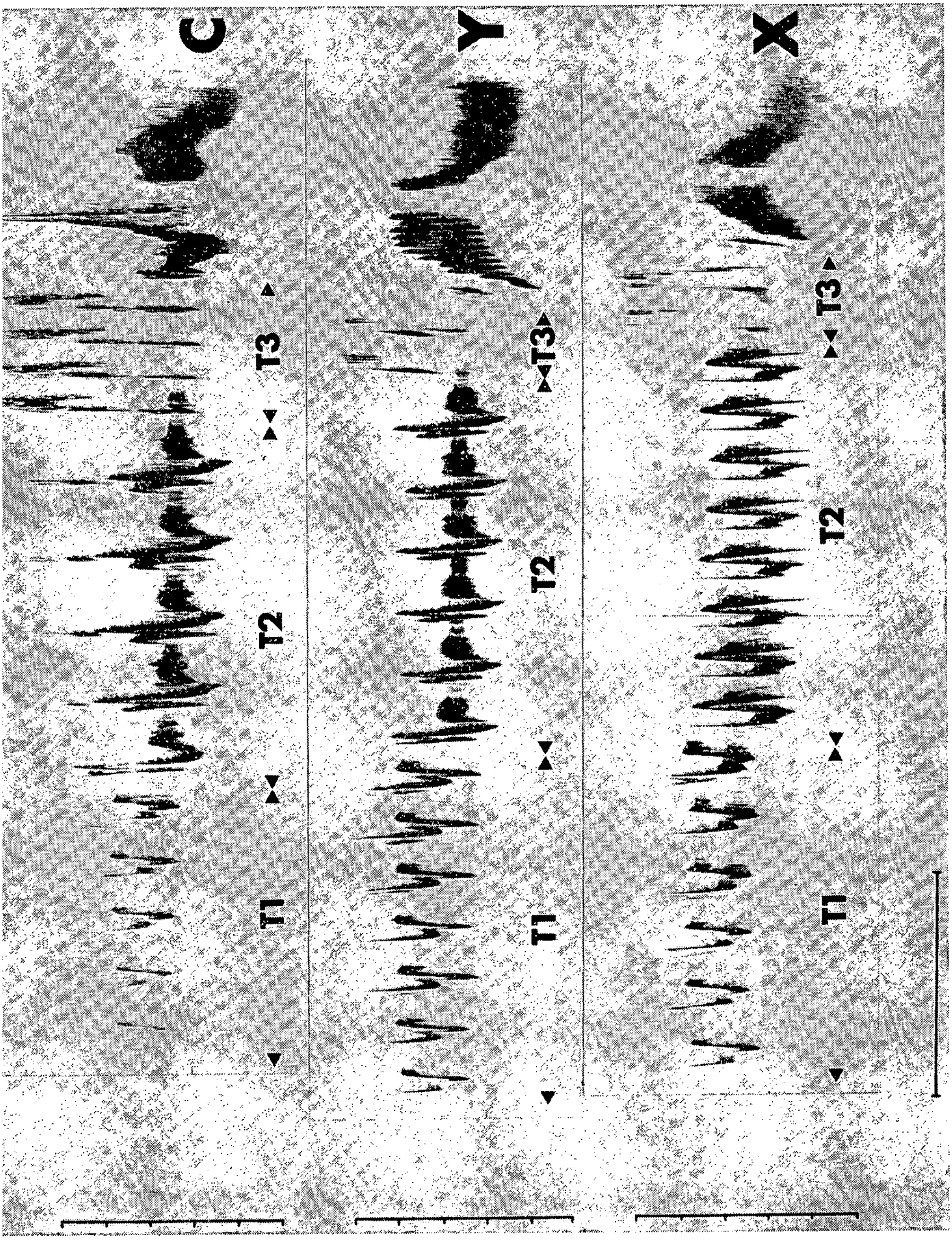
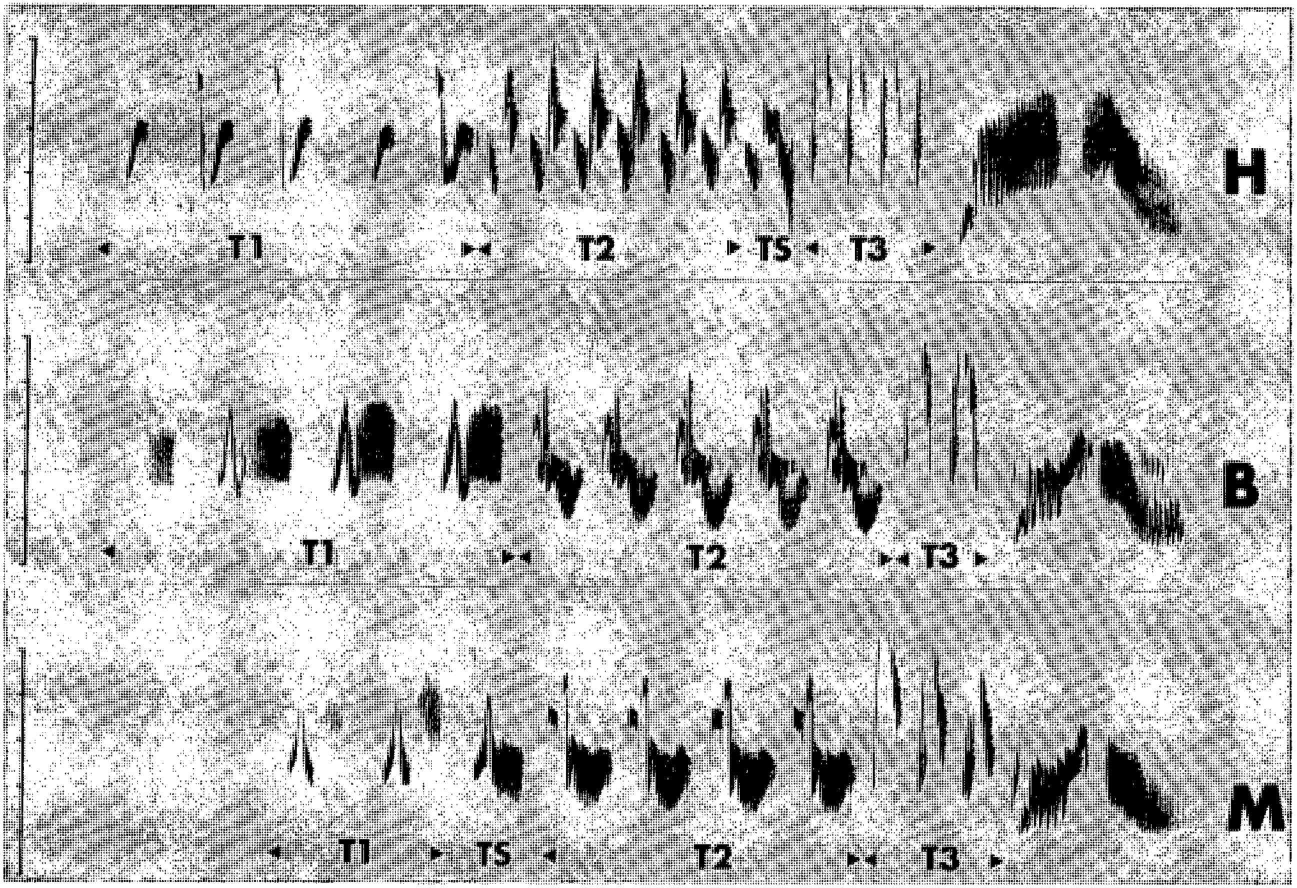


Fig. 4. Sonagrams of song types H, B, M, C, Y and X to illustrate the features which they have in common. For further details see legend to Fig. 2.


H
T1
T2
T5
T3
B
T1
T2
T3
M
T1
T5
T2
T3

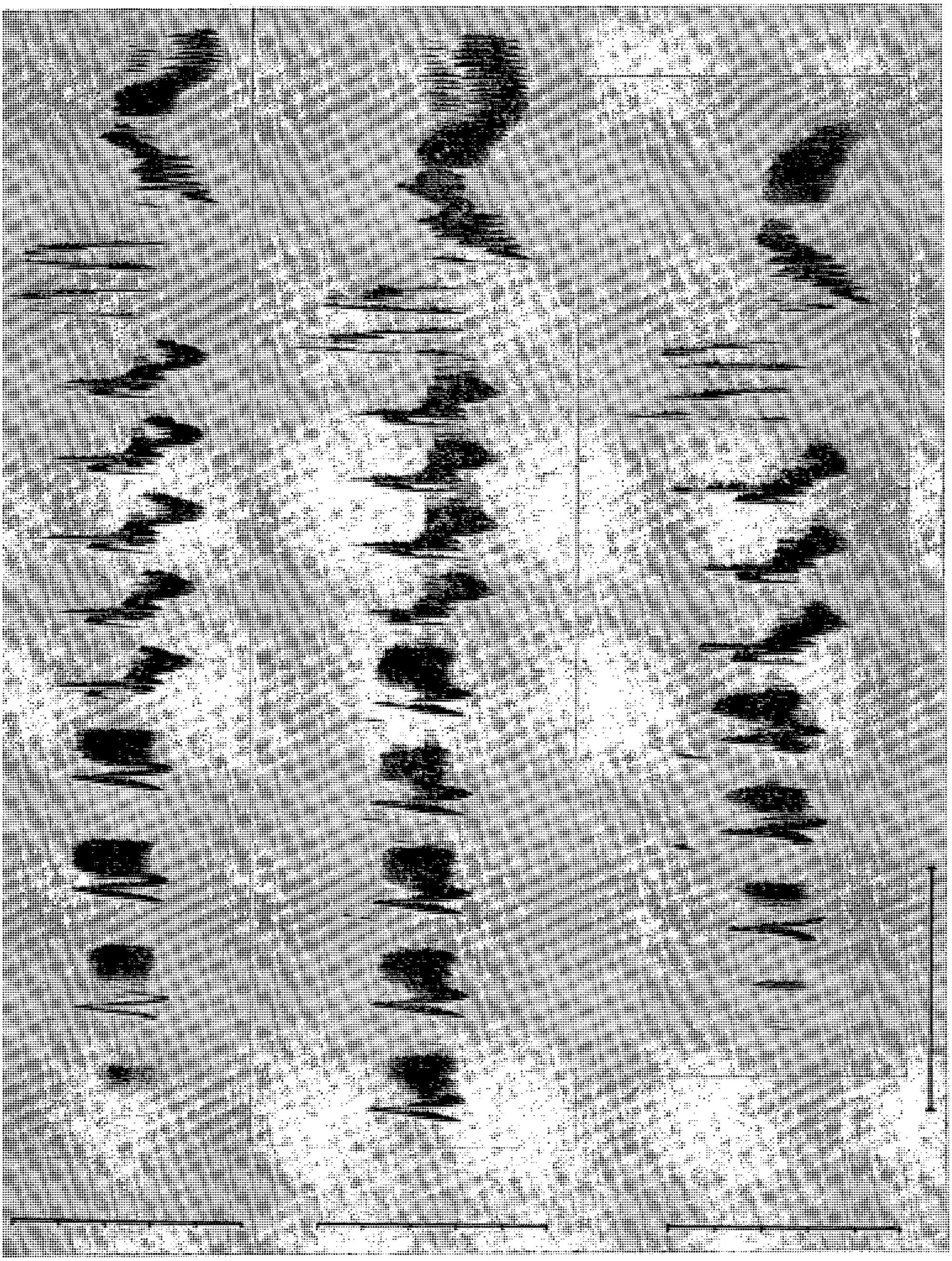


Fig. 3. Sonagrams illustrating variations in the number of syllables in a phrase of song type B. The three songs shown were produced by different individuals. For further details see legend to Fig. 2.

In Table 2 the number of syllables comprising section T2 of this song type are tabulated for each of the 14 birds for which a reasonable sample was available. Although the within-individual variation is considerable, an analysis of variance revealed a highly significant difference between individuals (F = 46.2; d.f. 11,442; p<.001). This was also true for an equivalent analysis of section T1 (F = 36.0; d.f. 11,447; p<.001). No analysis of T3 was conducted because in most birds this section consists of two syllables in all the songs recorded (see Fig. 3): this feature is one of the most reliable ways of distinguishing by ear between this song type and others, such as C and M, which sound very similar. Table 2 also suggests that the number of syllables in T2 may vary between localities, the figures for Finstown being, on average, higher than those for Balfour and Woodwick. However, the between localities component of the analysis of variance just failed to reach significance for either T2 (F = 3.1; d.f. 2,11) or T1 (F = 3.7; d.f. 2,11). This may be because the woods are not fully isolated from each other so that birds which have learnt a song type in one wood may subsequently sing it in another. A possible candidate for this movement between woods would be bird B1, which has a distribution of syllable numbers in T2 more similar to that of Finstown birds than to others from Balfour (see Table 2).

TABLE 2

Data on the variability of section T2 of song type B

	Number of syllables								
Bird	2	3	4	5	6	7	8	9	Mean
F1			8	13	1				4.7
F2			5	6					4.5
F3					8	12	6	2	7.1
F4		1	1	10	12	4			5.6
F5				16	27	8			5.8
F6				4	7	5	2		6.3
F7		1	6	8	19	3			5.5
F8	1	4	53	102	9				4.7
F9			3	7	1	1			5.0
B1		2	1	6	10				5.3
B2	3	11	2						2.9
B3	1	15	6	1					3.3
B4		14	2						3.1
W1		6	5	1					3.6

The 14 individuals for which reasonable samples of this song type are available are shown on the left. The figures in the body of the table indicate the number of times each individual was recorded singing this song type with the number of syllables shown along the top. Birds are from three different localities: Finstown (F), Balfour (B) and Woodwick (W).

combined here because of their closeness and the similarity of the song types found in the two places. It is clear from the Table that the prevalence of different types varies from wood to wood. Some song types were found commonly in one locality but either rarely or not at all elsewhere. Thus types A and J were most typical of Finstown, G and H of Balfour and F and M of Trumland and Woodwick. Other types were more widespread, C being common at both Finstown and Balfour and B in all three locations. Geographical variation therefore exists even within this small area, but not so strongly as to suggest that the different sub-populations are totally isolated from each other. For example, it seems certain that a bird with both types G and H at Finstown had moved there after learning these songs at Balfour, and it is also likely that the birds at Balfour with types A and D had learnt them in or around Finstown.

Seven of the song types recorded were shown by only one individual. As will be discussed below, some of these may have arisen from more common types as a result of errors in the learning process. In two cases, however, the birds concerned had no song types in common with any others recorded (a bird at Finstown which only sang type E and one at Balfour with types W and Z), and it is probable that these birds had learnt their songs in a different locality before moving into the area.

Variation within a song type.

As songs are passed culturally from one individual to another, the possibility exists that copying is inexact and that this leads to individual differences in the rendering of each song type. Small differences in amplitude and frequency are not easy to measure and, as mentioned earlier, the form of elements within a song type is remarkably consistent. By contrast, the number of syllables in each section of the trill varies both within and between individuals. The song type most appropriate for analysis of this variation is type B, as this was produced by several birds in each of the three main localities. Fig. 3 shows three sonagrams of this song type as produced by different birds to illustrate this variation in syllable numbers.

Fig. 2. Sonagrams of two of the song types (A and F) found in Orkney to illustrate the terminology used in the text in describing chaffinch song. Each song can be spilt into a trill and an end phrase, and the trill can be further split into sections (T1, T2, etc.) in which successive syllables are near identical. Unrepeated notes found during the trill are referred to as transitional syllables (TS in the lower sonagram). In this and the other figures the sonagrams were prepared using the wide band setting to give the best temporal resolution. They provide a plot of frequency against time. The frequency scale on the left runs from 1 to 6 kHz and each song lasts for around 2-3 seconds (the time bar in this and subsequent figures is 0.5 seconds long).

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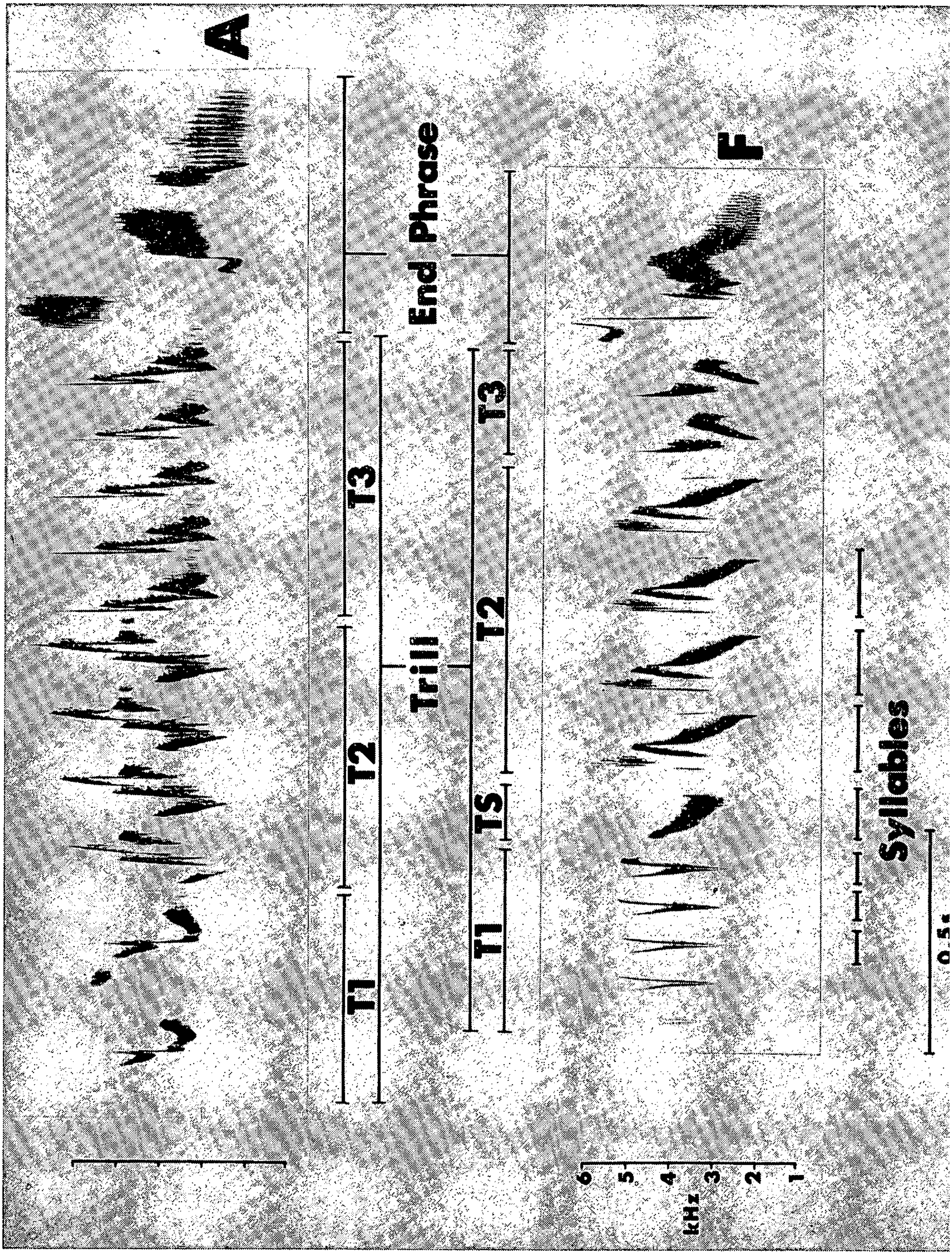
A
T1
T2
T3
End Phrase
Trill
T1
TS
T2
T3
F
Syllables
0.5 s
kHz
6
5
4
3
2
1

The following terminology will be used in describing the songs (see examples illustrated in Fig. 2). Each song may be split into a *trill* followed by a complex terminal flourish or *end phrase*. The series of elements comprising the trill may be further split up into sections in each of which successive *syllables* are nearly identical. The units of repetition within the trill will be referred to as syllables: in some cases these appear to be single notes, but in others several separate notes can be seen on the sonagram within a particular syllable. The trill of both the songs in Fig. 2 has three sections, but some other types have fewer and some more. In Fig. 5, for example, song type J has two sections in the trill, while song type G has four. These sections will be referred to as T1, T2, *etc.* In some cases a single syllable of a different type occurs between two sections of the trill, and these will be referred to as *transitional syllables* (TS). Examples of this are the syllables between T1 and T2 in song type F (Fig. 2) and also in type J (Fig. 5). The word trill is therefore reserved for syllables which are repeated, others being designated as transitional or as part of the end phrase.

3. RESULTS

Prevalence of song types in different localities.

Sixteen different song types were identified and 14 of these are illustrated in Figs 2-6, no good quality recordings being available of the other two. As the 41 individuals recorded during 1977 averaged 2.2 song types each, this means that there were many cases in which the same song type was sung by several individuals.

Table 1 shows the number of birds, in each of the three main areas studied, which were known to possess each song type. Woodwick and Trumland are

TABLE 1

Number of repertoires known to include each song type found in three different localities

Song type	Finstown (16 birds)	Balfour (15 birds)	Trumland & Woodwick (6 birds)
X	1	0	0
Y	1	0	0
E	1	0	0
N	1	0	0
J	4	0	0
A	6	1	0
D	7	1	2
C	10	4	0
B	9	4	3
H	1	9	0
G	1	9	0
K	0	1	0
W	0	1	0
Z	0	1	0
F	0	0	3
M	0	0	2

Sound spectrograms (Kay-Electric Sonagraph No. 6061A) were prepared of the different song types found and of all song types about which identification was uncertain. With practice many of the more distinctive song types could be identified by ear, but identification was made much easier by recording a sample of the songs of each individual and comparing them with sonagrams during replay at 2.4 cm/s. Identification was later checked by sonagraphic analysis. Each new song type discovered was assigned a letter, by which it is labelled throughout this paper. In theory the decision as to whether a song differs sufficiently from those already described to be called a new type could be difficult; in practice very few problems of this sort were encountered. As will be seen, the same song type, as produced by different individuals or repeated by the same individual, may show variation in the number of elements in each phrase, but the general form of the elements remains closely similar and quite distinct from those in other song types. In the few cases where intermediates were discovered, or where one type showed a small but consistent difference from another, the divergent song was assigned to a type of its own. This seems the most reasonable approach because of the existence of cases where birds possessed two closely similar, but consistently different, song types in the same repertoire, indicating that they were themselves able to distinguish these small differences, at least during learning.

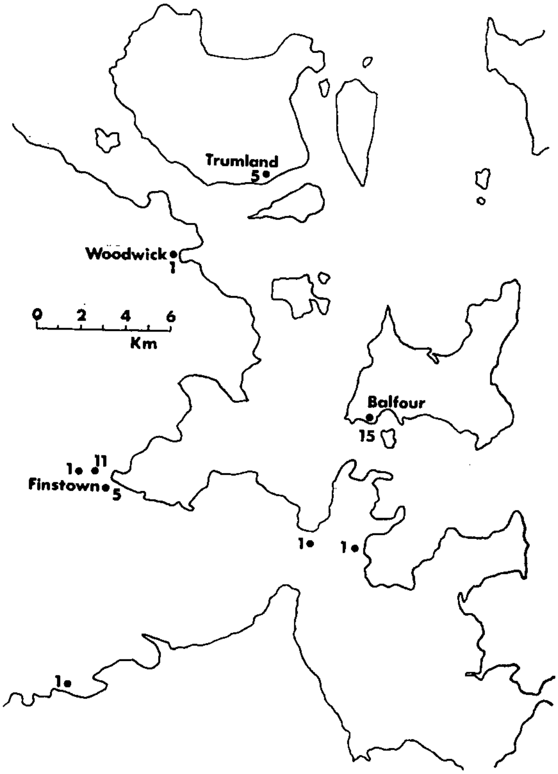

Fig. 1. Map of the part of the Orkney islands in which chaffinch songs were recorded. The black dots indicate recording sites and the numbers next to them the number of individuals recorded at that site.

influences their relationships with other males and with females in the population to which they belong. In the case of the chaffinch no such study of the songs of individuals within a small area has been carried out and the present paper aims to fill this gap.

Most of the work to be reported concerns the distribution and classification of song types in the Orkney Islands, Scotland and the inferences which their examination allows for the way in which cultural evolution normally occurs in the wild. The Orkney chaffinches are particularly suitable for the study of cultural evolution, in the same way that island populations have proved useful in studying genetic evolution, because groups of individuals within the area are relatively isolated from each other. Although the islands cover an area of several hundred square kilometers, they are windswept and thus support very little woodland. Most of this was planted in the latter half of the last century and it is doubtful if chaffinches bred in the islands prior to that time. Today the population probably amounts to only about 50 pairs, the majority of them in three main woods 11-15 km from each other on separate islands, but with isolated pairs in smaller pockets of woodland elsewhere. This situation makes it possible to record the song of a high proportion of the males present, so that a reasonably complete survey may be made of the song types in the area and how these are distributed between different individuals and different woods.

2. MATERIALS AND METHODS

Preliminary fieldwork was carried out during May-June 1976 and more detailed surveys in April-May of 1977 and 1978. Unless otherwise mentioned, the results to be discussed are taken from the 1977 season. In the first year recordings were made with a Nagra III tape-recorder, but subsequently use was made of a Uher 4200 IC with Grampian DP4/X microphone mounted in a fibreglass parabolic reflector 50 cm in diameter. The tape speed used was 9.5 cm/s. The woods visited and number of birds recorded in each are shown in Fig. 1. Efforts were made to locate all singing males in this area and it is unlikely that many escaped detection. The only part of Orkney where chaffinches are known to breed but which was not covered was the island of Hoy, the nearest point on which is 15 km south-west of Finstown; the population studied is therefore relatively isolated from others.

Individual chaffinches may have up to six song types in their repertoire (MARLER, 1956), but as some birds have types which they rarely use (HINDE, 1958; SLATER & INCE, in prep.), it is never possible to be sure that the complete repertoire of a particular individual has been recorded. To maximise the chances that its full repertoire would be found as many songs were recorded from each individual as possible. The main Finstown population of 16 birds was examined in the greatest detail, making it certain that any song types which were undetected in their repertoires were rarely sung: even so, two birds which had been recorded in 1977 were found to have additional song types in 1978. An additional difficulty is that song output varies considerably with stage of the breeding cycle (tending, for example, to be high during incubation and low during care of the young) and also, for reasons which are unclear, between different individuals. Thus some of the song types of relatively silent individuals may escape detection.

Behaviour, 71, 1-2

CULTURAL EVOLUTION IN CHAFFINCH SONG

by

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(With 6 Figures)

(Acc. 20-II-1979)

1. INTRODUCTION

In a long and important series of experiments, THORPE (1958a, b) demonstrated that young chaffinches (*Fringilla coelebs*) learn the fine details of their songs from other individuals during the first 13 months of their lives. Birds taken as nestlings could be tutored with tape-recordings in the autumn and winter and would, in the following spring, reproduce these tutor songs with a high degree of fidelity. Such birds would even learn unnatural songs in which the final portion had been artificially transposed to the middle. On the other hand, it was difficult to teach birds which had been caught in the autumn anything but normal chaffinch song, suggesting that some learning had taken place before they were caught. The general form which song should take had therefore been established by the first autumn while fine details could be added by learning from conspecifics in the following spring when the birds began to sing themselves.

Despite our knowledge of this remarkable learning process, partially completed well before the young bird starts to sing, the advantage gained by the cultural transmission of song remains obscure, although several possibilities have been raised by NOTTEBOHM (1972). As MARLER (1952) noted, the form of chaffinch song shows considerable geographical variation, probably because divergences arise through errors in the copying process. Such spatial variation in song has been studied in many species, but it remains questionable whether it is in itself an important phenomenon or simply a byproduct of the role played by learning in ontogeny (ANDREW, 1962). The significance of vocal learning is more likely to be found by studying the impact which it has on the songs of individual males and the way in which it

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[1] We are grateful to the many people in Orkney who have given permission for recordings to be made on their land and, in particular, to Mr and Mrs BIRLEY of Woodwick, Major and Mrs RITCHIE of Trumland, the late Mrs SCARTH of Binscarth and Mr and Mrs ZAWADSKI of Balfour, in whose woods the majority of the recordings were made. This research is financed by a grant from the Science Research Council.

Condor, 82:285–290

CHANGES WITH TIME IN THE SONGS OF A POPULATION OF CHAFFINCHES

S. A. INCE
P. J. B. SLATER
AND
C. WEISMANN

ABSTRACT.—A comparison has been made between 23 song types recorded from Chaffinches in Stanmer Great Wood, Sussex, U.K. in 1960, and the total of 36 that were sung there in 1978. Eight of the earlier song types showed clear similarities with those present in 1978: in three of these the differences were minor, but in the other five they were substantial enough for the songs to have been classified as different types had they been found in the same population at the same time. With all other song types, the differences were too great for song types to be compared between the two sets of recordings. While at any one time some song types are shared in more or less identical form among many individuals in a population of Chaffinches, these results show that the form of song types changes through time. These changes may occur because rare song types are not copied by other birds and become extinct in the area, because new song types are introduced from elsewhere by birds moving into the area and because mistakes in copying may lead to new song types being generated.

All the songs of Chaffinches (*Fringilla coelebs*) have certain features in common. The first part, or trill, may be split into two to four phrases within which there are units, referred to here as syllables, that are repeated in more or less identical form. The songs shown in Figure 1 are an example in which the trill has three phrases, the syllable structure being the same within a phrase but differing among them. The final part of the song, after the trill, is the end phrase, a note complex in which the elements are not usually repeated.

Within this pattern there is much variation both among birds and among the songs in an individual's repertoire. In a study of the songs found in the Orkney Islands (Slater and Ince 1979) we found that this variation is discontinuous, the songs falling into discrete types. Within a song type the intervals between syllables and the structure of the syllables themselves are very similar among birds. On the other hand, the number of syllables in a phrase varies considerably both among individuals (see Fig. 1) and among repetitions by the same individual. The best criterion for distinguishing between song types is therefore the form of the syllables. In assigning songs to types, we have used any consistent difference in form, no matter how slight, to indicate that two songs should be classified as separate. Some song types are very similar to each other, but, as the variation is not continuous, they can be separated by playback at slow speed or by inspection of sonograms. Our criteria for classifying songs into types appear similar to those used by the birds, as the most similar of the song types we have found can appear as two separate types in the repertoire of one bird (see Slater and Ince 1979).

Young male Chaffinches learn the details of their songs from conspecifics during the first 13 months of life (Thorpe 1958). The fact that some of the song types in an area are very similar to each other indicates that new types may arise by mistakes being made during copying. Comparison between types suggests that such mistakes may involve gradual change as the song is passed down through several successive individuals or sudden major changes, such as the mixing up of phrases from two different song types (Slater and Ince 1979). By contrast, some of the song types in an area bear little relation to any others and have probably been introduced by immigration of individuals after their songs were learnt.

The reconstruction of changes in song by analyzing the similarities and differences among the song types found in a population at a particular time is analogous to tracing the probable course of genetic evolution by an examination of living species. However, as cultural evolution is a more rapid pro-

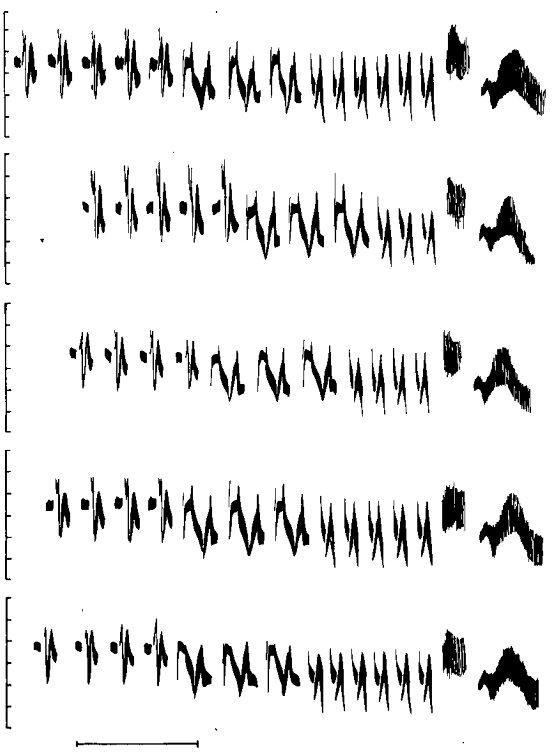

FIGURE 1. Five sonograms of the same song type (type B), as sung by five different Chaffinches in Stanmer Great Wood, Sussex in 1978. In this and the other figures the scale at the side runs from 1–7 kHz and the time bar beneath is 0.5 s long.

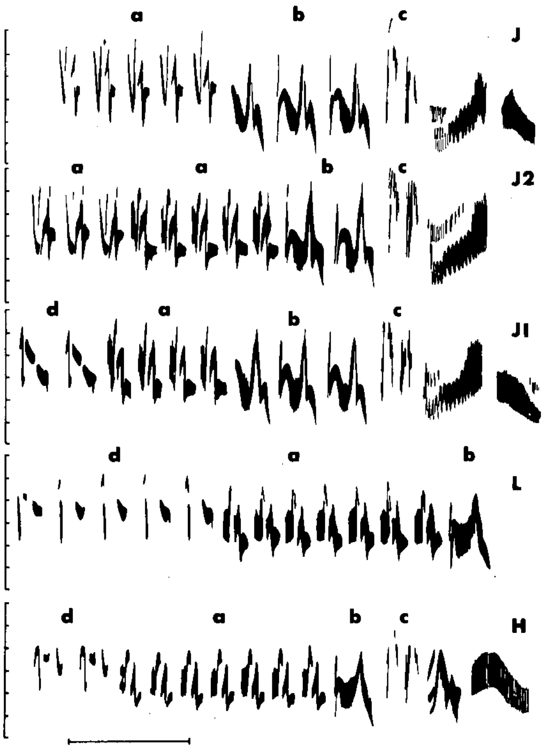

FIGURE 2. Five song types sung in Stanmer Great Wood in 1978. Compare with Figure 3.

cess, it is feasible to examine changes through time as well, to determine whether immigration and inaccuracies in copying lead to changes in the songs present in an area over time. This paper is concerned with a study of this latter type, made possible by two sets of recordings made at the same place 18 years apart.

METHODS

Between 30 May and 7 June 1960, C. W. recorded as many Chaffinch songs as possible in Stanmer Great Wood, Sussex, U.K. close to the site on which the University of Sussex was subsequently built. These recordings were made with an EMI L2A tape recorder and Sennheiser MD21 microphone mounted in a 90-cm parabolic reflector. The tape speed used was 38 cm/s but the recordings were copied at 19 cm/s before analysis. About 22 individuals were recorded. This survey was not complete and so cannot indicate the relative frequencies of different song types. Chaffinches usually have more than one song type in their repertoire (Marler 1956), and sonographic analysis showed that these recordings included 23 distinct song types: these were assigned numbers. Eighteen years later, in summer 1978, S. A. I. surveyed completely the songs of all the male Chaffinches in Stanmer Great Wood. These were recorded at 9.5 cm/s on a Uher 4000 tape recorder using a Grampian DP6 microphone and 50-cm parabolic reflector. The 42 birds present had an average of 2.9 song types each and, sharing of song types being common, the number of distinct types found was 36. These are labelled throughout this paper by letters, followed by numbers where necessary. With both samples, the classification of songs into types was based on any consistent difference in form that was found between them (see below).

The two sets of recordings were compared by taking each song type found in 1978 and finding the song type from 1960 to which it was most similar. Sonograms, prepared with a Kay-Electric Sonagraph No. 6061A using the wide band setting, were used in making these comparisons. The figures illustrating this paper are tracings from these sonograms; the quality of the original recordings, particularly those from 1960, was often not adequate to use the actual graphs. Each set of recordings was traced without reference to the other.

RESULTS

Figures 2 and 4 show two groups of song types recorded in 1978, within each of which there are strong similarities. The differences among the songs within these groups illustrate the differences in structure that allow song types to be classified as distinct. Lower case letters in these figures label syllables that have features in common and may therefore have evolved from a common original. In some cases the similarities are so strong that they have almost certainly done so. However, caution is required here because, for example, the *b* and *c* syllables in Figure 2 closely resemble elements we

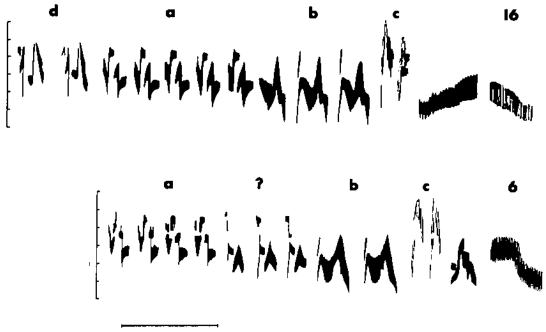

FIGURE 3. The two song types recorded in Stanmer Great Wood in 1960 that are most similar to those in Figure 2, which were recorded in 1978.

have found in Chaffinch songs in Orkney, about 900 km from Stanmer (see Slater and Ince 1979). Given the distance involved and the variation found in song over comparatively short distances, this is likely to be due to convergence rather than evolution from a common precursor. The mechanism of song production in Chaffinches may be particularly prone to generating elements of these types. For this reason, we restrict ourselves here to a comparison among songs that have more than one syllable type in common, a situation which, given the wide variety of syllable types, would be very unlikely to arise by chance.

Figure 3 shows the two song types recorded in 1960 that were most similar to those in Figure 2. Type 16 is most like type J1, the strongest differences between them being in the *d* syllable and the more drawn out end phrase in type 16. The last part of type 6, from syllable *b* onwards, is virtually identical to that of type H, but the earlier sections of these two songs are clearly distinct. Thus, although song types 16 and 6 include elements that are of the same form as those of the songs shown in Figure 2, no song type found in 1978 was identical with either of these earlier types.

A comparison of the song types shown in Figures 4 and 5 yields similar conclusions. Type 18 is most like type C or type S, but the end phrase differs from either, as does the detailed structure of syllables earlier in the song. Type 11 is like type A1, but A1 lacks a component in the end phrase and also in the syllable type *e*. Type 10 is perhaps most closely allied to type A in syllables *g* and *h*. However, there is again a difference in that type A has a very brief end phrase which lacks the two final components of that in type 10, and the introductory elements also differ between them.

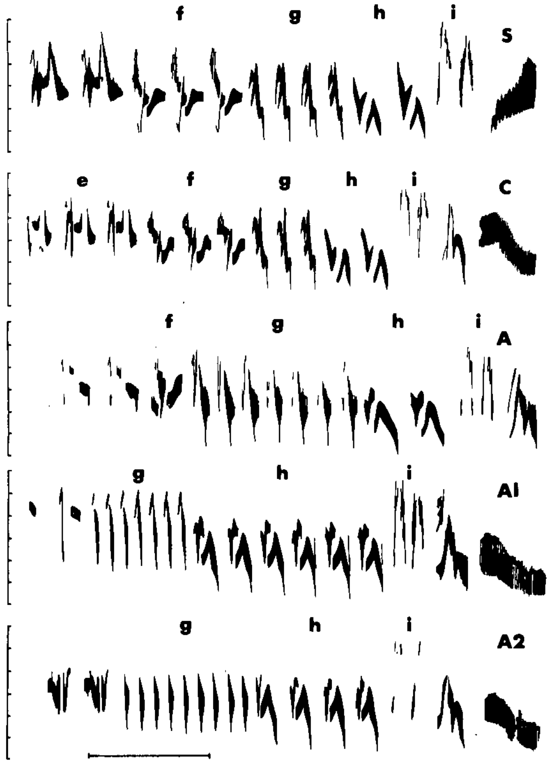

FIGURE 4. Five song types sung in Stanmer Great Wood in 1978. Compare with Figure 5.

Many of the other song types found in 1978 showed no clear similarity to any of those recorded in 1960. The only three other cases where resemblance was sufficient to suggest that the two types had a common derivation, or that the earlier type had evolved into the later, are shown in Figure 6. In each pair, differences between syllable types can be seen, although these are

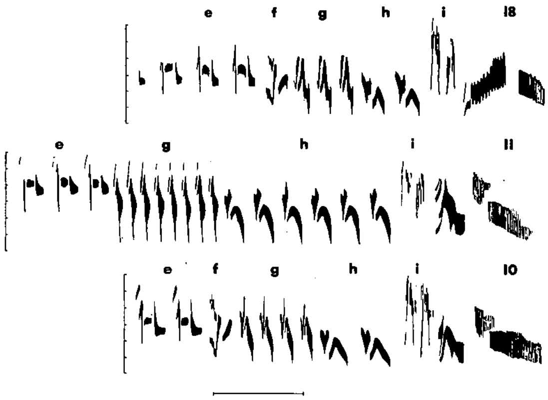

FIGURE 5. The three song types recorded in Stanmer Great Wood in 1960 that are most similar to those in Figure 4.

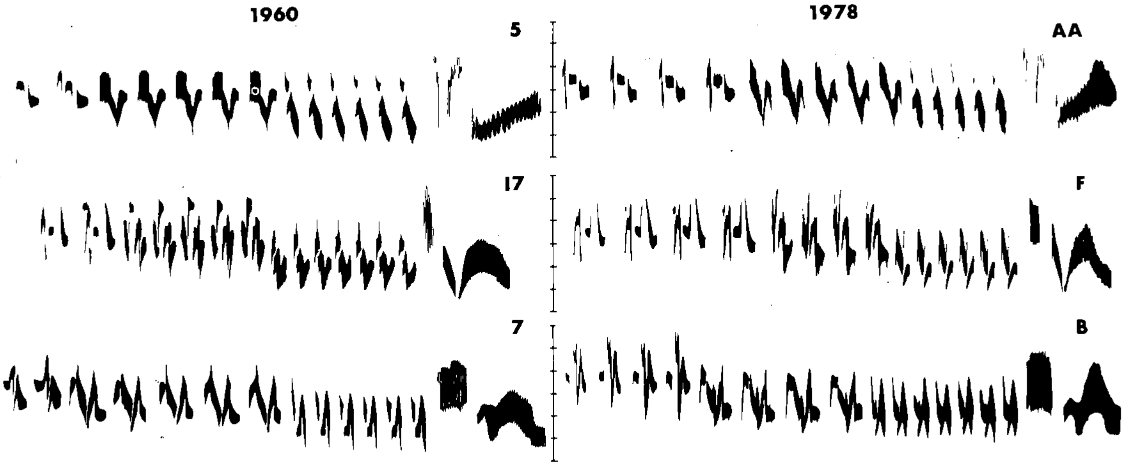

FIGURE 6. Three song types recorded in 1960 compared with their nearest equivalents recorded in 1978.

minor in some cases and could have resulted simply from small changes in amplitude modulation leading to different aspects of a particular syllable being emphasized. Types 5 and AA appear to be the most similar. The main difference lies in the second phrase, syllables of which are longer in type 5 than in type AA. This variation is greater than that usually found within a song type; measuring the intervals between equivalent points in the syllables of this phrase for these two songs yields a coefficient of variation of 10.6%, which is considerably greater than normal within a song type (see Table 1). Despite this quantitative difference, however, song types 5 and AA might well be classified as the same because of their overall similarity in form.

Types B and 7 look rather more different from the tracings in Figure 6 than comparisons of the original sonograms suggest; the recording of type 7 was particularly poor, with the result that small details could not be traced accurately. However, these two types can be compared in more detail by examining the interval between equivalent points in successive syllables of each phrase. This is possible here, and in comparisons with song types C and F, because these three types were recorded from several birds in 1978 so that the variation among them could be measured for comparison with the earlier song types. These data are shown in Table 1. The results confirm the similarity between type B and type 7, the intervals in the latter falling within

TABLE 1. Comparisons of the interval between the same points in successive syllables for each phrase of the three song types that were most common in 1978 with their nearest equivalents in 1960. Times given are in milliseconds; CV = coefficient of variation.

		Phrase			
Song type		1	2	3	4
B (N = 14)	Mean interval	139	182	89	
	Range	131-151	169–204	82–98	
	CV	4.94%	5.29%	4.96%	
7 (N = 1)	Interval	139	178	95	
F (N = 10)	Mean interval	184	122	84	
	Range	174–197	117–139	78–91	
	CV	5.17%	4.29%	4.53%	
17 (N = 1)	Interval	178	116†	86	
C (N = 10)	Mean interval	185	153	100	161
	Range	174–204	142–167	98–106	144–167
	CV	5.59%	5.66%	2.96%	4.24%
18 (N = 1)	Interval	201	*	121†	197†

* No comparison can be made here because there was only one syllable in the second phrase of song type 18.

† These figures fall outside the range of intervals given above. This may suggest some divergence, although with only a single sample of each song type from 1960, numbers are too small for statistical testing.

the range of those recorded from 14 birds singing the former. The elements in the second phrase of type 17 are repeated slightly more rapidly than any of those recorded for type F, suggesting a small divergence between these song types, though not one which would be likely to yield statistical significance with a larger sample. On the other hand, comparison of type C with type 18, shows a more substantial discrepancy in the timing of the third and fourth phrases which is in keeping with the greater difference in form between these types (see Figs. 4 and 5).

DISCUSSION

These results show that substantial changes have taken place in the song types found in a population of Chaffinches during the course of 18 years. Some individual syllables have remained very much the same over time (e.g., *b* in Figs. 2 and 3 and *h* in Figs. 4 and 5), but others have changed considerably, and there has also been reassortment of syllables between song types. Of the 23 song types recorded in 1960, eight showed clear relationships with those of 1978, and the three of these shown in Figure 6 had persisted with only minor changes. Even in these cases, however, the changes might have been sufficient for the earlier and later forms to be regarded as different song types if both had been found in the population at the same time. As with species of organisms, it is easier to classify forms present at one time than variants recorded at different times.

Both our observations on territory ownership and the analysis of banding recoveries by the British Trust for Ornithology (R. J. O'Connor, pers. comm.) suggested that about 60% of male Chaffinches survive from one breeding season to the next. The average duration of a cultural generation is thus approximately two years, so that 8–10 generations would be expected in the course of 18 years. However, in a population of 42 birds, one or two individuals would be expected to be over seven years old, meaning that some song types could have passed through considerably fewer generations, thus giving greater conservatism. Another factor countering change may be how common a particular song type is in the population. Not only are these types more likely to be included in the repertoire of long-lived individuals, but also young birds may have more than one model available to copy if two adults are singing the same type near them. Individual idiosyncrasies would therefore be less likely to pass on from one bird to another. It may be for these reasons that the two song types which were most common in 1978, B and F, sung by 22 and 16 individuals respectively, were also those most clearly related to types recorded earlier.

No previous study has examined cultural changes over the length of time covered by this analysis. Even so, the evidence suggests that the speed of cultural change differs considerably among species. For example, while Snow (1968) found no change in song types over a period of three years in the Little Hermit hummingbird (*Phaethornis longuemareus*), Thompson (1970) found two years to be sufficient for most song types to have changed from those previously found in a population of Indigo Buntings (*Passerina cyanea*). In Saddlebacks (*Creadion carunculatus*), cultural mutations are infrequent, but Jenkins (1978) was able to observe a number as they happened by following a small population through five years. The exact speed of change found by any study doubtless depends on mortality rates as well as on the exactitude of copying. If many individuals died in a particular year, as might have been the case in the present study for the unusually hard winter of 1962–63, the apparent speed of cultural change might have been enhanced by a subsequent influx of birds who had learnt their songs elsewhere. In general, however, male birds nest close to their natal area (Greenwood and Harvey 1976) and we have found that male Chaffinches tend to occupy the same territory in successive years. In our Sussex population of 42 birds, only one had a repertoire in which none of the song types were shared with any others; this again suggests that birds tend not to move long distances after song learning has ceased. Thus the introduction of song types from elsewhere is unlikely to be a major source of change; most of the differences observed have probably resulted because some song types that are sung by only one or a few individuals become extinct and because new ones are formed when copying is inexact.

The original intention of the 1960 recordings was to trace parallels between the songs of Chaffinches at Stanmer and those of the same species in New Zealand. The entire New Zealand population is known to be derived from 66 birds caught in Stanmer Park and transported there in 1870. The comparison would be interesting but, from our observations on the changes which can occur over 18 years, it seems unlikely that close parallels would be found between two populations that have been separated for nearly a century. Thielcke (1974) reported no differences in song between European Chaffinches and those recorded in New Zealand. However, this is only in the general characteristics of song rather than in the details considered here.

ACKNOWLEDGMENTS

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CHAFFINCH SONG TYPES: THEIR FREQUENCIES IN THE POPULATION AND DISTRIBUTION BETWEEN REPERTOIRES OF DIFFERENT INDIVIDUALS

by

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(With 2 Figures)

(Acc. 3-VII-1980)

INTRODUCTION

In common with many other bird species, male chaffinches (*Fringilla coelebs*) often have a repertoire of different song types (MARLER, 1956; HINDE, 1958). The songs in each bird's repertoire are learnt from other individuals during the first year of life (THORPE, 1958). Within a population of birds many individuals may share a single song type, the elements in all phrases of which are identical in form, although they may differ both within and between individuals in the number of times that they are repeated. On the other hand many song types are peculiar to single individuals and may either have been introduced into the area after they were learnt or have arisen because mistakes were made during copying. SLATER & INCE (1979) argue that new song types appear in the population for both these reasons, some having clear similarities to the song types already present, whereas others are quite distinct from them.

In this paper we consider a number of aspects of the frequencies of song types and their distribution between repertoires. As new song types can be regarded as arising through the occurrence of "cultural mutations", there is an analogy between song type frequencies and gene frequencies. We apply the theory developed by EWENS (1972) to determine whether the distribution of song types is equivalent to that of neutral genes or whether it differs and so suggests that song types vary in the

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[2] We are grateful to Dr B. CHARLESWORTH for his advice on the application of genetic models to our data. This work is financed by a grant to P. J. B. S. from the Science Research Council.

likelihood that they are transmitted. We also test several hypotheses about the distribution of song types between repertoires. Do repertoires tend to be of a particular size? Are the different song types found in the population distributed independently and randomly among them? Do rare songs tend to be found together in the same repertoires? Do larger repertoires have more rare songs? All these questions require the comparison of the observed distributions of song types with statistical models. Generating appropriate models for data of this type is not as simple as it might at first seem, for reasons which we shall discuss. The techniques are, however, likely to prove useful in making similar comparisons in other bird species.

The analysis was carried out because it is likely to shed light on developmental questions, such as whether individuals learn their songs from more than one other bird and how often copying is inexact, as well as functional questions, such as the significance of variation in repertoire size.

METHODS

Data were obtained by recording song from all the male chaffinches in Finstown, Orkney, in 1977 (16 individuals) and in Stanmer Great Wood, Sussex, in 1978 (42 individuals). In each place the territories were mapped and, although the birds were not marked, individuals could be identified unambiguously by their locations and the song types which they had in their repertoires. Recordings were made using a Uher 4000 tape-recorder and microphone (usually Grampian DP4X) mounted in a 50 cm diameter parabolic reflector. The tape speed used was 9.5 cm/s.

Song types were identified by recording as many songs as possible and preparing sonagrams on a Kay 6061A Sound Spectrograph of a sample of songs from each bird. Those recorded songs not sonagrammed were compared with sonagrams during replay at 1/4 speed to ensure that they belonged to a type already recorded as sung by that individual. Sonagrams were prepared in all cases of doubt. At least 50 songs, and in some cases several hundred, were recorded from each bird. As birds sometimes possess song types which they very rarely use, it is never possible to be sure that the complete repertoire of a particular individual has been recorded. It is, however, unusual for a song type possessed by a bird not to appear in a sample of 50 songs. Taking 30 birds for which songs were classified into types, a mean repertoire size of 2.80 was found from a mean sample of 319 songs; had the calculation been based only on the first 50 recorded songs, the size of three repertoires would have been underestimated and the mean size would have been 2.67. The only circumstance in which repertoire size was likely to have been underestimated was where birds sang infrequently and had song types which comprised a small proportion of their output. To avoid this problem, we studied birds which sang little particularly intensively. For both study areas, the mean repertoire size found was greater than that reported by MARLER (1956) suggesting that we have been relatively successful in recording complete repertoires.

Each song type was assigned a letter for identification. Song types from different birds were given the same letter if the form of all the elements comprising them was the same. A song which showed a consistent difference from those previously found was assigned a new letter. The distinction between song types is discussed in more detail by SLATER &

INCE (1979): as the variation is discontinuous, the allocation of songs to types is not a difficult one.

The development of statistical models and the methods used to compare them with the results obtained will be described in the appropriate sections of the results.

RESULTS

Frequencies of song types in the populations.

Fig. 1 shows the frequency of different song types in the Sussex population for which the data are most extensive. The 42 birds recorded averaged 2.9 song types each and these belonged to 36 different types. Twenty-one song types were sung by only one individual each, but three song types were sung by 15 or more birds.

How might such a distribution be produced? The process of cultural transmission of song types from adults to young birds with copying errors and immigration producing new types and sampling fluctuations and emigration extinguishing existing types, is analogous to the process of genetic transmission of alleles across generations. The simplest hypothesis is that the frequencies of the different song types reflect a population of equally fit song types in equilibrium. This can be examined by using the statistical test incorporated in the FORTRAN computer program in Appendix 4 of EWENS (1972), designed to detect departures from neutrality amongst alleles. Tested in this way the Sussex data yielded an

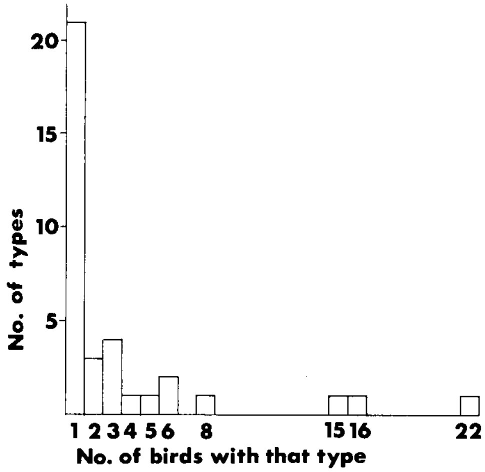

Fig. 1. Distribution of song types in the Sussex population. The histogram shows the number of song types plotted against the number of birds singing each of them: thus 21 song types each occurred in only one repertoire, while the commonest song type was sung by 22 of the 42 birds in the population.

F ratio of 0.65 (df = 248, 34; n.s.). There is thus no evidence to suggest that song types are other than selectively neutral: they appear to arise and be lost from the population at random without the transmission of some being favoured over that of others.

"Mutations" occur more frequently in the transmission of song types than in the copying of genes. Nevertheless, a graphical extrapolation of data in EWENS' Table 1 allowed a very rough estimate to be made of the frequency with which new song types arise in the population. This was approximately 16%. However, little faith can be placed in this figure because its calculation involved making assumptions about the influence of overlapping generations and about the effective population size. We have used computer simulation to obtain a better estimate of the likely rate of mutation amongst song types. Simulations were run with mutation rates varying from 10-20% and with a population of 121 songs, matching that in our Sussex data. At the start, all these songs were of the same type, but we simulated the changes that would take place over 100 years given a particular mutation rate and mortality of 40% per annum (based on ringing data from the British Trust for Ornithology). The number of song types found rose rapidly in the first ten years and tended to fluctuate about a mean thereafter, new types being counterbalanced by extinctions. Table 1 gives a summary of the results of three runs for each of three mutation rates. In all cases the program generated over 20 song types, some of which were represented only once in the final output, while others were much more common. The general form of the output was therefore similar to that of the original data. The 10% mutation rate results in fewer song types and a smaller number of cases of a type being

TABLE 1

Results of simulations of cultural evolution run at three different mutation rates

Mutation rate	No. of song types obtained	No. of song types occurring in only one repertoire	No. of repertoires in which most common song occurred
10%	24.3	9.0	32.3
15%	37.0	17.6	16.3
20%	45.0	22.3	14.0
Numbers in Sussex population	36.0	21.0	22.0

Results given are the means of three runs at each rate. Each simulation started with a single song type and ran for 100 years with an annual mortality of 40% and a constant population of 121 song types.

unique to a single bird than in the original data. This low mutation rate also leads to some types being very much more common than any were found to be in the populations we studied, suggesting that this rate is lower than that which exists in nature. The 20% rate, by contrast, leads to too many song types none of which is as frequent as the commonest ones in the original data. The best fit was obtained at the 15% mutation rate, with which both the number of song types produced and their frequency distribution matched the data rather closely.

These simulations suggest that about 15% of songs sung by young birds setting up their territories are new to the area, but do not allow us to decide the proportion of this due to mutation and that due to introduction. While the distribution of song types between birds makes it clear that most birds settle to breed in the same area as that in which they learnt their song types, occasional birds may move into the area having learnt their songs elsewhere (SLATER & INCE, 1979). Such immigration may account for some of the cases where new song types appear in the population. We can, however, conclude that the distribution of song types in the population is adequately accounted for on the assumption that birds copy their songs from other individuals at random and that less than 15% of these transmissions involve inaccuracies in copying leading to the creation of new types.

Number of song types in repertoires.

Individual male chaffinches have repertoires of between one and six song types. Fig. 2 shows the distribution of these repertoire sizes in three sets of data: those from our two study areas and that given by MARLER (1956). The variation in these data is quite considerable, yielding coefficients of variation of around 40% in each case (see SLATER, 1980). The simplest model which can be applied to distributions of this sort is the zero-truncated Poisson distribution, the distribution expected if birds learn one or more song types independently with the same fixed probability.

Theoretical distributions based on this model are also shown in Fig. 2. The results from Cambridge and from Sussex differ significantly from these (Cambridge, $\chi^2_4 = 22.82$, $p < .001$; Sussex, $\chi^2_4 = 12.75$, $p < .02$). Those from Orkney, while also showing a surplus of intermediate sized repertoires, do not reach significance, probably because of the small sample size ($\chi^2_4 = 2.98$). The Sussex data are probably the most suitable for a comparison of this sort, the sample size being relatively large and the mean repertoire size being the highest found. We can therefore be confi-

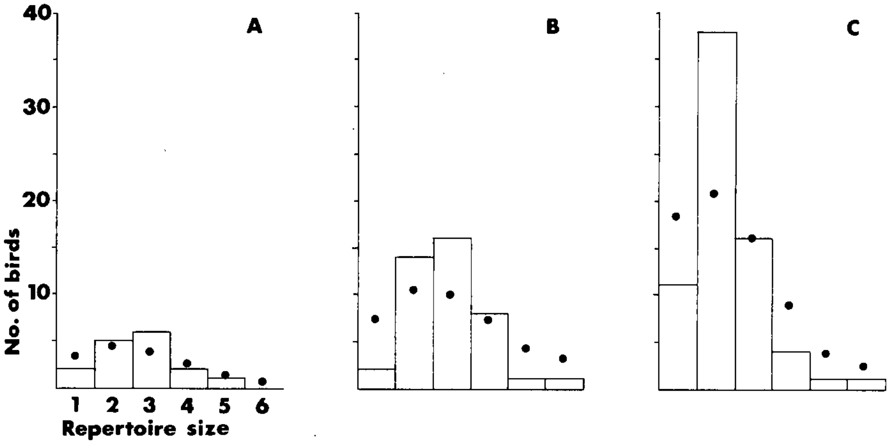

Fig. 2. Frequency of repertoire sizes of 1-6 song types in three different populations: A. Orkney (Mean = 2.7); B. Sussex (Mean = 2.9); C. Cambridge (Data from MARLER, 1956; Mean = 2.3). The black dots indicate the frequencies expected if repertoire size followed a zero-truncated Poisson distribution.

dent that the divergence in the distribution of repertoire sizes from that expected for this sample is a genuine one. We can conclude that song repertoires in this species tend to have a typical size of 2-3, with repertoires larger and smaller than this being rarer than expected on the basis of this simple model.

An alternative version of the same model also deserves consideration. This is the hypothesis that birds learn songs independently and with the same fixed probability, but that they may learn the same song type more than once. This idea is attractive for other reasons: unpublished data on the sequence in which different song types are produced, and on their relative frequencies, suggest that some birds may have the same song type twice in their repertoire and use it as if it were two separate types. Thus the repertoire sizes observed for some birds may be smaller than they actually possess. It is not easy to calculate the distribution of repertoire sizes which would be expected if repertoires were built up in this way. However, an estimate can be obtained by simulation, and the expected values shown in the third column of Table 2 have been obtained in this way. These are based on the supposition that birds in the Sussex population have built up their repertoires by drawing song types at random from the distribution of those available without the constraint that one type can only be learnt once. An iterative technique was used so that the observed mean repertoire size homed in on that found in the population (2.9 song types per bird). It did so when the actual repertoire size,

TABLE 2

Observed distribution of repertoire sizes in the Sussex population compared with that expected on two different hypotheses

Repertoire size	Number of birds with that repertoire size		
	Expected on Hypothesis 1	Observed	Expected on Hypothesis 2
1	7.2	2	6.5
2	10.4	14	11.8
3	9.9	16	10.6
4	7.2	8	7.3
5	4.1	1	3.9
6	3.3	1	1.8
	$\chi^2_4 = 12.75$		$\chi^2_4 = 8.87$
	$p < .02$		$.10 > p > .05$

Hypothesis 1: That birds learn one or more song types independently with the same fixed probability. Hypothesis 2: That birds learn songs independently with the same fixed probability but may learn the same song type more than once.

that including repetitions of the same song type as separate songs, averaged 3.26 and yielded the distribution shown in Table 2. This fits the data more closely than the earlier model ($\chi^2_4 = 8.87$, $.10 > p > .05$), but again predicts the occurrence of more large and small repertoires than was actually observed. However, as the discrepancy is not significant, it is possible that repertoires are built up at random in this way.

The distribution of song types among repertoires.

As chaffinches learn their songs from other individuals, it is possible that they might copy their complete repertoire from one other bird (for example, their father). If this were the case one would expect to find certain combinations of song types very frequently while other combinations were rare or absent. The alternative hypothesis, that song types are distributed independently and randomly across repertoires, appears more likely from inspection of the data. Unfortunately it is difficult to test this hypothesis statistically because the large number of song types produces many combinations with small expected values. The problem would not be alleviated by obtaining a larger sample, since such a sample would contain more song types. However, two lines of evidence support the hypothesis of independence. First, for repertoires of size 2, the expected values for independent combinations of the three most common song types (B, C and F) in the Sussex population have been calculated. The results are given in Table 3. Although a formal test is inappropriate,

TABLE 3

Combinations in which the three commonest song types (B, C and F) occurred in repertoires of two song types

Combination	Observed	Expected frequency
BC	1	0.73
BF	0	0.69
CF	1	0.50
BX	6	3.11
CX	1	2.26
FX	2	2.12
XX	3	4.55

Note: X is used to denote any of the other 33 song types found in the population.

it is clear that the observed and expected values are similar. Second, there are no clear trends in the frequencies of these three song types in different repertoire sizes and thus the hypothesis of independence appears reasonable. It seems therefore likely that repertoires are usually built up by copying from more than one other individual.

The distribution of rare songs.

The examination carried out above concerned only common song types because the others occur in very few repertoires so that the combinations in which they are found cannot easily be examined. However the distribution of rare songs, defined here as those noted in the repertoire of only one bird, can be studied both among and within repertoire sizes.

TABLE 4

Incidence of rare songs in repertoires of different sizes

Repertoire size	Frequency of that size	No. of slots in repertoires of that size	No. of slots occupied by rare songs	
			Observed	Expected
1	2	2	0	0.35
2	14	28	3	4.86
3	16	48	7	8.33
4	8	32	9	5.55
5	1	5	0	0.87
6	1	6	2	1.04

$\chi^2_4 = 5.70$

$.10 > p > .05$

Table 4 shows that the incidence of rare songs is independent of repertoire size. This argues against the possibility that birds can copy a small number of song types exactly but, where repertoire size is large, the additional types are generated by innovation. Instead, it appears that large and small repertoire sizes are as likely to contain rare songs. However, Table 5 shows that, within a given repertoire size, rare songs are not randomly distributed. Repertoires tend to contain too few or too many rare songs compared with chance expectation.

TABLE 5

The number of rare songs found in the same repertoire

	Number of rare songs		
	0	1	≥2
Observed no. of repertoires	30	5	7
Expected no. of repertoires	24.68	13.99	3.32

$\chi^2_1 = 10.99$ $p < .001$

Note: Expected values were calculate separately for each repertoire size and each number of rare songs and then combined for statistical testing.

DISCUSSION

In this paper we have shown that the relative frequencies of different song types in a population of chaffinches, with some types occurring in many repertoires and many types occurring in only a single repertoire, can be simply accounted for. The distribution fits that predicted by Ewens (1972) for neutral alleles, and closely similar distributions can be generated by computer simulations in which copying of song is normally exact but is less accurate on about 15% of occasions so that new song types are created. This 15% mutation rate is likely to be an overestimate as new song types can arise in the population through immigration as well as through mistakes in copying. The good fit of this simple model to the data suggests that songs are copied at random by young birds so that some song types are not selected for copying or copied more accurately than are others. Slater & Ince (1979) suggested that common song types might be more conservative than rare ones because young birds would often have more than one model available to them when learning so that minor individual idiosyncracies would be less likely to pass from one individual to another. If the accuracy of copying also depended on the number of repetitions of a particular song type that was heard, common types would also be expected to be less prone to change. The present results suggest, however, that neither of these factors is of importance.

The random copying of song types, with transmission errors occurring on a small proportion of occasions, suggests that the song types present in a population should change gradually over a matter of years. INCE, SLATER & WEISMAN (in press) compared the 36 song types in our Sussex population with 23 which had been recorded in the same wood 18 years previously and found only three which were similar enough to be considered as belonging to the same song type. Ten runs of a computer simulation based on these data and with a 15% mutation rate predicted the occurrence of 3.2 in common: again, a close fit to the data.

Other results reported in this paper suggest that, as well as the songs which are copied being chosen at random from the population, birds do not normally copy all their song types from the same individual. If they did so, the same combination of song types would tend to occur in several repertoires while other combinations would be rare or absent. However, there was no evidence that song types were other than randomly distributed between repertoires, although the small number of birds with a given song type made it impossible to test this statistically. The only departure from randomness found in the distribution of song types between repertoires was that individual birds tended to have either too many or too few rare song types. This result may arise for either or both of the following reasons. First, immigrant individuals may introduce rare songs into an area and may arrive having learnt more than one of their song types elsewhere. Second, some individuals, perhaps those hatched late in the season, may have less opportunity for learning the precise details of song than do others. As a result, their copying may be less exact and their repertoire more likely to have several new song types in it.

The main departure from randomness which we have found is in the distribution of repertoire sizes. This did not follow the zero-truncated Poisson distribution which would be expected if the probability of learning a song type was independent of the number already learnt. Instead, repertoires tended to be of a typical size, 2-3 song types, with fewer than expected either smaller or larger than this. Although the variation in repertoire size is great, it is not as great as this particular model would predict. A possible functional reason for this is that stabilising selection is in operation, birds with large or small repertoires being at a disadvantage compared with those having 2-3 song types, for reasons which remain to be explored. On the other hand, repertoire size could be constrained by opportunities for copying. A bird can only learn song types to which it is exposed and there may be a tendency for repertoire size to be influenced by the number of different song types which the young bird hears.

A different model of how repertoires might be built up, based on the idea that birds might learn the same song more than once, so that some individuals have a repertoire size larger than that observed, gave a rather closer fit to the data. While computer simulations based on this model also predict more large and small repertoires than were found in the Sussex population, the discrepancy is not significant. This suggests that at least some of the departure from randomness in repertoire size distribution may be because song types are not learnt at random, but songs are, so that the same type can be represented more than once in an individual repertoire. In some ways this is a simpler model for song learning than that which assumes that one song type can only be learnt once. Following on from the suggestion by KROODSMA (unpublished) that repertoire size may be limited by available "neural space", one can think of each individual as having a number of "memory slots" into which song types can be placed. The hypothesis that types are learnt randomly and independently of each other makes it necessary to assume interaction between slots so that one slot cannot contain the same song type as that already occupying another. If, however, songs are copied into different slots according to the frequency with which they are heard, then the same song type can occupy more than one slot, and it is not necessary to assume an interaction between slots. Further work to test this idea, involving the hand-rearing and training of young birds, is in progress.

The fact that the observed distribution of repertoire sizes and that expected on this hypothesis for song learning are not significantly different, makes it more likely that the distribution of repertoire sizes results simply from the random occurrence of opportunities to learn. If so, it is not necessary to provide a special functional explanation for why some repertoire sizes are more frequent than others. Some less tractable questions do, however, remain to be answered. Why does song have to be learnt? Why is it normally learnt so accurately? Why do birds have the capacity to learn more than one type?

SUMMARY

In a population of chaffinches (*Fringilla coelebs*) some song types are produced by many individuals while others occur only in the repertoire of single individuals. This frequency distribution of song types fits that predicted from a model for the frequency of neutral alleles, suggesting that song types are copied at random rather than some being favoured over others. Both comparison with this model and computer simulations suggest that the "mutation rate" in song copying is around 15%, changes in this case arising either

through immigration or because of inaccuracies in copying. Such a rate of change would also lead the songs present to change with time to much the same extent as we have found.

No evidence could be found that particular combinations of song types tended to occur more often than expected in the same repertoire, suggesting that repertoires are built up by copying from more than one individual. Rare songs (those unique to a particular individual in the population) do, however, tend to cluster in the same repertoire, probably because some of the birds possessing them are immigrants. Repertoire size clusters at around 2-3 song types but is not significantly different from that predicted if birds can learn the same song type more than once so that their observed repertoire size is smaller than that which they actually possess.

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ZUSAMMENFASSUNG

In einer Population von Buchfinken (*Fringilla coelebs*) werden einige Gesangstypen von vielen Individuen erzeugt, während andere nur im Repertoire von Einzeltieren vorkommen. Ein Vergleich der Häufigkeitsverteilung von Gesangstypen mit einem Modell für die Frequenz neutraler Allele ergibt, dass die Imitation von Gesangstypen ein zufälliger Prozess ist (d.h. es gibt keine bevorzugten Gesangstypen). Sowohl der Vergleich mit diesem Modell, als auch Komputersimulationen ergeben eine 'Mutationsrate' von ca. 15% für die Gesangsimitation. Bei dem hier beschriebenen System entstehen die Veränderungen durch Einwanderung oder durch Ungenauigkeiten beim Imitieren. Diese Veränderungsrate reicht aus, um die tatsächlich beobachteten Veränderungen zu erklären.

Es wurden keine Hinweise dafür gefunden, dass in demselben Repertoire bestimmte Kombinationen von Gesangstypen häufiger auftreten würden als erwartet. Die Repertoires werden also durch Imitation von mehr als einem Individuum aufgebaut. Seltene Gesänge (d.h. solche, die nur von Einzeltieren in einer Population erzeugt werden) haben die Tendenz, gehäuft innerhalb desselben Repertoires aufzutreten, vermutlich weil die Vögel, die sie produzieren Einwanderer sind. Die häufigste Repertoiregrösse liegt bei 2-3 Gesangstypen, unterscheidet sich aber nicht signifikant von der, die man erwarten würde, wenn die Vögel denselben Gesangstyp mehr als einmal lernen könnten. Das würde bedeuten, dass ihre beobachtete Repertoiregrösse kleiner ist als die, die sie in Wirklichkeit besitzen.

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Chaffinch Song Repertoires: Observations, Experiments and a Discussion of their Significance

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With 7 figures

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Abstract

In Part I data are presented on the relationship between song repertoires and territory in the chaffinch (*Fringilla coelebs*), on the ways in which individual males use their repertoires, and on the responses they show to song playback both inside and outside their territories. In Part II theories which have been put forward to account for the existence of song repertoires are discussed and criticised, and their possible relevance to this species examined. It is suggested that the most plausible reason for repertoires in chaffinches is that birds which possess them are more likely to be able to produce songs which intruders and neighbours find aversive.

Introduction

Many species of passerine birds have repertoires of different song types (see Krebs and Kroodsma 1980). The average size of these varies greatly from species to species: while some normally have only one song (e.g. white-crowned sparrow, *Zonotrichia leucophrys*, Baptista 1975; splendid sunbird, *Nectarinia coccinigaster*, Grimes 1974), others may have over 100 (e.g. mocking bird, *Mimus polyglottos*, Wildenthal 1965; short-billed marsh wren, *Cistothorus platensis*, Kroodsma 1977). Numerous theories have been put forward as to why birds have song repertoires (see Krebs 1977a; Smith and Reid 1979), and the main aim of this paper is to discuss these in relation to the song of one particular species, the chaffinch (*Fringilla coelebs*).

Male chaffinches have from one to 6 different song types (Marler 1956; Slater 1980): repertoire size is therefore small and relatively easily assessed, yet shows considerable variation. The chaffinch is a good species on which to

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analyse the significance of repertoire size because it has been studied extensively from numerous viewpoints: information is, for example, available on song learning (POULSEN 1951; THORPE 1958 a, b; SLATER and INCE in press), on geographical variation in song (CONRADS 1966; MARLER 1952; METZMACHER and MAIRY 1972; SLATER and INCE 1979; THIELCKE 1969), on the temporal organisation of song (HINDE 1958; SLATER and LESTER in prep.), and on the distribution of particular song types, their frequencies in the population and in the repertoires of neighbours (CONRADS 1979; SLATER et al. 1981; SLATER and INCE in press). All these studies provide relevant information and some further observations and experiments will be presented in the first part of this paper. Part II consists of a detailed discussion of the likely significance of repertoires in this species, drawing on the extensive literature on the subject as well as the results presented in Part I.

Part I: Observations and Experiments on Repertoires

In this section results will be presented on three different topics relevant to the significance of repertoires in the chaffinch. First, the relationship between the size and content of repertoires and aspects of territory ownership will be examined. Second, observations will be described on the way in which birds use their repertoires. Lastly, I shall give the results of experiments on the response of territory owners to the playback of song from loudspeakers placed either within or outside their territories.

Methods

Observational Data

The data to be presented here were collected partly in the woods at Finstown in the Orkney Islands, U.K. (59° N, 3° 6′ W), and partly in Stanmer Great Wood, Sussex, U.K. (50° 51′ N, 7′ W). The emphasis in these two sets of recordings was rather different and each will be used to analyse those aspects to which it is most appropriate. Nine birds were recorded in Orkney, the sample size ranging from 266 to 1839 songs. These data will be used to illustrate the proportions with which different songs are used. The Sussex data involve 42 birds, but fewer songs from each of them: the territories were, however, mapped and their areas assessed for the 27 individuals for which we could be confident that we had covered their complete territories and had studied the songs of all their neighbours. Territory boundaries were mapped by walking in various directions from a central position in each territory with a cassette recorder playing a tape loop of chaffinch song. In most cases this led the territory owner to follow the observer until the boundary was reached, when the bird would usually stop and sing. At least 50 songs were recorded from each bird and repertoire size was determined by sonagraphic analysis and playback at 1/4 speed (for further details see SLATER et al. 1981). Only those birds from which over 100 songs had been recorded were used to assess the proportion of different song types in the output. The recordings in Orkney were made between 14th April and 2nd June 1978, those from Sussex between 12th March and 5th June 1978. In both cases the majority were made during May and most individuals were only recorded during a short period within this time. Thus the sample is primarily of birds whose females were incubating and, being over a relatively brief period, the proportion of different song types in the output is unlikely to be affected by seasonal changes. In only one of the birds recorded in Orkney was there a suggestion of such changes.

Experimental Data

Two types of playback experiments were conducted. In the first 11 territorial males in Orkney were tested with three different song types: one possessed by a neighbour, one possessed by themselves and one from elsewhere in the islands. Two birds did not respond at all and are excluded from the analysis. Each song type was recorded on a tape loop giving one reproduction every 15 s and played back for 5 min from a speaker (Poly-planar P20) in the centre of the bird's territory using a Sony 153D recorder. Each bird was tested once with each category of song, but a test was repeated once if the bird failed to show any response in case this was due to absence from the territory; all tests of the same bird were on different days. There was no evidence of declining responsiveness over the small number of trials, but birds did differ greatly in the extent to which they responded and the way in which they did so. For example, some individuals would perch close to the loudspeaker and call repeatedly while others would fly silently to and fro above it. With birds behaving in such very different ways it is not possible to obtain a useful overall measure of responsiveness to playback. Only the form of the response shown will be considered here; a full consideration is inappropriate as the results are similar to those of Pickstock and Krebs (1980).

Two territorial males in Orkney with relatively large repertoires (4 song types) and few neighbours were tested with another form of playback. This consisted of playing song from loudspeakers placed outside their territory. These birds were given a series of tests ($N = 24$ and 32 respectively), half with one or other of the four songs in the repertoire and half with four other songs from another part of the islands. Each song was played once every 15 s from a speaker 10 m inside the territory of a neighbour using the same equipment as above, and playback was continued until the bird stopped singing or until 16 replies had been recorded. Playback was only commenced when the bird was singing and the data collected consisted of the sequence of songs during playback; this was compared with sequences during normal song recorded on different days to assess the influence of playbacks. A hand-reared captive male, which was kept in a cage in a sound proof chamber, was tested in a similar way. He had been trained with tape recordings of three song types, two of which he had learnt. He was given 12 trials with each of these two and 12 with a third song type he had not heard before. Each song type was played on a tape loop once every 30 s for 5 min, and all three were played each day at ½ h intervals, their sequences being balanced between days. Once again the songs produced in response to playback were recorded.

All the statistical tests employed throughout the Results section are two-tailed.

Results

1. Territory and Song Repertoires

Chaffinch territories, like song repertoires, vary very considerably in size. Territories measured by Marler (1956, p. 76) had an average size of around 7000 m^2 with a range from about 1000—12 000 m^2. 11 territories in an Orkney wood averaged 4400 m^2, while the 26 we have measured in Sussex gave a mean of around 26 000 m^2, with range of 6000—65 000 m^2. The small size of territories in Orkney may well be related to the longer daylength for foraging in the north, the lack of feeding competition from other species (particularly tits *Parus* sp., which are absent from the islands) and the fact that all territories bordered on fields in which the birds could spend some of their time feeding. The great variation in Stanmer Wood is probably related to the heterogeneity of the habitat there with the largest territories occurring in areas of larch plantation and where the density of beech trees was great so that there was little undergrowth. The smallest territories occurred in open ornamental park and in woodland with greater species diversity and dense undergrowth, like that in Orkney where territory size was similar. The great variation in territory size, both at Stanmer and between these studies, may relate both to habitat quality and to that of the territory holding individuals.

There was no suggestion of a correlation between repertoire size and territory size in the Sussex population ($r_s = +.026$, $n = 27$, n.s.). As birds vary considerably in the extent to which they share songs with other individuals in the population, it seemed possible that repertoire size as such is less important than repertoire quality: the ability that a given repertoire gives its possessor to match the songs of intruders or of neighbours. Several possible measures of this gave no clear relationship to territory size. There was only a weak positive correlation between territory size and the number of birds in the wood as a whole that the individual could match with at least one song type ($r_s = +.191$, n.s.) or the average number that it could match with each of its song types ($r_s = +.171$, n.s.). Neither was there any tendency for birds with large territories to be able to match more of their neighbours with at least one song type ($r_s = -.054$, n.s.) or a higher proportion of all the songs possessed by their neighbours ($r_s = -.121$, n.s.). Thus territory size does not seem to be related in any simple way to repertoire size or quality.

It would almost certainly be more appropriate to look for a relationship between repertoires and territory quality than territory size. The closest we can come at this stage to examining this point is to compare the repertoires of neighbouring birds. The territory quality of neighbours is likely to be similar because the habitat does not change over short distances and, indeed, neighbours do tend to have similar sized territories (correlation of territory size of each individual with mean size of neighbours' territories: $r_s = +.398$, $n = 26$, $p < .05$). Thus, if repertoire size is related to habitat quality, neighbours should have similar repertoire sizes. No such effect can be seen in Table 1, or is found when the repertoire size of each bird is correlated with the mean repertoire size of its neighbours ($r_s = +.167$, $n = 42$, n.s.).

The only influence of territorial neighbours on repertoire size which I have been able to detect is shown in Fig. 1: there is a significant negative correlation between repertoire size and the number of neighbours that an individual has ($r_s = -.354$, $p < .05$).

Table 1: The relationship between the repertoire sizes of neighbour pairs. Figures in the body of the table give the number of pairs in which the two birds had the repertoire sizes shown above and to the left. Expected values in brackets are based on chance association

Repertoire sizes	1 and 2	3	4, 5 and 6
1 and 2	28 (28.1)	27 (23.0)	12 (15.9)
3		14 (18.9)	14 (13.1)
4, 5 and 6			12 (9.0)

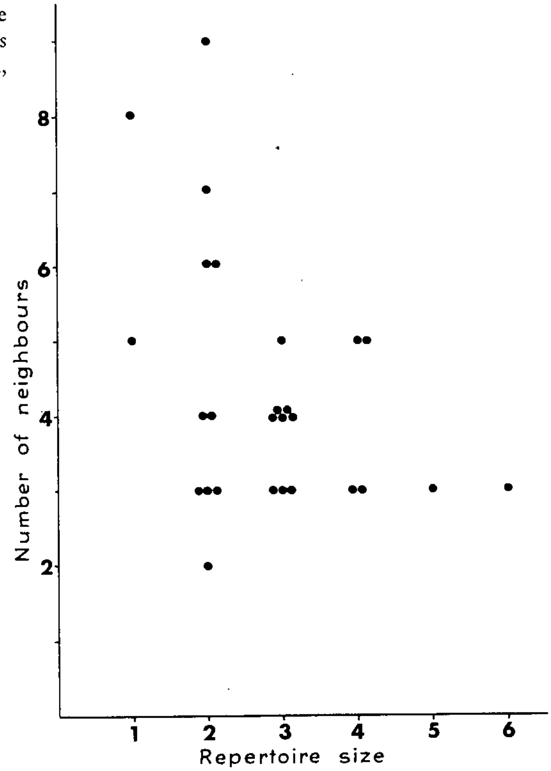

Fig. 1: Correlation of repertoire size with number of immediate neighbours for 27 birds in Stanmer Great Wood, Sussex (r_s = —.354, $p < .05$)

2. Repertoire Use

As with many birds which have small repertoires of song types, male chaffinches produce a series of songs of one type before switching to another (Hinde 1958) and individuals with larger repertoires tend to sing all their songs in turn before embarking on a second bout of any one of them (Slater and Lester in prep.). Table 2 shows the mean bout lengths and proportion of different song types in the output of the 9 birds from Orkney for which there are large samples of songs. In several of the individuals the songs occur in approximately equal proportions, but in others this is not the case and one or two of the birds had songs which they sang very rarely. Mean bout length does not vary with repertoire size (Kruskal Wallis test, H = 3.09, d.f. = 3, $.50 > p > .30$) although it does show a slight tendency to be smaller in birds with larger repertoires (Fig. 2). Lack of significance here may stem from the strong differences between individuals, as well as those between the songs of the same individual. Within repertoires of three or more songs the most frequent songs tend to occur in longer bouts ($r_s = +.931$, n = 19, $p < .001$) but, where the proportions of different songs vary rather little, individuals tend to show similar bout lengths for their different songs. Here it can be seen from Table 2 that some birds (e.g. bird 3) typically sing in very short bouts, whereas others (e.g. bird 2) sing longer series of each of their song types.

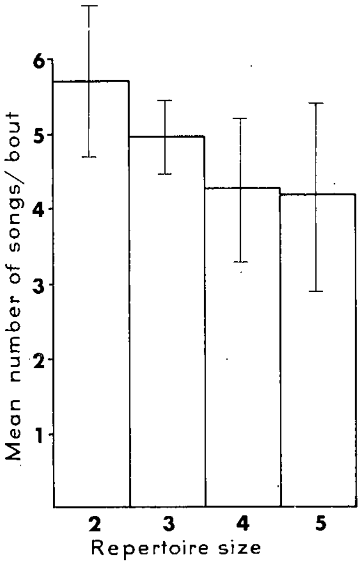

Fig. 2: The relationship between the mean number of songs sung in a bout of one song type and the repertoire size of the bird. Data are from 9 birds in Orkney. Ranges shown are standard errors

One reason why birds sing some of their song types more often than others may be that they are influenced by the songs possessed by their neighbours. Fig. 3 shows the proportion of a song in the output of a particular individual expressed as a percentage of that which would be expected if all the bird's song types were sung equally (to allow for differences in repertoire size) plotted against the number of neighbours the bird had with that song type. Detailed statistical testing is not easy because the songs in a single repertoire are not independent. There is, however, some suggestion from these data that birds sing a higher proportion of a song type when one or more neighbours

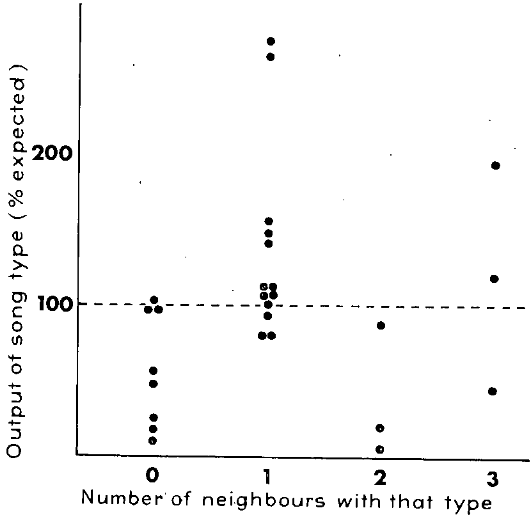

Fig. 3: The proportions of particular song types sung by 9 birds in Orkney plotted against the number of neighbours possessing each type. The proportion of each song type produced is expressed as a percentage of that expected if all the songs in a bird's repertoire were produced with equal frequency

Table 2: The percentage of different songs in the output of 9 birds from Orkney and the mean bout length of each song type

Bird	Song type	%	Mean bout length	Total songs recorded
1	B	27.5	4.6	417
	D	72.5	11.3*	
2	B	45.9	7.4	266
	C	54.1	6.2	
3	B	44.1	2.2	406
	C	55.9	2.6	
4	B	59.9	6.1	411
	C	40.1	5.2	
5	B	36.4	4.7	718
	C	31.9	4.9	
	D	31.8	5.1	
6	A	48.8	5.9	858
	D	45.3	6.3**	
	J	5.8	2.8	
7	A	26.3	3.7	950
	B	28.6	3.6	
	C	20.0	2.5**	
	D	25.1	3.5	
8	A	68.7	11.1	1839
	B	5.2	1.6	
	J	14.1	3.7**	
	Y	12.1	4.4	
9	A	53.3	7.0	1041
	B	39.3	7.0	
	D	0.5	1.5**	
	N	1.6	2.4	
	X	5.3	2.5	

Significant differences between bout lengths: * $p < .02$, Mann-Whitney U test; ** $p < .001$, Kruskal Wallis test.

possess that type than when none do (Fisher exact test, $p < .05$). This is not a strong effect, probably because birds cannot sing all their songs more than expected when all are shared with neighbours. It is also not apparent in our Sussex data, probably because these data are less extensive with only just over 100 songs having been recorded from some individuals included in the test.

The results in Fig. 3 might also arise if birds sang more of those songs in their repertoire which are common in the area without necessarily being affected by neighbours directly. No such effect could be found in the data from Orkney ($r_s = +.192$, $n = 27$, n.s.) or from Sussex ($r_s = -.065$, $n = 59$, n.s.) when the number of birds in the whole wood possessing a particular song type was correlated with the proportion of that type in the output of each bird singing it corrected for repertoire size.

3. Responses to Playback

There is a weak tendency for male chaffinches to respond more to song types possessed by neighbours than to types only from another wood when

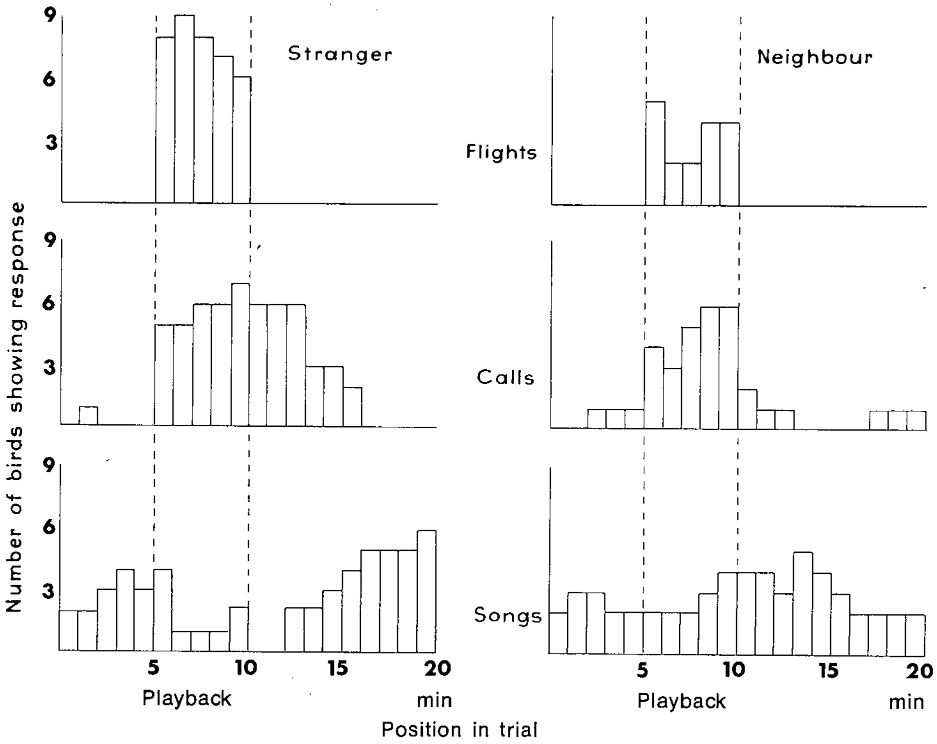

Fig. 4: The number of male chaffinches showing flights, calls and songs during playback tests involving song types not found in the area and those possessed by at least one neighbour (same 9 birds tested in each case). Data are plotted separately for each test minute with observations lasting for four 5 min periods with playback during the second of these

these are played inside their territories (Fig. 4). The most frequent reaction of male chaffinches to song playback on the territory is to fly up and down over the loudspeaker or to perch close to it and call, and more birds showed calling and flights in response to stranger song than to neighbour song. As Fig. 4 shows, where response is strong, as it is to stranger song playback, song is actually suppressed, although it rebounds after playback ceases. The lesser response to neighbour song may result because a bird at a distant point on its territory cannot discriminate between the song of a neighbour on his own territory and the same played from a loudspeaker rather closer at hand. The responses shown indicate that song played within a bird's territory is a very disturbing stimulus to a male chaffinch but not one to which he responds by singing.

The second series of playback experiments consisted of testing two singing males with song played from nearby but not on the territory. Brief details will also be given of the results from a captive bird played songs from outside his cage. The two different situations are examined together as all three birds responded by singing. In the wild males the playback was arranged from an adjacent territory and had the advantage that this stopped the neighbour

Table 3: Responses of birds to playback of songs in their own repertoire from outside their territories. Comparison of percentage matching with that expected by chance

Bird	Song type	N*	% matching	% expected
7	A	80	35.0	26.3
(Wild)	B	48	33.0	28.6
	C	48	85.4	20.0
	D	16	81.0	25.1
8	A	64	84.4	68.7
(Wild)	B	64	9.4	5.2
	J	64	20.3	14.1
	Y	64	18.8	12.1
Fr	B	157	47.1	53.8
(Captive)	F	137	44.5	46.2

* N = Number of responses over which the percentage matching was assessed. This varied according to the exact experimental procedure. Statistical treatment is inappropriate as successive songs are not independent.

from singing (as above) thus removing a source of complication. All birds were active singers and were tested with some songs which were in their repertoires and some which were not.

Both wild birds tended to move to the part of their territory closest to the loudspeaker and continue singing when playback began. If the song played was in their repertoire, they had a tendency to match it (Table 3) which grew over the first few responses (Fig. 5). On the other hand the sequential organisation of the song remained very similar to that which they showed in normal singing, although the proportion of unusual transitions (those which occur less than expected in normal song) was greater during playback in both birds and significantly so in one of them (Table 4). They thus showed a tendency to match and a slight tendency to make unconventional transitions, though not one which completely altered the sequencing of their songs. The

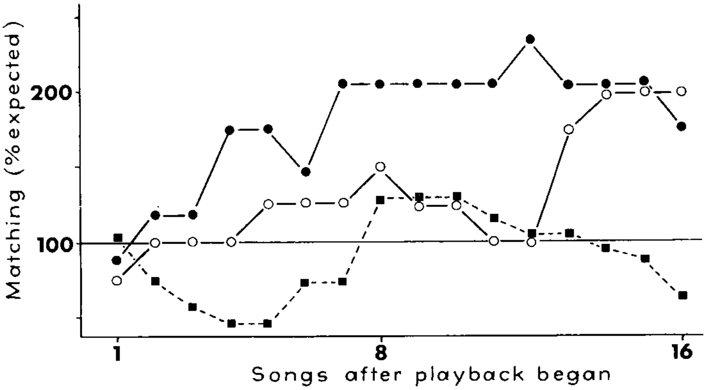

Fig. 5: Matching during playback of songs in the bird's own repertoire for the three birds tested. The number of matched responses is expressed as a percentage of that expected if the bird's singing was unaffected by the playback, and plotted for the first 16 responses given by each bird after the playback session began. Captive bird: ■ - - - ■

third bird showed much less of an effect, perhaps because he was a hand reared bird which had only previously heard three song types, two of which he had learnt. He showed no sign of matching either of these two (Table 3) and, with his small repertoire, sequencing could not be examined. His response to a third song type which he had not heard before included "chink" vocalisations on 5 out of 12 trials, while he did not produce these on any of the trials with the songs which he possessed and had heard frequently during training. The strangeness of this song may have been responsible for the stronger response, rather more like that of the wild birds tested with speakers on their territories.

Table 4: Song sequences during normal singing and during playback. The matrices show, for each bird, the number of instances in which the song type on the left was followed by that above. Homogeneous transitions are not considered and the figures in brackets are expected values which take this into account. Departures from random sequencing are analysed using χ^2 as is the extent to which sequencing during playback differs from that during normal song

(a) Bird 7

Normal singing	A	B	C	D
A		33 (20.4)	18 (23.4)	12 (19.1)
B	17 (20.6)		25 (26.2)	26 (21.2)
C	24 (22.0)	20 (24.3)		25 (22.7)
D	19 (17.5)	11 (19.3)	29 (22.3)	

χ^2 = 20.3, d. f. = 5, p <.01

Playback	A	B	C	D
A		6 (4.3)	8 (9.8)	3 (2.9)
B	7 (7.5)		11 (10.4)	3 (3.1)
C	9 (7.5)	3 (4.5)		3 (3.0)
D	1 (2.0)	1 (1.2)	4 (2.8)	

Data too few for testing

	Common transitions*	Uncommon transitions*
Normal song	156	103
Song during playback	26	23

χ^2 = 0.44, d. f. = 1, n. s.

* Common transitions are defined as those which occur more frequently than expected during normal song. The test detects whether more unconventional transitions take place during playback.

Table 4 (continued)

(b) Bird 8

Normal singing	A	B	J	Y
A		9 (28.9)	45 (35.5)	35 (24.5)
B	37 (27.2)		7 (13.5)	6 (9.3)
J	16 (32.7)	37 (13.2)		4 (11.2)
Y	29 (22.1)	5 (8.9)	8 (11.0)	

$\chi^2 = 89.3$, d. f. = 5, $p < .001$

Playback	A	B	J	Y
A		6 (15.7)	12 (6.9)	9 (4.3)
B	20 (15.9)		12 (13.6)	6 (8.5)
J	1 (7.8)	24 (15.1)		2 (4.2)
Y	8 (5.3)	11 (10.2)	1 (4.5)	

$\chi^2 = 33.4$, d. f. = 5, $p < .001$

	Common transitions	Uncommon transitions
Normal song	183	55
Song during playback	73	39

$\chi^2 = 4.74$, d. f. = 1, $p < .05$

Discussion

The results presented here allow some tentative conclusions to be reached about chaffinch song repertoires. No suggestion could be found that a larger repertoire, or one containing more common song types, enabled individuals to maintain larger territories. A large territory could be taken to indicate that the individual was particularly effective at territorial defence, but it is as likely that large territories occur where the habitat is suboptimal so that a greater area is required to ensure sufficient food for breeding. Thus the fitter individuals would be more likely to nest at higher densities and, if repertoire size is a measure of fitness, this should be inversely related to territory size. On the other hand repertoire size should be positively related to territory quality (Howard 1974; Krebs 1977 b). Because of the diversity of the habitat it is not easy to obtain any measure of territory quality in our population, although long-term studies might indicate that certain territories or areas of the wood were more productive in terms of nestlings than others. As neighbouring territories are similar in size and likely also to be similar in quality, the repertoire sizes of neighbours were examined, but no suggestion was found that these were related.

No easy explanation can be put forward to account for the finding that birds with smaller repertoires tend to have more neighbours. Individuals which learn songs while they are setting up their territories would be expected to obtain larger repertoires if they had more neighbours to copy from so that this result is in some ways the opposite of expectation. However, we have found that chaffinches have no more song types in common with their neighbours than would be expected by chance and that they are capable of learning songs as fledglings (SLATER and INCE in press). The extent to which songs are learnt from neighbours is therefore doubtful. The correlation between repertoire size and number of neighbours might therefore be expected to be low, but there is no obvious explanation for the fact that it is negative.

As far as repertoire use is concerned, the observations reported here suggest that some birds use the different songs at their disposal more or less equally while in others this is far from being the case. Where the proportions of different songs are similar, individuals tend to sing a bout of each type in succession without returning to the first until their repertoire has been exhausted. In the data from Orkney, departures from equality of song use have been found to relate to sharing of songs between neighbours, songs being used more than expected if they are shared and less if they are unshared. It seems most likely that this effect arises through the influence of matched countersinging in raising the proportion of shared songs in the output.

All the data on proportions of different songs in the output of individual birds were collected over a short period of time to avoid, as far as possible, the influence of seasonal changes in proportions. These sometimes occur in captive chaffinches (HINDE 1958; pers. obs.) and in wild individuals (Dr. H.-H. BERGMANN pers. comm.; pers. obs.), and may be related to the overall amounts of singing shown by different neighbours and to the stage of the breeding cycle. It is certainly true that song output varies with the breeding cycle being, for example, high when the female is incubating and low subsequently when the male assists in caring for the young. It is also the case that some birds sing very much more than others regardless of the stage of the season. This may relate to stability of neighbour relations, birds in settled areas with familiar neighbours singing less than those which suffer more intrusions from neighbours and others.

The playback experiments which were carried out were aimed at testing the response of territorial males to the song of others. The results of song playback from a loudspeaker on the bird's territory were in agreement with those reported by PICKSTOCK and KREBS (1980) in indicating a weak tendency for males to respond more to stranger song than neighbour song. Similar results have been reported for many other species (e.g. WEEDEN and FALLS 1959; HARRIS and LEMON 1976; GOLDMAN 1973). In chaffinches, where response is strong the birds usually call repeatedly or may fly up and down over the loudspeaker but they do not tend to sing. Thus, while song is certainly a signal to other males to keep out, it does not appear to be used in the active repulsion of intruders. By contrast, playback from the territory of a neighbour led the two individuals tested in the field to approach and sing actively from the nearest point to the speaker within their own territories. As also reported by HINDE (1958), they showed some tendency, where this was possible, to match the song played. These experiments therefore point to song having a role in the relationship between neighbouring birds. It may also intimate ownership to other potential intruders even though it does not appear to be used in expelling those that do encroach.

Part II: Why Do Chaffinches Have Song Repertoires?

There have been many suggestions as to why birds have song repertoires (see KREBS 1977a; SMITH and REID 1979 for accounts), but it is not easy to discriminate between these by either observation or experiment. Given the diversity of singing behaviour in birds it is particularly true that findings on one species may not be relevant to another. It is also the case that in any one species several different selective forces may have combined to give rise to repertoires. Especially if these forces pull in different directions, so giving features of singing behaviour which are a compromise, the evidence for any one of them may be very weak. In this section I would like to consider a number of ideas which have been put forward in the literature to account for the evolution of bird song repertoires, together with some which appear not to have been proposed before, and discuss their relevance to what is known of singing in chaffinches, both from previous work on the subject and from the data presented in Part I of this paper.

Theories for the Evolution of Repertoires

1. *Different songs have different functions.* This has been suggested for a number of species (e.g. by MORSE 1970; LEIN 1972; SMITH et al. 1978). There is, however, no evidence of this in chaffinches: song types do not fall into categories of which all birds have representatives and which could convey different messages, birds vary greatly in repertoire size with a sizeable proportion having only one type (MARLER 1956; SLATER et al. 1981) and, as shown here, song sequencing differs rather little between normal song and response to playback. These features would not be expected if songs varied in their contexts.

2. *Repertoires arise because females prefer males with more varied song (intersexual selection).* Males with more song types may be chosen by females if repertoire size somehow reflects male fitness. Evidence for this comes from species in which males with large repertoires have been found to mate earlier (HOWARD 1974; CATCHPOLE 1980) and circumstantial evidence implicates it where repertoire size is large and singing stops after pairing (CATCHPOLE 1973, 1976). It is less likely in those species, such as the chaffinch and the great tit (*Parus major*, KREBS 1977b) where repertoire size is small and variable, and where pairing is completed very early in the song season. Many chaffinches

are paired soon after song starts in February, yet the most active singing period is usually when the female is incubating in May and June.

3. Repertoires arise through intrasexual selection. Males with large repertoires are better able to obtain and keep high quality territories. Howard (1974) argues that this is the major selection pressure behind the extreme elaboration of repertoires in mocking birds as he found repertoire size in this species to be best correlated with a measure combining territory size and quality; Yasukawa et al. (1980) also argue that this is the most important factor leading to repertoires in red-winged blackbirds (*Agelaius phoeniceus*). Krebs (1977b) found repertoire size and territory size to be correlated in great tits, but only after correcting for "neighbour pressure", arguing that this leads territories to be smaller in the centre than on the edge of the wood. He suggests that territory size and quality are likely to be related in his study area as the habitat is fairly uniform. These arguments are not strong but, as later work has shown larger repertoires to be more effective in keeping out intruders (Krebs et al. 1978) and that males with larger repertoires have greater lifetime reproductive success (McGregor et al. 1981), intrasexual selection does seem a likely reason for repertoires in the great tit. The evidence would be stronger, however, if good reasons could be put forward as to why it has been impossible or disadvantageous for individuals with smaller repertoires to build up larger ones, and why repertoire size should be related to ability at territory maintenance. In the chaffinch we have been unable to find clear relationships between territory size and repertoire size or quality and, as the number of birds involved is quite large, this is unlikely to be due to shortage of data unless the effect is very small. It is nevertheless likely that the main function of repertoires in this species lies in some aspect of territorial defence because of the distribution of singing through the season (with the peak during incubation for many birds), the existence of countersinging between neighbours and the responses we have found to song playback. It is thus worth considering ways in which larger repertoires might assist in territory maintenance and also why repertoire size is so small and variable in this species. There are several possible ways in which repertoires may function in territory maintenance.

3a. Large repertoires reduce habituation on the part of the listener. Hartshorne (1956, 1973) suggested that birds switching often between songs were able to sing more continuously without the performance becoming monotonous, and amassed a good deal of evidence to demonstrate a relationship between continuity and versatility of song. This has been questioned by Dobson and Lemon (1975), but analysis by Kroodsma (1978) suggests that the basic relationship does hold: as a result birds with smaller repertoires tend to sing less continuously than those with large ones which can generate more immediate variety in their output. The most basic and important question is, however, whether this is in any way related to habituation on the part of singer or listeners. Invoking habituation as a fundamental phenomenon which cannot be got round without song becoming elaborate or discontinuous is a very weak argument. It could equally be argued that the hearer will not habituate if it is advantageous not to do so regardless of the form of song.

Why then might the continuity and versatility relationship exist? I think it most likely to be because continuous and discontinuous songs serve rather different functions. Song in continuous singers seems likely to have arisen primarily through intersexual selection, leading to great elaboration. Continuity is possible here because the individual is not listening for a reply, whereas in discontinuous singers the song is primarily a signal between males, a system which does not require extreme elaboration of repertoires but does require that an exact message be received by the hearer (hence the high redundancy in many species with the same song being repeated several times before a switch) and the interpolation of short intervals between songs so that the singer can listen for possible replies. This seems a much more likely reason for HARTSHORNE's correlation than those previously proposed, which are made unlikely by the assumption that habituation is inevitable.

3b. The Beau Geste effect. KREBS (1977a) argued that birds with large repertoires may exclude intruders by creating the impression that there is more than one individual on their territories. In a recent test YASUKAWA (1981) has found evidence compatible with this idea in red-winged blackbirds, but points out that none of the possible tests is very strong and that the data could easily be interpreted in other ways. There are a number of difficulties in applying this idea to chaffinches, some of which are also true of other species. First, song repertoires are highly variable (SLATER 1978; CONRADS 1979). KREBS (1977a) suggests that intruders might take repertoire size into account when assessing the number of individuals present by comparing the number of songs heard with their own repertoire size. Thus birds with relatively large repertoires would often be mistaken for more than one individual. This is a weak argument based, like that on habituation, on the idea of a basic phenomenon which cannot be circumvented by selection. Why should birds not take variance into account as well as repertoire size? Second, SLATER et al. (1981) showed that similar songs are as likely in the same repertoire as dissimilar ones, while a Beau Geste bird would be expected to maximise differences. Third, as I have shown here, birds have some songs which they very seldom sing while a Beau Geste bird would be expected to use all songs equally. Fourth, as SLATER (1978) suggested, this hypothesis would predict immediate switching between song types to maximise apparent variety, just as HARTSHORNE (1973) predicted immediate variety to cut down on habituation. KREBS (1978) replied to this point, but his reply was based on the idea that the listener needed to identify precise song types in the output of the singer and should therefore be presented with a series of the same type to make this possible. This is not the case: all that is required for Beau Geste is that one type be heard as different from another. If two songs in a row are the same such a difference does not exist; if they belong to different types however it will always be possible that the difference will be detected regardless of how noisy the channel is. Thus the more short term variety the larger the repertoire size would appear to be (see Appendix for a more formal statement of this idea). Seen from another angle, if all chaffinches sang a single song type, a mutant bird with two types would most effectively mimic the presence of two birds on its territory by alternating those types as two birds would do if they were present. Finally, is the allied point that neighbours would not be expected to show matched countersinging because this reduces the variety in the area and should therefore encourage intruders. For all these reasons the Beau Geste hypothesis does not seem very likely to apply to chaffinches. It also seems implausible as a general idea because of the assumption that selection would not lead to listeners seeing through the deception.

3c. Song repertoires indicate length of ownership. Particularly in species in which repertoires become larger with age (e.g. NOTTEBOHM and NOTTEBOHM 1978), or change during the breeding season (HALL-CRAGGS 1962), their size or state of development could give listeners an indication of length of ownership of a territory. It might thus benefit a possible intruder to avoid birds with large repertoires as these would be more likely to have been present for longer and thus have a nest and eggs or young making the territory more valuable to them. Repertoire size would also indicate proven ability at territorial defence, and this again might deter potential intruders. Such a mechanism could lead to progressively larger repertoire sizes (as with intersexual selection). It is not applicable where repertoire size is small and, as in chaffinches, where it is fixed early in life (THORPE 1958 a), but I put it forward as a possible alternative to intersexual selection for the origin of very large repertoires.

3d. Larger song repertoires are more likely to include particular song types. In its broadest form this hypothesis suggests that certain song types are more effective as deterrents than are others. Thus the larger a bird's repertoire, the more likely he is to include them. There are several reasons why some song types may be more effective than others.

1. If there was a correlation between particular song types and fighting ability, birds might avoid songs possessed by individuals which had previously beaten them in a fight through a simple conditioning mechanism. Thus the larger the repertoire the more likely it would be to contain a song or songs found frightening by a particular intruder (or attractive to a particular female by an equivalent argument). There is little direct evidence for effects such as this but experiments on the deterrent effect of repertoires (e.g. KREBS et al. 1978) could as easily be compatible with this hypothesis as with ones suggesting that repertoire size as such is important.

2. If song is passed from father to son then individuals may be better able to exclude brothers from their territories because their songs will match more precisely than will those of nonrelatives and it is advantageous to both to avoid competition. TREISMAN (1978) proposed that birds might then benefit from learning other song types and thus pretending relationship where this did not exist. The passing of song from father to son has been reported for a few species in the laboratory (IMMELMANN 1969; NICOLAI 1959) but does not appear to be common. One must also be cautious about generalising from laboratory experiments to the situation in the wild. Chaffinches can learn complete songs as fledglings (SLATER and INCE in press) but it is not known how common this is or how much of it would be from the father. There is no suggestion that birds with like songs tend to nest on adjacent territories as has been predicted if relatives share songs (TREISMAN 1978). This therefore seems

an unlikely hypothesis as far as neighbour relations are concerned although other intruders, looking for territories to take over, could still be excluded and may be a more important selective force on repertoire development than are neighbours which have, after all, got territories already.

3. A third related theory concerns the suggested importance of song matching in relations between neighbours. Although the effect found here (see Part I) was not very strong, in many bird species matched countersinging is normal between territorial neighbours. ARMSTRONG (1973) suggests that matching may enable birds to "name their opponent" in song duels; BERTRAM (1970) argues that matching is the equivalent of flinging an insult back at a rival; LEMON (1968) considers matching to be involved in "territorial homeostasis"; KREBS et al. (1981) suggest that matching may act as a graded signal in territorial disputes. All of these ideas seem unlikely to apply to the chaffinch as sharing between neighbours is only at a chance level (SLATER and INCE in press). This is probably because chaffinches do not learn further songs after the first 13 months of life (THORPE 1958 a). If matching of neighbours was really important as a reason for repertoire development, the capacity to learn songs from those neighbours would be likely to have evolved so that birds would share at least one song type with each neighbour. In chaffinches, with

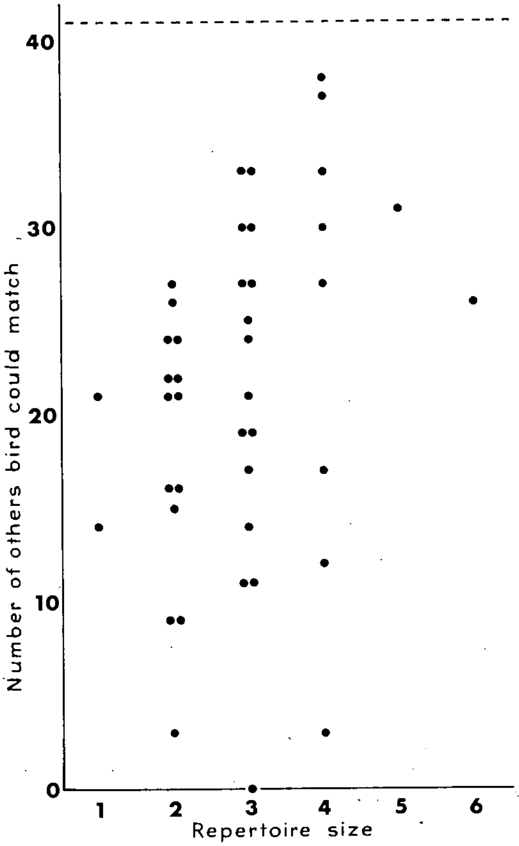

Fig. 6: Repertoire size and ability to match other individuals in the population with at least one song type for 42 birds in Stanmer Great Wood, Sussex. For each bird the plot shows how many of the 41 others in the wood it was capable of matching

the song types possessed by neighbours independent of one another, the mean number of song types shared by neighbour pairs was 0.67. KREBS et al. (1981) give a figure of 0.65 for great tits, a species with a similar repertoire size to the chaffinch, so that I would argue here also that matching between neighbours is unlikely to be a major reason underlying the evolution of repertoires. Similar arguments cannot be made about the matching of intruders who are not neighbours as, in that case, the more songs an individual possesses the more likely he is to be able to match an unknown individual from the population. Fig. 6 shows that there is a great deal of variation around this basic trend because birds with songs unique to themselves, either because they learnt them elsewhere or because their copying was not exact (see SLATER et al. 1981), can match no others while those with very common songs can match many even with a small repertoire. The fact that larger repertoire size does not necessarily increase the capacity to match, a point also noted by KREUTZER (1979) in cirl buntings (*Emberiza cirlus*), may help to explain why repertoire size is so varied.

4. Lastly, a larger repertoire size will make an individual more likely to sing one or more song types which were possessed by the previous owner of its territory (see PAYNE 1978 for a similar argument). Playback experiments on many species, including the chaffinch (PICKSTOCK and KREBS 1980; results reported in Part I), suggest that males respond less to the songs of neighbours than to those of strangers. A young bird setting up its territory for the first time may therefore incur less aggression from its new neighbours if it sings one or more songs similar to those that the neighbours had heard previously on the same boundary. Larger repertoires, or ones which included more common song types, would increase the chances of this. By experience the young male would also be likely to learn which of his songs were most effective in excluding neighbours and which led to antagonism. As a result he might well come to sing some types more commonly than others.

Conclusions

Of all the many theories of repertoires outlined above, those concerned with producing particular song types, either because they were possessed by the previous territory owner or because intruders respect and avoid them, seem, at this stage, the most plausible in the case of the chaffinch. While the data are not conclusive, many characteristics of chaffinch song would fit in with such functions:

(i) Song is learnt extremely accurately in over 85 % of instances (SLATER et al. 1981). This accuracy is essential to any matching theory but would not be necessary for any theory which suggested that repertoires existed simply to increase variety.

(ii) During singing males repeat one song type several times before switching to another. As distinct song types can be very similar (CONRADS 1979; SLATER and INCE 1979), such redundancy is likely to be necessary so that the listener can identify the song type accurately.

(iii) Singing birds produce bouts of each song type in turn before returning to the first again. This increases the chances of presenting an intruder with a type which is aversive, for whatever reason.

(iv) Songs are separated by intervals of several s (HINDE 1958), making it possible for the individual to listen for responses of intruders and to check the location and response of territorial neighbours.

(v) Neighbours do not share song types more than expected, suggesting that matching between neighbours is not of primary importance.

(vi) Birds do not learn new songs after 13 months of age (THORPE 1958 a), a point problematic for other theories but reasonably compatible with this one. If birds benefit largely from matching intruders and producing the songs of the previous territorial owner, then copying from neighbours is not necessarily advantageous. It is more likely to be of advantage to have a complete repertoire when first setting up the territory.

(vii) The large repertoire size variation may well simply result from differences between individuals in learning opportunities, bearing in mind that where matching is important song must be learnt precisely if it is to fulfil this function.

(viii) Given that some songs are copied inaccurately, if matching is important, repertoire size is less likely to relate to measures of territory worth than is repertoire quality, as discussed earlier. The lack of correlation between repertoire quality, as measured in Part I, and territory size may be because this measure of quality does not take account of similarities with the song types sung by the previous occupant.

(ix) Some birds sing a disproportionate amount of certain song types. These may be those types the individuals have learnt to be particularly effective in excluding intruders, possibly because they were possessed by the bird's predecessor in the same area.

In all these respects chaffinch song seems to fit well with the idea that repertoires help birds to match particular song types and thereby assist in excluding other individuals from their territories. This evidence is, however, primarily circumstantial. To achieve greater certainty what is needed is information on how effective different song types, both rare and common in the area, are at excluding intruders, more sophisticated measurements of territory quality to relate to repertoire measurements and, finally, long term studies to see whether birds setting up territories tend to have similar song types to those they succeed.

A final point is worth making, and this concerns the relationship between repertoires and song learning. NOTTEBOHM (1972) proposed that the development of bird song originally took place without learning playing a part and suggested various reasons why selection might have favoured a move to vocal learning. Learning is likely to lead to greater variability in song, if for no other reason than that transcription errors during learning are very much more frequent than those occurring during genetic transmission (SLATER et al.

1981). Birds with relatively fixed songs could match many different individuals (perhaps even all members of their own species if song was particularly stereotyped) with a single song type. With the move to vocal learning, and the greater variety between birds that this generated, precise matching of other individuals could only be achieved where copying was exact and would be made more likely by the possession of more than one song type. If matching is important, the evolution of song learning may therefore have been followed by the evolution of repertoires in species, such as the chaffinch, which have a small number of song types usually copied from other individuals very precisely.

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Summary

Repertoire size in the chaffinch (*Fringilla coelebs*) varies from one to six song types. No relationship could be found between territory size and repertoire size, nor with measures of repertoire quality made on the assumption that common song types would be more effective than rare ones. The different song types in a male's repertoire are often used very unequally. Playback of song within the territory of a male leads him to call or fly up and down over the speaker and also depresses his singing if response is strong. Playback from a neighbouring territory leads to approach and singing, with a tendency towards matching in two out of three birds tested if the song played was in their repertoire. However, matching was not very strong and was constrained by the tendency to sing songs in rather stereotyped sequences.

These results, and those of previous work on this species, allow some consideration of the likely significance of song repertoires. The evidence is against chaffinch repertoires having arisen because different song types have different functions, because females prefer males with larger repertoires, because larger repertoires reduce habituation, because they suggest the presence of more individuals or because they give a measure of age or length of ownership. In a species such as this where song learning is usually very accurate their most likely significance lies in the ability they confer to produce songs which are the same as those of other individuals. Such an effect may involve matching songs which are the same as those of neighbours, or of possible intruders. Alternatively it may involve producing songs which neighbours or intruders do not possess but find aversive because of past experience. Amongst reasons for the latter is suggested the hypothesis that young males may benefit if they can produce songs which match those of the previous occupant of their territory.

Zusammenfassung

Das Repertoire des Buchfinken (*Fringilla coelebs*) umfaßt ein bis sechs Gesangstypen. Es konnte keine Beziehung zwischen der Größe des Reviers und der des Repertoires gefunden werden, auch keine zu dessen Beschaffenheit, die in der Annahme untersucht wurde, daß häufige Gesangstypen wirksamer sind als seltene. Die einzelnen Gesangstypen im Repertoire des Männchens ertönen oft mit unterschiedlicher Häufigkeit. Tonbandwiedergabe von Gesang innerhalb seines Reviers veranlaßt das Männchen zu rufen oder über dem Lautsprecher auf und ab zu fliegen. Bei starker Reaktion hört das Tier auf zu singen. Tonbandwiedergabe in einem benachbarten Revier löst Annäherung und Gesang auf. Dabei neigen die Tiere dazu, ihren eigenen Gesang dem dargebotenen anzupassen, vorausgesetzt, dieser ist im eigenen Repertoire enthalten. Diese Angleichung ist jedoch nicht sehr stark ausgeprägt und wird durch die geringe Veränderlichkeit der Gesangsfolgen eingeschränkt.

Diese Befunde, zusammen mit denen aus vorangegangenen Arbeiten über dieselbe Art, erlauben einige Betrachtungen über die vermutliche Bedeutung von Gesangsrepertoires. Die Befunde sprechen gegen die Deutungen, die Repertoires der Buchfinken seien entstanden, weil verschiedene Gesangstypen unterschiedliche Funktionen haben oder weil Weibchen diejenigen Männchen bevorzugen, die die größeren Repertoires besitzen; oder weil größere Repertoires Habituation verhindern; oder weil sie die Gegenwart mehrerer Individuen vortäuschen; oder weil sie ein Maß für das Alter oder die Besitzdauer sind. Bei einer Art wie Buchfinken, die ihre Gesänge gewöhnlich sehr genau lernen, liegt ihre Bedeutung am wahrscheinlichsten in der Fähigkeit, die eigenen Gesänge denen anderer Individuen anzugleichen. So kann es dazu kommen, daß der Revierinhaber dasselbe singt wie Nachbarn oder Eindringlinge, oder er singt etwas, daß nicht zu ihren Gesängen paßt, sie aber aufgrund früherer Erfahrungen abstößt. Neben einer Reihe anderer Gründe, die für letztere Funktion sprechen, wird auch angenommen, daß es für junge Männchen vorteilhaft sein kann, wenn sie Gesänge haben, die denen des vorangegangenen Revierbewohners gleichen.

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Appendix

Song Repetition and Repertoire Size Assessment

Using arguments from signal detection theory, KREBS (1978) suggests that song repetition may be advantageous for birds conforming with the Beau Geste hypothesis i. e. which have been selected to impress others with the size of their repertoires. However, his reasoning assumes that a single signal has a low probability of detection (0.24) and that the probability of detection rises to more than four times this value if the signal is repeated four times. While repetition will certainly make a signal more likely to be detected, such a very great improvement is highly improbable. It is true, as KREBS argues, that a bird listening to the sequence AAAABBBBCCCC will detect more of the song types on average than one which hears ABC, but this is not a reasonable comparison as the total number of songs heard is not the same. Nor is the problem a simple one in signal detection: the task which the bird has is to detect whether a song type heard is the same as or different from others it has heard previously and so assess the repertoire size of the individual to which it is listening.

Fig. 7 shows the number of song types which should be detected on average in two sequences of 25 songs in each of which 5 song types are repeated 5 times, but in one case the sequence is AAAAABBBBBCC... and in the other it is ABCDEABCDEAB... In both cases the probability of identifying a song type well enough to distinguish it from others is 0.5 the first time it is heard and rises with repetitions according to the formula $p_n = 1 - (1 - p)^n$ so that it approaches an asymptote. As the Figure shows, immediate switching gives a greater apparent repertoire size, unless the listener hears the whole sequence, and this would be so for all probability values and also for other likely forms of improvement in detection with repetition such as that depending on $\sqrt{n}$ (GREEN and SWETS 1966). The only case where it would not hold is in the improbable circumstance that the rate of improvement, instead of approaching an asymptote, rises with number of repeats. This is the case that KREBS considered. One assumption made for the plots in Fig. 7 may mean that this model underestimates the effectiveness of immediate switching. It is assumed that the bird hearing a song on several occasions sharpens up its memory of that song and becomes more likely to be able to distinguish it from others. While this seems reasonable where the same song is repeated several times in a row it is less likely when other songs are interposed between repeats. This type of sequence will lead to greater apparent variety and to greater difficulty in achieving an accurate assessment of repertoire size. It might therefore be an even more effective strategy for the Beau Geste bird than it appears to be in Fig. 7, the hearer being confused into thinking the repertoire greater than it actually is.

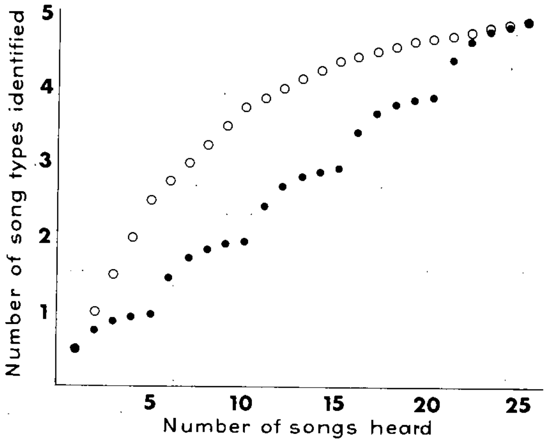

Fig. 7: The number of song types detected in the repertoire of a singing bird by a listener hearing a sequence of 25 songs. The singer has a repertoire of five songs sung either in the sequence ABCDEABCDE... (o ——— o) or with five repetitions each in the sequence AAAAABBBBB CC... (●——— ●). In both cases the probability of a song type being identified as a new one when first heard is 0.5, but successive repetitions raise the probability of identification towards an asymptote at 1.0

These arguments suggest that the advantages of repetition proposed by KREBS (1978) would only be found under the very special circumstances which he considered: low initial probability of detection and greater than linear increase in this with repetitions. More realistic assumptions lead to the conclusion that a listener is likely to detect more song types if these are sung with immediate variety than if each is repeated several times before the bird moves on to the next.

SONG DEVELOPMENT IN CHAFFINCHES: WHAT IS LEARNT AND WHEN?

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In his classic study of song development in the Chaffinch *Fringilla coelebs*, Thorpe (1958) concluded that young birds learn the details of their songs from other individuals during the first 13 months of life. Birds which were hand-reared and kept in auditory isolation developed abnormally simple songs without clear phrasing. If, however, such birds were trained with tape-recordings of normal song during the winter and spring of their first year the songs which they developed were normal. Some hand-reared birds showed evidence of learning songs in which the terminal flourish had been artificially transposed to the middle but birds caught in the autumn would not do so. From this Thorpe argued that young males learn the basic structural features of Chaffinch song in their first summer before the males around them have ceased to sing but do not add the fine details until the following spring, when they start to sing themselves and hear the songs of their territorial neighbours.

Many of the birds which Thorpe trained developed songs which were loosely based upon the songs which they heard rather than being accurate copies of them. However, our observations in both Sussex and Orkney suggest that song copying is extremely accurate on at least 85% of occasions, many of the birds in a small area sharing songs which are near identical (Slater & Ince 1979; Slater, Ince & Colgan 1980). The fact that birds singing in small copses out of earshot of others have been found to have songs similar to those of individuals in nearby woods suggests that birds may sometimes learn song in detail before setting up territories. Although all birds we have followed from one year to the next retained the same territory, we have found instances of birds singing song types otherwise unknown in their wood but typical of an area some distance away (Slater & Ince 1979). This again argues that birds can learn their songs before setting up territories. The main opportunity for them to do so would be before mid-July in the previous year, when they themselves were nestlings or fledglings and the males around them had not yet stopped singing. Thorpe's experiments did not include training as early as this, doubtless for the simple reason that learning the detailed structure of song at that stage seemed unlikely; Poulsen (1951) had also found that the song of two young birds which had been caught in autumn was similar to that of hand-reared isolates. However, more recent demonstrations that fledglings can learn song in other species (see Kroodsma 1978) makes the possibility worth investigating in Chaffinches. It may be because of such learning in their first summer that autumn-caught females later injected with testosterone and trained by Kling & Stevenson-Hinde (1977) produced normal songs which bore little relation to those on the tutor tapes.

If young Chaffinches normally learn their songs from territorial neighbours then birds in adjacent territories would be expected to share song types to a greater extent than more distant individuals. In this paper we examine the frequency of song sharing between neighbours and then go on to discuss results on hand-reared birds which shed light on the exact stage at which song is learnt. They also provide interesting information about exactly what young birds learn: is it simply the form of

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the elements in each phrase or is their number and the temporal organization of song output influenced by experience as well?

METHODS

The relationships between the songs of neighbours were analysed using the songs of all the individuals which sang in Stanmer Great Wood, Sussex, in summer 1978. The wood is approximately 2·5 km long and a maximum of 500 m wide. The territories of the birds were mapped and at least 50 songs were recorded from each individual. Representative songs from each bird were sonagrammed with a Kay Sonagraph No. 6061A (wide band setting) and others were compared with these during playback at slow speed. In this way the songs of each bird were separated and its repertoire size determined. Each song type was given a letter—and in some cases an additional number—for identification and this same label was applied to the songs of other individuals where the form of the elements in each phrase and of the flourish was the same. The 42 individuals recorded had a mean repertoire size of 2·9 songs and these belonged to 36 different types when classified by this means. Further details of the separation of songs into types, together with sonagrams showing songs of the same and of different types, will be found in Slater & Ince (1979) and Ince, Slater & Weismann (1980). As there are discontinuities between song types, rather than song being continuously variable, the separation of songs into types is not a particularly difficult task.

Birds to be hand-reared were taken from the nest, under licence, between 5 and 14 days of age and kept subsequently in sound proof chambers with artificial light maintained on the same day length as that outside. The main mixture on which nestlings and fledglings were fed was that described by Lanyon & Lanyon (1969), although we have also tried variants of the mixture used by Thorpe (1958). Chaffinches are not easy to hand-rear compared with other birds of which we have experience, partly for dietary reasons but also because they are susceptible to various infections. As a result we have only succeeded, following two seasons in each of which several broods were taken, in obtaining song from two individual males. The results of these are, however, illuminating as they had received very different training from each other: the exact training procedure will be described with the results.

RESULTS

SHARING OF SONG BETWEEN NEIGHBOURS

To assess whether songs are shared more or less often than expected between neighbours, the results for each song type found were analysed separately, with the analysis covering all the 15 song types found to be sung by more than one bird. Given the number of birds singing a particular type and the arrangement of the territories in the wood, it was calculated how many pairs of neighbours would be expected to share that type if it was randomly distributed through the wood. This was compared with the actual amount of sharing between neighbours found (see Table 1). Because the pairings are not independent of one another it is not possible to test the difference statistically but it is clear that there is no evidence for neighbours sharing more than they should do by chance. Table 1 also compares the sharing between near neighbours (those separated by only one territory) and chance expectation. This gives similar results.

These results are surprising because they suggest that the range of song types found does not vary from one part of the wood to another as it has been found to do between different localities (Slater & Ince 1979). It is clear that birds learn their

TABLE 1

Sharing of song types between Chaffinches which are neighbours (on adjacent territories) and near neighbours (separated by a single territory). Figures show the number of pairs of birds sharing a particular type compared with that expected if songs were randomly distributed between territories

Song type	Pairs of neighbours sharing		Pairs of near neighbours sharing	
	Observed	Expected	Observed	Expected
B	21	20·8	32	34·0
C	12	11·5	14	17·0
F	11	9·4	17	16·9
H	4	2·0	5	2·7
A	3	1·5	7	2·7
Gl	1	1·2	0	1·5
Others	2	2·7	4	3·8
Total	54	49·1	79	78·6

songs mainly within the area in which they set up territories but not necessarily from their immediate or near neighbours. This raises the possibility that learning is often completed in the previous summer well before the young birds start to sing themselves. This was one of the hypotheses tested with hand-reared birds.

SONG LEARNING IN HAND-REARED BIRDS

Bird Ch

This bird was obtained at about 14 days of age, on the point of fledging. His father had three song types each of which had been recorded and he was trained with one of these (type K) for 42 days starting on the day after he was taken into captivity. The song was played for two hours per day on a cassette recorder using a 30 s loop with a single song on it. Thus the bird heard approximately 240 songs per day. The last day of training was 18 July, around the time when wild Chaffinches cease singing. The next spring the bird was heard to be in sub-song on 21 February and received a further 42 days of tuition from that date onwards with a different song type which he had not heard previously. He was in full song by 1 March and was recorded extensively during and after the spring training period. He only produced one song type and this was nearly identical with that he had heard the previous year except for the detailed form of the terminal flourish (see Plate 2). There was no evidence that tuition in the spring had influenced him.

Bird Fr

This bird was about 11 days old when obtained on 28 June and was given no tuition thereafter until the next spring. He then received 30 days of tuition with 240 repetitions per day starting on 12 February, just after Chaffinches in the wild had started to sing, although he was not himself recorded as being in sub-song until 28 February. The tuition was split into three 10-day periods, one each with three different songs recorded in Orkney which the bird had not heard before. The first of these he failed to reproduce but he subsequently produced a perfect copy of the second (type F) and a near perfect copy of the third (type B; see Plate 3). In the case of type B he never included the second part of the flourish.

These results show that young Chaffinches are capable of learning the detailed structure of song elements in their first summer as well as in the following spring.

TABLE 2

Comparison between number of elements in phrases of Chaffinch tutor songs and the mean and coefficient of variation (c.v.: standard deviation as percentage of mean) for the same measure in songs of pupils

		Phrase 1	Phrase 2	Phrase 3	*n*
Song type K					
Tutor		7	10	—	1
Pupil (Bird Ch)	Mean	6·6	10·1		40
	c.v.	21·4%	21·5%		
Song type F					
Tutor		12	5	3	1
Pupil (Bird Fr)	Mean	17·5	7·9	3	29
	c.v.	23·8%	9·8%	0%	
Song type B					
Tutor		6	7	2	1
Pupil (Bird Fr)	Mean	10·7	9·9	2	43
	c.v.	8·9%	11·4%	0%	

Analysis of the output of these two birds suggested that some other aspects of song production are less dependent on experience. In both cases the young birds were trained with tape loops on which there was only a single song. Unlike natural song this did not therefore show variation between repetitions in the number of elements in a phrase. Variation was, however, introduced by the young birds in the case of most phrases (see Table 2). The lack of variation in the last phrase of song types F and B is also true of wild birds and is probably because these phrases are very brief. Examination of 15 longer phrases of wild birds yielded coefficients of variation ranging from 9·6 to 17·5%. Three of the phrases of these two birds show variation in excess of this despite the constant number of elements on the tutor tapes. It seems that much of the variation in this feature between repetitions by the same bird is intrinsic to the copier rather than occurring because accurate copies have been made from a variable model. In bird Ch the mean number of elements in a phrase matches that on the tutor tape rather well; in Fr, by contrast, it was much greater for each of the four phrases which varied. Some of the songs produced by this bird were in excess of 4 s in length, which is quite exceptional for a Chaffinch.

Other differences between the tutor tapes and the song output of these two birds lay in the temporal organisation of singing. During a bout of singing, both these birds sang at a rate of one song every 5–15 s, as is typical of Chaffinches in the wild, rather than the slower rate of production used on the tapes. Bird Fr also switched frequently between song types, producing a few of one type then a few of the other rather than long periods of a single type. Again the match of this to the behaviour of wild birds is evidence for an intrinsic rate of switching which was not modified as a result of abnormal experience.

DISCUSSION

If young Chaffinches learned all their songs from territorial neighbours in their first spring then, given that they show a strong tendency to occupy the same territory

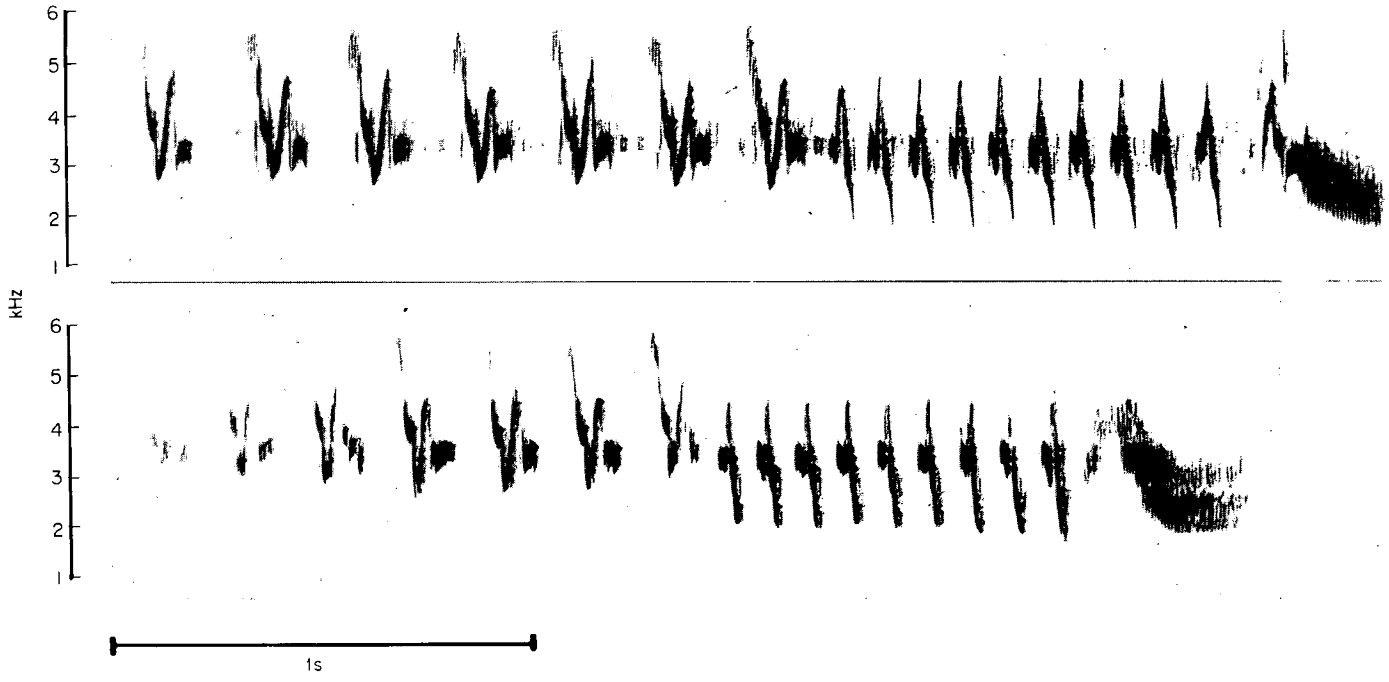

PLATE 2. Song type K as recorded on tutor tape (above) and as subsequently produced by Chaffinch Ch (below). Time bar beneath is 1 s long and frequency scale is graduated from 1 to 6 kHz.

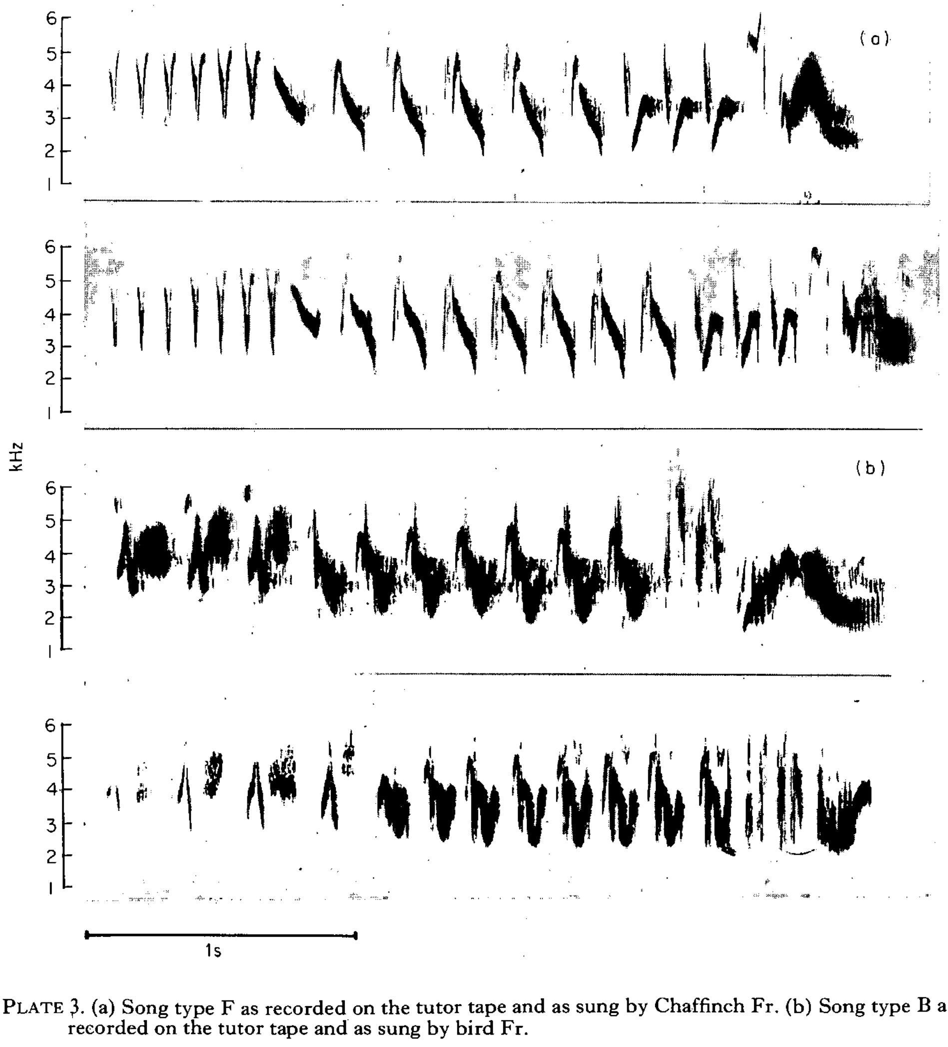

PLATE 3. (a) Song type F as recorded on the tutor tape and as sung by Chaffinch Fr. (b) Song type B as recorded on the tutor tape and as sung by bird Fr.

in successive years, neighbours should share particular song types frequently. This does not, however, appear to be the case. While the frequencies of different song types differ between woods a few kilometres apart (Slater & Ince 1979), we have found no evidence for systematic changes over the shorter distances examined here. Birds are no more likely to share songs with neighbours than with any other individuals in the wood. This suggests that, while birds clearly learn their songs within the general area where they subsequently sing them, they do not necessarily do so from territorial neighbours. Given the seasonal pattern of Chaffinch song there are two other possibilities. One is that first year birds may find and set up territories late and learn from older birds which they hear in full song while they are searching for a vacant area. The other is that birds may learn songs in the previous summer when they are fledglings and immediately thereafter.

Our results on the two hand-reared birds show that learning can take place at both these stages, bird Ch having learnt one song as a fledgling and bird Fr two while coming into song in his first spring. It may seem doubtful if birds in the wild normally learn as early as Ch was found to do, as both Poulsen (1951) and Thorpe (1958) reported that autumn caught birds kept in isolation developed abnormal songs. However, whether or not birds actually learn in their first summer must depend on whether they hatch early enough to hear adults singing: those hatched early in May will be exposed to over two months of song while others, hatching in July, do not fledge until after song has ceased for the season. Although both our hand-reared birds were over 10 days old when taken from the wild, neither showed signs of having learnt songs as nestlings, perhaps not surprisingly as adult males sing very little when feeding their young and the father would be the most likely model at this stage. Bird Ch also failed to learn a song he was played in his first spring. This could have resulted from the extensive tutoring he had received the previous year or from the spring tutoring being too late in relation to the development of his singing. Thorpe (1958) found that birds, once in full song, would not learn further song types. It is more difficult to account for the failure of bird Fr to learn the first of the three songs with which he was tutored but he provided no evidence of having done so: although this song was played before he was in sub-song Thorpe (1958) gives ample evidence for learning at that stage.

The results of these hand-reared birds illustrate a number of points. First, Chaffinches are capable of learning the detailed structure of song elements in the year of their birth, many months before they start to sing themselves. This has previously been found in some other species (e.g., Diltus & Lemon 1969, Marler 1970), but it has not previously been shown in Chaffinches. Second, as would have been predicted from song sharing in the wild (Slater & Ince 1979), the copying of song can be extraordinarily precise. The learning of song type F by bird Fr is more precise than any previously reported for this species (see Fig. 2). Third, as Thorpe's results also showed, birds will reproduce songs which they have not copied precisely. The failure of bird Fr to produce the latter part of the flourish of song type B is a clear example of this.

Young Chaffinches learn the exact structure of the individual elements which comprise their songs. By contrast, the number of elements in a phrase is either unlearnt or not copied with anything like the same precision. As the work of Hinde (1958) also showed, the temporal pattern of singing in hand-reared birds is very like that of wild individuals even though they have been trained with a very different pattern. Interestingly, these aspects of behaviour which do not appear to be modified by experience also vary considerably between individuals. For instance, in Chaffinches with repertoires, some will repeat a particular song type 10–15 times before switching to another while others average only 2–3 repetitions. It may be that the number of repetitions, both of elements in a phrase and of one song type before switching to another, are features which have little significance in communication and do not therefore have to be precise. It is often supposed that behaviour which is unlearnt is necessarily rather fixed. But the variation in these aspects of song could also result from their selective neutrality permitting a great deal of genetic variation rather than from any influence of experience. Indeed, if these features are of little consequence for communication, there is no reason why selection would have favoured learning having a rôle in their development. By contrast, it may be precisely because very accurate copying is required that learning has been selected for in the transmission of song structure.

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SUMMARY

Male Chaffinches share no more songs with territorial neighbours than would be expected by chance, suggesting that some song learning occurs before young birds set up their territories. Hand-reared birds are capable of learning song both in their first spring and in the previous summer: one young bird produced a good copy of a song which he had only heard as a nestling and fledgling eight months previously. While song learning involves accurate copying of individual elements, the variation in number of elements in a phrase and the temporal pattern of singing shown by hand-reared birds were similar to that of wild birds rather than being influenced by the tutor tapes.

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Incestuous Mating in Zebra Finches

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Abstract

Zebra finches (*Taeniopygia guttata*) were tested in quadruplets in which they had the choice of mating with a close relative or a non-relative. The majority of birds chose to mate incestuously and possible reasons for this finding are discussed.

Introduction

It has frequently been suggested that inbreeding has, or is likely to have, deleterious consequences, either through reduction in the variability of offspring or because of the greater likelihood that disadvantageous or lethal genes will be expressed (see, for example, MAYNARD SMITH 1978). On the other hand, mating with highly dissimilar individuals may also carry penalties. At an extreme, sterile hybrids between species may result but, even within a species, too much outbreeding may lead to the breakup of coadapted gene complexes and may therefore be selected against (NOTTEBOHM 1972; BATESON 1978 a, b). Thus, where choice is available, animals might be expected to choose mates which are not too closely and not too distantly related to themselves, assuming that they are capable of assessing degree of relatedness. BATESON (1978 a) has shown that the approach and mating preferences of quail (*Coturnix coturnix*) are compatible with this notion of "optimal outbreeding", relatedness in this case probably being assessed visually by the physical features which are shared between relatives. In mice, GILDER and SLATER (1978) showed that females preferred the smell of distantly related males of the same strain as themselves to either that of their brothers or that of males of a different strain. Once again smell may be a feature which diverges in line with genetic differences and so could provide a measure of relatedness (AVERHOFF and RICHARDSON 1976).

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Bird song may be another such feature in species where young males learn their songs from their fathers early in life. Although learning can occur in fledglings in a number of species (e.g. cardinal *Richmondena cardinalis*: DITTUS and LEMON 1969; white-crowned sparrow *Zonotrichia leucophrys*: MARLER 1970; chaffinch *Fringilla coelebs*: SLATER and INCE 1982) whether this learning is normally from the father is uncertain. Laboratory experiments have shown young birds to learn from their father or foster-father in the bullfinch (*Pyrrhula pyrrhula,* NICOLAI 1959), the Bengalese finch (*Lonchura striata,* DIETRICH 1980), and the zebra finch (*Taeniopygia guttata,* IMMELMANN 1969). The zebra finch case was especially striking as young birds would learn from a foster-father of a different species even when members of their own species were singing in the same room. Zebra finches are particularly appropriate for studies of mate choice as they breed rapidly and easily in captivity, young birds being mature at three months of age, and IMMELMANN's work suggested that cues to relatedness might be passed from generation to generation. MILLER (1979) found that female zebra finches, when mature, preferred the song of their father to that of a strange male; they also preferred it to a song which differed from it only slightly, but not as strongly. This suggests that song might be used as a cue to assess relatedness when choosing a mate, although the preference found by MILLER was always for the closest possible relative.

The experiments to be reported here were commenced with a view to testing whether mating preferences of zebra finches were affected by relatedness.

Methods

A breeding colony of zebra finches was set up using 20 birds purchased from a local dealer in 1977. All the birds were selected as having wild-type plumage and, the parentage of the individuals being known, brother-sister mating was avoided in the choice of pairings. The offspring of these original pairs were therefore related to each other by a coefficient of relationship (r) of 1/8 or less. Subsequent matings avoided pairs in which both birds were drawn from the same lineage and so involved relationships which were not as close as 1/8. Pairs which bred successfully were left together to produce further broods. The young birds were removed from their parents at 50 days of age and kept thereafter in monosexual groups in the same room as the breeding cages. Some of the later birds were from breeding stock set up in 1980 using birds from the Bielefeld colony donated by Prof. K. IMMELMANN. All pairs bred in individual cages (60 × 45 × 30 cm) supplied with a nest box and hay for nest building.

Testing was carried out when the young birds were at least 90 days of age. However the exact age of the individuals used in a particular test varied considerably as the same individual was sometimes used in several choices with different relatives. In choice tests four individuals, two of each sex, were placed in a cage twice the size of a normal breeding cage and supplied with two nest boxes and with hay for nest building. One week later an observer, who was unaware of the relationships between the individuals, watched the cage for 30 min to assess which male was paired with which female. In the majority of cases this was obvious, as the members of a pair would sit together, move around together and frequent a particular nest box. Where preferences were not clear the quadruplet was left together for up to a further week and the assessment procedure repeated. In a few cases, where for example both females seemed to prefer the same male, the results had to be discarded as showing no clear choice.

Otherwise the preferences were simply scored according to whether the birds involved had paired with a relative or a stranger. Each quadruplet was counted as a single trial as the preference of one pair was determined by that of the other. After a result was obtained from a quadruplet, the birds in it were returned to stock cages in which they were kept in monosexual groups for at least 14 days before being used in another test.

The main results to be discussed concern three different types of quadruplet: one type in which the two males were the fathers of the two females (N = 6); one in which the two females were the mothers of the two males (N = 10); and one in which each bird had a choice between members of the opposite sex which were a sibling from the same brood and a stranger respectively (N = 9). In none of the quadruplets were the birds of the same sex related to each other. All four birds in each test were therefore provided with a choice of mating with a close relative ($r = 1/2$) or with a stranger ($r < 1/8$). A few other tests were also carried out involving brothers and sisters from different broods and cousins but these results were not sufficiently extensive to be worth discussing. While the two birds of the same sex in each quadruplet were sometimes the same as in a previous test, no bird ever met the same bird of the opposite sex in two tests. In total the 25 quadruplets tested involved 66 different individuals.

As song seemed a likely cue that birds might use in assessing relatedness the songs of the original males and of a selection of their offspring and their grandsons were recorded and sonagrams of them prepared. A brief account will be given of comparisons between them. Each bird used was also assessed for its plumage characteristics. Although the original birds of the colony were all of the wild type, and their male descendants continued to be so, some of the females in subsequent generations showed divergent plumage of either the fawn or white types. If individual experience of relatives has an important role to play in mate choice, it must therefore be borne in mind that some of the choices presented to males in these experiments were between individuals which were very easy to discriminate between.

Results

The results of the choice tests are shown in Table 1. In all three types of quadruplet the majority of pairings were with relatives rather than strangers. This was most clear amongst the quadruplets involving mothers and their sons of which there were sufficient for the result to reach significance ($p < .02$). The father/daughter results may have failed to achieve significance simply because there were too few birds available for tests in this category to be as numerous. The brother/sister tests, although biased towards incestuous mating, were only mildly so and it is very unlikely that a significant effect would have been found with an increased sample size.

Table 1: Mating preferences of zebra finches. Figures give the number of quadruplets of each type in which birds paired with strangers or with relatives. Significance levels given are from two-tailed sign tests

Quadruplet type	Mating between relatives		Mating between strangers
Father / daughter	5	p = .22	1
Mother / son	9	p = .02	1
Brother / sister (same brood)	6	p = .50	3
Overall	20	p = .002	5

Taking all the results together (see Table 1) they show a strong tendency for birds to mate incestuously when given the choice between pairing with a close relative and with an individual to which their relationship is much less strong. There seems to be a stronger tendency for parents to mate with offspring than for siblings to mate with each other, although the coefficient of relationship is the same in both cases. This may stem from experience, the parent being the yardstick by which prospective mates are judged.

A possible complication in these results comes from the fact that the same bird was sometimes used more than once in different quadruplets, although always with different potential partners. Of the 66 birds used, 21 were tested more than once, in most cases only twice but in some up to five times. It is possible that successive choices by the same bird are not independent of each other. For example, individual differences might lead some birds to choose relatives consistently more, or they might become better at making the discrimination as a result of repeated experience in the testing situation. Of the 21 birds given two or more tests, 15 chose relatives on all occasions and none chose non-relatives on every test. On the basis of the birds tested only once, one would have expected 10.4 of these birds to choose identically on all tests, giving a significant difference ($\chi^2 = 4.05$, $p < .05$). Thus there is some evidence for an effect of this nature, although it is weak compared with the main finding and could not have been responsible for making this significant.

If birds assess relatedness by comparing potential partners with their memory of parental features, the failure of quadruplets containing siblings to reveal clear preferences may arise because of discrepancies between siblings and parents. The plumage differences amongst females, not present in our original colony but which arose subsequently, might be one reason why a young male's sister might look quite different from his mother. Gross plumage differences do not, however, appear to be required for the discriminations we have found: of 13 quadruplets in which the females were of a different morph, 11 gave incestuous mating, while 9 out of 12 were incestuous when both females were similarly marked ($\chi^2 = 0.32$, n.s.).

If females choose mates using song as a cue and the father's song as a basis for comparison, then the extent to which fathers and sons share songs may be important. We have examined the songs of 22 father/son pairs. In no case was every element type the same in both birds, and in a few none of the father's elements were sung by the son. However, in the majority there was some evidence of cultural transmission of element types from father to son. This topic will be considered elsewhere (CLEMENTS and SLATER, in prep.), as careful description and quantification is required to determine whether similarities between elements are due to transmission or chance, and element types are not easy to classify objectively into anything but broad categories (PRICE 1979).

Discussion

The results presented here were unexpected, although they are compatible with those of MILLER (1979) on song preferences in this species. We have found that zebra finches prefer to mate with close relatives rather than with strangers. A number of functional explanations could be suggested to account for this. First, if zebra finches do prefer to mate so as to achieve an optimal degree of outbreeding (BATESON 1978 a, b), then they might in these tests be choosing the less undesirable of two alternatives. A complete stranger, and particularly one with very different song or plumage, may be less close to the ideal than is a near relative, so that the latter is chosen. In an interesting discussion of the theory underlying the idea of optimal outbreeding, BATESON (1980) has suggested that the optimal mate may sometimes be as close as a first cousin. A second alternative explanation for our findings is that it is advantageous for zebra finches to inbreed as much as possible. The disadvantages of inbreeding may not be so great when animals live in a relatively predictable environment so that selection does not favour the production of varied offspring (in other words, amongst K-selected species) as suggested by MATHER (1943). Inbreeding may also ensure that the offspring have exactly the right characteristics for that environment. However, this argument seems unlikely to apply to zebra finches as they live in an environment aspects of which are extremely unpredictable. Nevertheless it is possible that individuals have different strategies for coping with that environment and it benefits them to choose partners with similar adaptations.

A third possible reason for the results presented here is that they arise as a result of the unnatural situation in the laboratory. It is not easy to test functional hypotheses in the laboratory because the environment is so different from that to which the individuals being tested are adapted. In most bird species females disperse further than males (GREENWOOD 1980), so that the chances of relatives mating are very slight. The zebra finch is nomadic (KEAST 1958) and both sexes seem to disperse considerable distances as individuals ringed at colonies are seldom recovered in the same area (ZANN, pers. comm.). Dispersal alone could make the chances of inbreeding negligible without any specific mechanisms to stop it during mate choice. On the other hand, something akin to optimal outbreeding might be achieved by dispersal over a particular distance followed by a choice of mate as like the bird's parent as could be found. If this was the case, experiments in the laboratory, where dispersion is excluded, would show that individuals chose to inbreed as much as possible. Another barrier may preclude inbreeding with parents in wild populations. This is that zebra finches are monogamous and pair for life at an early age (IMMELMANN 1962). Members of the parental generation will not normally be available for mating at this stage and most pairing will be with members of the same generation.

The choice of mates found here is likely to have resulted from early experience. IMMELMANN et al. (1978) have found that imprinting leads wild-type and white zebra finches to mate within their respective groups when given a choice of partners. The preferences of both sexes are likely to be involved in this and in the present results. It is well known that early experience influences mate choice in male zebra finches (e.g. IMMELMANN 1972). Recently SONNEMANN and SJÖLANDER (1977) have shown cross-fostered female zebra finches to prefer the species on which they had been imprinted and Miller (1979) has also found female zebra finches to show preferences amongst the songs of males of their own species. In most of the tests reported here choices, if based on plumage, would have had to be made using subtle cues as such gross differences were not present. Our results show that this preference for the imprinted type extends to more minor differences and to preferring the parent itself rather than an individual which is somewhat different.

In some of our tests the preferences of males could have been based on unnaturally large plumage differences between the two females in their quadruplet. The plumage differences between males in our colony were slight, and probably similar in extent to those between wild males (Immelmann 1962), but females might also have used song as a cue as this varies considerably between males. Immelmann (1969) described some remarkable cases of young zebra finches singing songs which were identical with those of their fathers or foster-fathers. Our results (Clements and Slater, in prep.), show less precise copying and may seem incompatible with these. However, Immelmann's cases of identical copying were in birds kept with the male which reared them for 80 days, considerably longer than were our birds. This difference in experience, as well as other social factors (Böhner, in prep.), may account for these differences in results. The difficulty of interpreting laboratory experiments where constraints are placed on the experience of young individuals means that the possible importance of song as a measure of relatedness must remain in question. To obtain perfect copying Immelmann (1969) had to leave young males with their parents until they were mature. An earlier separation is likely to be closer to the situation in the wild as adult males are often aggressive to their offspring even within the 50 day period which we used before separation. Despite this, however, the young might normally follow the father round even after this stage and pay particular attention to his song so that it is learnt in preference to the songs of non-relatives. Dietrich (1980) has found this to be the case in the Bengalese finch (*Lonchura striata*). However, Immelmann (1962) found that young zebra finches in the wild do not behave in this way but leave their parents and join flocks of non-breeding birds soon after their parents cease to feed them. More work is required on zebra finches in the wild, and on those in captivity given a choice of song models for various different periods, before it will be clear to what extent young birds in nature do learn the songs of their fathers. If they do so, such work may also help to decide whether this and other cues lead them to choose amongst possible mates so as to achieve a particular degree of inbreeding or outbreeding.

Summary

Zebra finches given the choice of mating with a close relative or a non-relative tend to choose the close relative. The effect is most striking when the pairings are between parents and their offspring and is probably based on the early learning of parental characteristics. The functional significance of this finding is discussed and it is suggested that it might stem from the abnormal

rearing situation in the laboratory, or arise because dispersion is normal in the wild but disallowed in the laboratory, or possibly because inbreeding is beneficial in this species.

Zusammenfassung

Zebrafinken, denen die Wahl gelassen wird, sich mit einem nahe verwandten oder mit einem nicht verwandten Tier zu paaren, neigen dazu, den nahe verwandten Artgenossen zu wählen. Dieser Effekt ist dann am ausgeprägtesten, wenn es sich um Paarungen zwischen Eltern und Nachkommen handelt, und ist vermutlich auf frühes Lernen elterlicher Merkmale zurückzuführen. Die funktionelle Bedeutung dieser Befunde wird diskutiert, und es wird vermutet, daß Verwandtenehen entweder durch die abnorme Aufzuchtsituation im Labor bedingt sind, oder dadurch, daß die normale Ausbreitung, wie sie im Freiland möglich ist, im Labor unterbunden wird, oder daß Inzucht bei dieser Art möglicherweise von Vorteil ist.

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MINIMISING ERRORS IN SPLITTING BEHAVIOUR INTO BOUTS

by

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(With 2 Figures)
(Acc. 20-X-1981)

INTRODUCTION

Where events of a single type are randomly distributed in time, the intervals between them follow a negative exponential distribution. Such a distribution, when plotted as a log survivor function, appears as a straight line the slope of which is proportional to the probability of a new event occurring with passage of time since the last event (Nelson, 1964; Slater, 1974a, b). Intervals between behavioural events do not, however, usually follow such a simple distribution: in particular, most activities normally occur in bouts with brief intervals being relatively common and long ones relatively rare. This gives rise to a log survivor function which is concave, descending steeply at first (high probability of a further event; intervals classified as within-bout), and subsequently much more gradually (low probability of a further event; intervals classified as between bouts). Such plots have proved extremely useful in many studies for choosing a time criterion for bout definition, the point where the slope changes most dramatically being that usually selected (*e.g.* Clifton, 1979; Culshaw & Broom, 1980; Petersen, 1976; Slater, 1974a, b, 1975).

Concave log survivor plots can be viewed as the sum of two or more negative exponential distributions (van Liew, 1962), as a combination of other distributions (Machlis, 1977) or as a single distribution in which the probability of a new event changes with time since the last. The idea that they are sometimes a combination of distributions has been cogently

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argued by Machlis (1977) and is supported by data, such as those of Nelson (1964), where there are behavioural criteria for distinguishing between the two distributions. Nelson found that the intervals between courtship events in a fish could be split into two distributions depending on the presence or absence of a dark mark on the male.

It follows from this reasoning that some intervals between events will always be misclassified when a time criterion is chosen for bout definition. Some of the intervals shorter than the criterion will be contributed by the between-bout distribution; some of the longer intervals will belong to the distribution of those within bouts (Fig. 1a). It is the purpose of this paper to explore the implications of this and, in particular, to consider the question of where the criterion interval should be picked to minimise the number of intervals misclassified in this way.

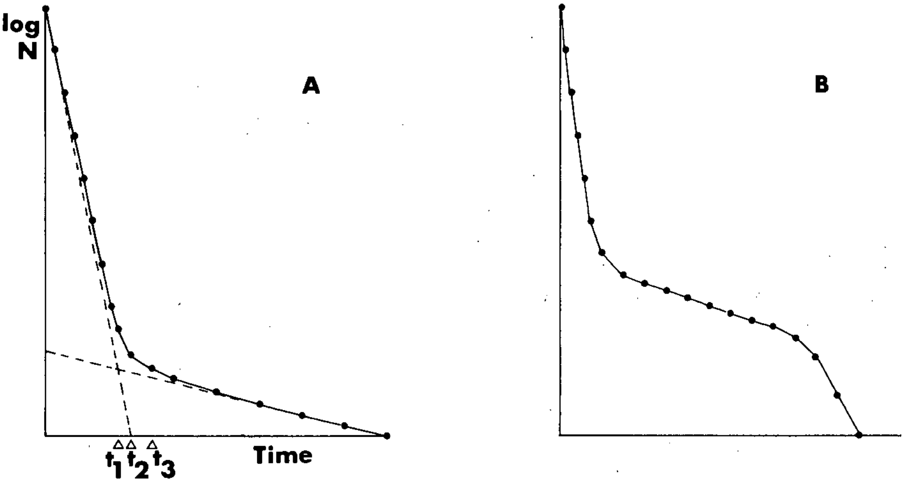

Fig. 1. (a) The curve is a typical log survivor function for intervals between behavioural events. Such a plot is of the number of intervals greater than a particular length plotted against that length. Three possible bout criteria are indicated. t_1 is that at which the two exponential functions which best fit the data cross, as suggested by Fagen & Young (1978); t_2 is where the slope of the curve changes most rapidly; t_3 is the point at which fewest intervals are misassigned. (b) An example of a log survivor function the tail of which cannot be easily fitted by a negative exponential distribution because the behaviour tends to occur cyclically, longer intervals being more common than those of intermediate length.

METHODS OF CRITERION CHOICE

Most of those who have used log survivor functions to choose bout criteria have done so by eye, a rapid change of slope at a particular point being taken to indicate the best position. Alternative methods are possible (see Fig. 1). For example, if the curve can be easily split into two negative exponential distributions, the place where these cross can be argued to provide a more objective criterion (FAGEN & YOUNG, 1978). The point where the two distributions cross is expressed by the formula:

$$N_w e^{-\lambda_w t'} = N_b e^{-\lambda_b t'} \qquad \ldots\ldots\ldots\ldots\ldots \quad (1)$$

where N_w and λ_w are the number of within-bout gaps and the rate of the process generating them, N_b and λ_w are the same for the between bout process, and t' is the criterion interval. As explained in the Appendix, this time interval is then given by:

$$t' = \frac{1}{\lambda_w - \lambda_b} \log_e \frac{N_w}{N_b} \qquad \ldots\ldots\ldots\ldots\ldots \quad (2)$$

This is the point at which the smallest amount of time is misclassified as both within bout when actually between or between bout when actually within. Because, by definition, within bout intervals are shorter than those between, use of this criterion will misclassify a larger number of within bout intervals than between bout ones.

Another method has been used by MACHLIS (1977). She found the best fitting negative exponential distribution for her data, then removed intervals in the shortest time bin and repeated the procedure until there was no significant difference between the data and the distribution against which they were being tested. Intervals in the remaining part of the distribution were then defined as being between bouts. While this method is certainly more objective than visual inspection of the plot, it does have some difficulties. One of these is that the criterion chosen depends on the significance level selected: if lower probabilities are required then a longer time interval will be selected. Second, the tail of the distribution may, in some cases, not be reasonably described by a negative exponential (Fig. 1b). This may arise for two main reasons. First, if observation periods are short then the distribution may curve downwards simply because it is not possible to record intervals longer than the length of those periods. Second, in some cases behaviour patterns may occur cyclically, in which case many of the gaps between bouts are likely to be similar in length so that the slope of the log survivor function will be great at that length. In both these cases it may be impossible to fit a negative exponential distribution to the plot and, even if such a distribution does fit, it is likely to lead to an unrealistic bout criterion interval being chosen.

Given these difficulties, and the technical problems of fitting theoretical distributions to data, it is not surprising that most recent studies have persisted in using visual inspection as a means of choosing bout criteria. How reasonable is this, and can it be made more effective?

MINIMISING NUMBERS MISASSIGNED

For many studies of bout organisation the important point in choosing a bout criterion is not to minimise the amount of time misclassified, as is done by the method of FAGEN & YOUNG (1978), but to minimise the number of intervals put in the wrong category. The problem is therefore to find the appropriate time intervals for this.

Fig. 2 shows three sets of points which are log survivor functions arrived at by the summation of pairs of negative exponential distributions. In each case the number of gaps in the within bout distribution is 1000 and that between bouts is 10, although the relative time courses differ in the three examples. The open points indicate the bout criterion interval which leads to the least misassignment of gaps to the opposite category from that to which they really belong. Table 1 illustrates this for the intermediate example, showing that the number of gaps misassigned reaches a trough at around this point (35 s). Using the symbols defined earlier, the number of within bout intervals wrongly classified as between bouts by this criterion (N_w') is given by:

$$N_w' = N_w e^{-\lambda_w t'} \qquad \ldots\ldots\ldots\ldots\ldots \text{(3a)}$$

and the equivalent number for between bouts is:

$$N_b' = N_b\,(1 - e^{-\lambda_b t'}) \qquad \ldots\ldots\ldots\ldots\ldots \text{(3b)}$$

It follows from this, as explained more fully in the Appendix, that the bout criterion to give the minimum number of misassignments ($N_w' + N_b'$) is:

$$t' = \frac{1}{\lambda_w - \lambda_b} \log_e \frac{N_w \lambda_w}{N_b \lambda_b} \qquad \ldots\ldots\ldots\ldots\ldots \text{(4)}$$

Applying this formula to the data given in Table 1, where $\lambda_w = 0.23$ and $\lambda_b = 0.023$, gives a value to t' of 33.4.

Several points are worth noting about the position of this criterion interval. First, it is considerably longer than that at which the two distributions cross (22.25 s in the example used in Table 1), and this will always

TABLE 1

Number of within and between bout intervals which are assigned to the wrong category by choosing various bout interval criteria for the curve labelled b in Fig. 2

Bout interval criterion (seconds)	Within bout intervals classed as between	Between bout intervals classed as within	Total misassigned
0	1000	0	1000
20	10	4.0	14.0
25	3	4.8	7.8
30	1	5.4	6.4
35	0.3	6.0	6.3
40	0.1	6.4	6.5
45	0.03	6.8	6.8
50	0.01	7.1	7.1
∞	0	10	10

be the case as $\lambda_w > \lambda_b$ by definition (compare equations (2) and (4)). The criterion of FAGEN & YOUNG (1978) would thus be a poor one for minimising the number of gaps wrongly classified. It is also true that the point is much closer to the between bout line than to the within bout one. The best criterion, as SLATER (1974b) suggested without formal justification, is therefore at a longer time interval than that at which the slope changes most rapidly, as illustrated in Fig. 2. This is the position where it is most suitable to choose a bout criterion in the case where two negative exponential functions are responsible for the distribution of gaps between events, and similar arguments can be applied to combinations of other likely distributions. It may sometimes be possible to fit such pairs of distributions to the data and choose the point of least misassignment in the same way as has been done in Table 1. But bout analysis may not be the most useful way of proceeding in these circumstances as, if this can be done, it will be possible to estimate the relevant parameters of the two underlying processes and proceed with analysis in terms of them. Bout analysis is most useful where the data defy simple mathematical description.

Whether the data consist of intervals between songs in a bird, bar presses in a rat or bites at food in a monkey, there is of course no way in which a criterion can be obtained which avoids misassignment altogether, assuming that two superimposed processes are involved. As a general rule the greater the difference in slope between the two processes the fewer intervals will be misclassified. Thus, in Fig. 2, point *c* misclassifies 8.6 intervals, point *a* misclassifies 2.9. In cases, such as *c* in

Fig. 2, where the slope of the log survivor function changes gradually because the underlying processes do not differ as much in rate as in the other examples, it is of doubtful value to split the data into bouts. This is partly because of the difficulty of choosing a criterion interval. But it is also the case here that a very high proportion of between bout intervals are misclassified as within bouts. Of the 10 interbout intervals in this example only 1.7 are detected so that the "bouts" discovered are actually combinations of several bouts. Of course, choosing a different criterion would, by definition, lead to greater misclassification: for example, a shorter criterion would lead to the detection of more "bouts" but these would be largely split up in the wrong places.

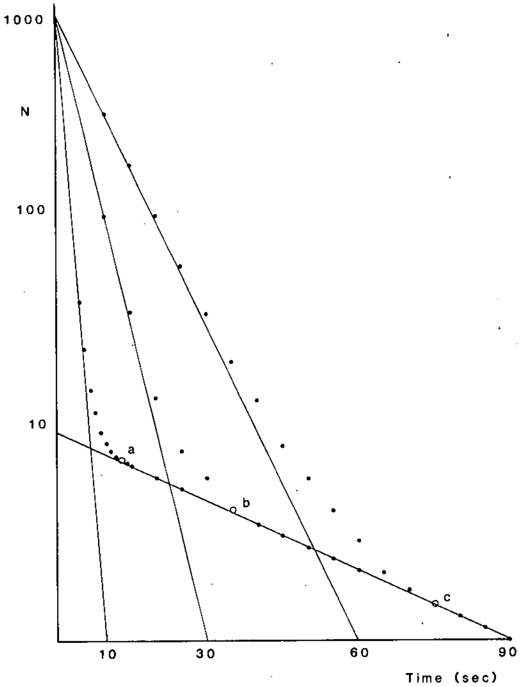

Fig. 2. The black dots show three log survivor curves obtained by summing the low rate negative exponential distribution (n = 10) with each of the three more rapid processes (n = 1000). The open circles indicate the bout criterion intervals which misassign the fewest within and between bout intervals to the opposite category.

Even where the bout criterion interval is relatively unambiguous, as in *a* in Fig. 2, the amount of misclassification involved may be a problem for analysis. In that case only 0.13 interbout intervals would, on average, be classified as intrabout, but 2.8 gaps which were actually between bouts would be categorised as within them. Put differently, if an animal showed 100 bouts of a particular activity only 73 would be detected: of these 28 would really be two bouts run together and two would be a single bout wrongly split. With such misclassification it is not surprising that, for example, correlations between bouts and the intervals that surround them tend to be rather low (see, for example, SLATER, 1974a). The actual correlation would have to be near perfect before the observed one achieved significance. One reason why bout analysis of feeding is often productive may be that this behaviour shows strong differences in rate between the within and between bout processes so that these difficulties are not pronounced (CLIFTON, in press).

CONCLUSION

There is no doubt that use of log survivor functions is the most useful means currently available for splitting behaviour into bouts. It is argued here that the best criterion for most purposes is that which assigns the fewest within and between bout intervals to the wrong category. In particular this is most suitable where the study involves examination of both the bouts and the intervals between them. For other purposes some divergence from this criterion point may be preferable. For example, if the interest is in the type of event which occurs at the start of bouts, choice of a long criterion will minimise the number of starts which are not actually commencements at all but events following within bout intervals wrongly classified as being between bouts. Where interest is in time allocated to different activities, as in studies of time budgeting, a criterion based on equalising time misassignment is most appropriate. This point, which is close to t_2 in Fig. 1, is that at which errors cancel out so that the time spent in the activity may be assessed.

In general, the aim of the methods outlined here is to make it possible to arrive at more objective bout criteria. But where discontinuities in the log survivor function are not sharp (*e.g.* *c* in Fig. 2) the amount of misassignment arising from any method will be so great that it would be better not to attempt any analysis which involves splitting behaviour into bouts.

SUMMARY

Some problems in using log survivor functions to split behaviour into bouts are outlined. It is argued that it is usually best to choose that bout criterion which leads to the fewest within and between bout intervals being assigned to the wrong category. A way of

doing this is illustrated and other possible criteria are considered. The influence of misassignment on data analysis is discussed and it is argued that where this is substantial analysis in terms of bouts may not be useful.

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APPENDIX

Derivation of Equation 2 from Equation 1.

$$N_w e^{-\lambda_w t'} = N_b e^{-\lambda_b t'} \qquad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

$$\therefore \frac{N_w}{N_b} = \frac{e^{-\lambda_b t'}}{e^{-\lambda_w t'}}$$

$$= e^{-(\lambda_b - \lambda_w)t'}$$

$$\therefore \log_e \frac{N_w}{N_b} = -(\lambda_b - \lambda_w)t'$$

$$\therefore t' = \frac{1}{\lambda_w - \lambda_b} \log_e \frac{N_w}{N_b} \qquad \ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Derivation of Equation 4 from Equations 3a and 3b.

$$N_{w'} = N_w e^{-\lambda_w t'} \qquad \ldots\ldots\ldots\ldots\ldots (3a)$$

$$N_{b'} = N_b(1 - e^{-\lambda_b t'}) \qquad \ldots\ldots\ldots\ldots\ldots (3b)$$

The total number of misassignments is $(N_{w'} + N_{b'})$. This may be minimised by differentiating with respect to t' and setting the derivative equal to zero, as follows:

$$\frac{d}{dt'}(N_{w'} + N_{b'}) = \lambda_b N_b e^{-\lambda_b t'} - \lambda_w N_w e^{-\lambda_w t'} = 0$$

$$\therefore\ \lambda_b N_b e^{-\lambda_b t'} = \lambda_w N_w e^{-\lambda_w t'}$$

$$\therefore\ \frac{\lambda_w N_w}{\lambda_b N_b} = e^{t'(\lambda_w - \lambda_b)}$$

$$\therefore\ t' = \frac{1}{\lambda_w - \lambda_b} \log_e \frac{N_w \lambda_w}{N_b \lambda_b} \qquad \ldots\ldots\ldots\ldots\ldots\ldots (4)$$

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BIRD SONG LEARNING: THEME AND VARIATIONS

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INTRODUCTION

Perhaps the greatest attraction of bird song, to scientist and layman alike, is its immense variety. In some birds songs are brief and discrete, while in others they can continue for long periods without a break; in some each male has but a single phrase which is repeated in identical form, in others the repertoire of phrases is so large that it is difficult to measure exactly; in some species neighbors tend to have similar songs, in others they do not. There are species in which the female sings as well as the male, there are those that sing at times of year far removed from breeding, there are those that sing loudly from conspicuous perches and those that sing quietly from the deepest undergrowth. With all this variety, generalizations about bird song, even if one restricts oneself to considering the songbirds (Oscines), are not easy to come by, and the knowledgeable will think of exceptions to every rule.

One likely reason for this variation is that the function of song differs among species. Three main functions for song have been suggested in the literature: that it repels rivals, that it attracts mates, and that it stimulates the female to lay eggs. There is some experimental evidence for each of these (e.g. Falls 1978; Wasserman 1977; Kroodsma 1976). However, there is no reason why, in a particular species,song should not serve more than one of these functions at the same time, and there are cases in which there is experimental evidence that both territorial defense and mate attraction occur in the same species (Krebs 1977; Krebs, Avery & Cowie 1981). Song may vary from species to species because they differ from each other in the relative importance of these functions and each function demands that song should be rather different, tending to pull it in opposite directions.

It may also differ amongst species because their social organisation is rather different. In some species the territorial function of song may be mainly through its utility in repelling incursions by neighbors, in others its role may be more to advertise occupancy to wandering intruders looking for vacant territories to take over. Song after pairing may cease to be advantageous for mate attraction in species where polygyny and stolen matings are rare, but continue to serve this function where this is not the case. In fact differences amongst species in many aspects of their way of life may have implications for features of their singing behavior, and the variety of song is not so surprising when these possible ramifications are considered.

It is not simple to devise experiments to examine the functions of song. Those that have been carried out have been concerned with simple qualitative questions, determining whether or not there is evidence in favor of a particular function, rather than quantitative assessment of the importance of different functions. Yet, if song can function in more than one way, some idea of the balance between these uses is essential as a contribution to understanding its variations. An alternative approach to the experimental is that involving correlations: can one relate variations in different aspects of song to each other and to variations in the way of life of different species ? While correlations can arise for many reasons without the correlated variables being directly related to one another, this approach can provide useful pointers on functional questions. For instance , it brought to light the relationship between continuity and versatility in bird song (Hartshorne 1956, 1973), which appears to be a genuine phenomenon (Kroodsma 1978a) even if it is open to a variety of interpretations (Slater 1981). A similar correlational approach is one that will be used, in a rather informal way, in this article.

The development of bird song is one aspect that has received a great deal of attention in the past decades. It has become apparent that learning has a part to play in the ontogeny of song in all or nearly all songbirds. Yet its exact role and the detailed schedule of development varies a lot from one species to another. Enough laboratory studies have now been carried out for this variation to be examined and related to differences amongst species in singing behavior in the wild. In this article I shall give a brief review of the literature on song learning, consider local and geographical variations in song in those species whose song development has received most attention, and end by discussing the link between song learning and the variation of song in the wild to explore the functional significance of these phenomena.

SONG LEARNING

One of the simplest ways to determine whether learning has a role in the development of bird vocalizations is to exclude the possibility of copying by raising young birds in isolation from other individuals. In the great majority of such "Kaspar Hauser" experiments, the effects have been profound. Isolate songs are often described as slower (e.g. Immelmann 1969; Kroodsma 1977; Ewert 1979), as including fewer elements (e.g. Poulsen 1954; Lemon & Scott 1966; Rice & Thompson 1968) and as being more variable (e.g. Marler, Kreith & Tamura 1962; Lanyon 1979). In some cases the basic structure of the song approximates to that typical of the species despite lack of opportunity for copying this (Guttinger 1979; Lanyon 1979), but in others the arrangement of song is abnormal (Ewert 1979; Marler et al. 1972; Thielcke-Poltz & Thielcke 1960). Occasionally isolated birds develop songs which appear to lie within the limits of variability of individuals in the wild, as suggested by Thorpe (1964) for single Corn and Reed Buntings (*Emberiza calandra* and *E. schoeniclus*). But subtle differences may still exist: Mulligan (1966) reported that the songs of Song Sparrows (*Melospiza melodia*) reared by Canaries (*Serinus canarius*) were approximately normal; however, Kroodsma (1977) repeated the experiment and found quite a number of differences from normal. The birds developed songs which were longer, of lower frequency range, with longer but simpler syllables, slower rate of syllable repetition and differences from normal in organization. The discrepancies therefore had many of the same characteristics as those found in other species. In another experiment, Lanyon (1979) found the young Wood Thrushes (*Hylocichla mustelina*) that he raised to sing near normal songs, but that wild birds did not respond to their playback, suggesting that the slight differences that existed were important. Few species have been reared in isolation from the egg and, unless this is done, learning before isolation could contribute to similarities between normally reared and Kaspar Hauser birds. It is probably true to say that no bird reared in isolation has developed fully normal song (Marler 1981). Experience has also been found to be necessary for the normal development of some passerine call notes, particularly amongst cardueline finches (Poulsen 1954; Mundinger 1970; Marler & Mundinger 1975), although not of others (Lanyon 1960), nor of many non-passerine sounds which have been studied (Konishi 1978). In the Ring Dove (*Streptopelia risoria*) and the domestic Fowl (*Gallus gallus*) calls develop normally even in birds that have been deafened

(Nottebohm & Nottebohm 1971; Konishi 1963). Thus, while learning is important in song development, it does not influence all bird vocalizations, and its involyement does not correlate simply with complexity for some quite simple sounds are learnt (Mundinger 1979).

The opportunity to hear adults singing is only one aspect of experience that may contribute to the development of song. It is often the case that young birds reared in groups develop songs that are more normal than those of individuals that are totally isolated (Thorpe 1958; Marler 1967). In some such cases grouped birds clearly copy each other and develop songs that are closely similar (Thorpe 1958; Waser & Marler 1977). However, this is not always so (Marler 1967), and another reason why song in grouped birds may be more normal is that they stimulate each other to sing and so gain more practice through which their song improves even without copying. Practice is an important aspect of song learning. Indeed song development can often be split into two phases between which some species show no temporal overlap: a memorization phase in which the young bird memorizes sounds that it hears, and a motor phase in which it matches its output to those sounds. This conceptualization of bird song development has been put forward most clearly by Marler (1970, 1976). He refers to young birds as being born with a "crude template" of what their species song should sound like. On its own this is insufficient to enable them to produce normal song, as the songs of isolated birds show, but it acts to exclude the copying of totally inappropriate sounds In other words, the bird has a rough idea of what it should learn and memorizes (at least in a form accessible for later production) only those sounds that fit in with this. As a result of learning the crude template becomes an exact template. This is often well before the bird begins to sing itself, so that the memorization appears to involve the storing of an auditory image rather than a motor program. When the bird starts to sing its output is matched to this image, in some cases with startling precision. Young birds which are deafened before they start to sing produce highly abnormal songs compared to those which are simply isolated at the same stage (Konishi 1964a, 1965a,b; Nottebohm 1968; Marler & Waser 1977). This suggests that it is necessary for them to hear the sounds of their own voices to match their output to the structure of songs they have learnt.

The general picture put forward by Marler is a theme on which there are a great many variations. The age at which the memorization phase of learning occurs is varied, being throughout life in some species but limited to a brief sensitive period in others. The extent to which the crude template limits what can be learnt also varies from species to species: some are constrained to a very small range of sounds while others have remarkable mimetic ability. The accuracy of learning is a third feature that varies, only the general features of song being picked up in some species while even the finest details are learnt and accurately reproduced in others. These variations in song learning deserve some attention here, for they may give us some insight into its functional significance and into the reasons for variations amongst birds in wild populations.

(a) Timing

The age at which song is learnt can be studied in the laboratory by training otherwise isolated individuals with tape-recorded songs at specific times and seeing whether any features of these songs are later reproduced. Field data, particularly of marked individuals, can also help by indicating whether or not the song of known birds changes over time. In most species song is a seasonal phenomenon and young birds, while they may be capable of learning at other times, as Thorpe (1958) showed in Chaffinches (Fringilla coelebs), will normally only have the opportunity to learn when adults are singing. Song is usually fully developed by the time that a young bird is one year old: in most species this means that learning can only occur in the first few weeks of life, unless adult males have stopped singing at that stage of the season, or in the following spring when song commences again and the young birds are starting to sing themselves. It is also possible that new songs can be learnt later in life after song is fully developed.

The extent to which learning occurs at these different stages varies from species to species. Attempts to train birds as nestlings have so far been unsuccessful (Thielcke-Poltz & Thielcke 1960; Marler 1970; Kroodsma 1978b). This is perhaps not surprising given the brevity of the nestling period and the early stage of development of hatchlings in altricial species. Nevertheless, it is possible that songs heard at this time may have a generalized effect without being copied exactly. By contrast, the evidence that some species can learn as fledglings is good, phrases heard at that stage being memorized and sung later. In the Zebra Finch (Taeniopygia guttata) learning is gradual and is completed by around day 66 of life, shortly before the young birds of this rapidly maturing species are fully adult (Immelmann 1969). In the White-crowned Sparrow (Zonotrichia leucophrys) memorization is almost entirely in the first two months of life, long before the birds sing themselves (Marler 1970), and the sensitive period for the Swamp Sparrow (Melospiza georgiana is similar (Marler & Peters 1977). Marler & Peters (1981b)have shown clearly that this species can produce syllables memorized eight months earlier without the need for rehearsal.

In other species learning can take place both in juveniles and in young adults the following spring (e.g. Poulsen 1954; Lanyon 1960; Lemon & Scott 1966). In the Chaffinch, Poulsen (1951) found two birds caught in the autumn and isolated thereafter to sing songs like those of Kaspar Hauser individuals. However, those caught by Thorpe (1958) at an equivalent time sang songs which were less abnormal although still different from those of wild birds. He suggested that the basic features of song were learnt in the summer and fine details added the next spring. More recently Slater (Slater & Ince 1982; Slater & Clements unpublished) has found some young birds to produce near perfect copies of songs which they only heard as fledglings as well as others they heard the following spring. Adult Chaffinches cease to sing in July, at a stage when some young birds are still in the nest. Thus young birds caught in the autumn and subsequently isolated may have had very different amounts of experience from each other and this will certainly influence whether or not they sing normally in the spring. The influence of hatching date is well illustrated by the results of Kroodsma & Pickert (1980). They raised Marsh Wrens (Cistothorus palustris) on short and on long days simulating those that would have been experienced by birds hatched in August and those hatched in June. Those kept on long days moulted later, showed more autumn sub-song and learnt more songs in their first autumn than those on short days. On the other hand those on shorter daylengths after hatching were more prepared to learn the following spring. Thus it is likely that the sensitive period and preparedness to learn of birds in the wild are influenced by daylength which in turn depends on their hatching date.

A proximate factor influencing the timing of sensitive periods in young birds may be their hormone levels. Testosterone stimulates song in most bird species (e.g. Poulsen 1951; Thielcke-Poltz & Thielcke 1960), and Nottebohm (1969a) found that a male Chaffinch castrated in its first winter would learn songs in its second spring, when it began to sing after injection with this hormone. Normally Chaffinches will not learn new songs after 13 months of age (Thorpe 1958). It it thus possible that testosterone influences not only the amount of song produced but the timing of the sensitive period for learning as well. Higher testosterone levels in birds on longer days might be a reason for Kroodsma & Pickert's results. As testosterone levels can be affected by many environmental factors, abnormal titers stemming from laboratory housing conditions may be a reason why individuals vary in their preparedness to learn songs in the laboratory.

The species considered above can learn songs either as juveniles or in the following spring, and which of these stages they learn at probably depends on the opportunities they have for learning. In other species, however, learning seems not to occur during the fledgling period and to be primarily in the spring when the young birds are setting up territories and can learn from neighbors. In a long-term study of wild Saddlebacks (Philesturnus carunculatus), Jenkins (1978) found young birds to sing songs identical with those of their neighbors but unlike those of their father and birds neighboring on his territory. Rice & Thompson (1968) showed that Indigo Buntings (Passerina cyanea) were still prepared to learn at 18 months of age, and Payne (1981b) found that their song was abnormal if they were isolated from 60 days onwards. Thus fledglings do not appear to learn in this case either and the sensitive period is mainly when the birds are beginning to sing themselves.

Once a young bird is in full song, it is common for no further learning to take place. In such species laboratory attempts to modify the songs of adults with tutors or with tape recordings are ineffective (e.g. Barrington 1773; Poulsen 1954; Thorpe 1958; Lemon & Scott 1966), and the songs of wild birds do not change from year to year (e.g. Blase 1960; Dowsett-Lemaire 1979). However, in some other species the capacity to learn new songs is not lost in adulthood and birds may change their repertoires during the season or from one year to the next (e.g. Laskey 1944; Guttinger 1979). This capacity to change songs in adulthood has been described for several thrush species (Hall-Craggs 1962; Farkas 1969; Marler et al. 1972) and is also true of Canaries (Nottebohm & Nottebohm 1978). In the Village Indigobird (Vidua chalybeata) all the birds in a display area have similar song and if a bird moves to a new area it changes its song appropriately (Payne 1981a).

From this brief review it will be apparent that there are strong species differences in the timing of the memorization phase of song learning. Most species that have been studied can be placed in one or other of four categories: (i) Those in which learning is restricted to a brief sensitive period at the fledgling stage, before the bird begins to sing itself; (ii) Those in which learning is primarily in young adults at the time that they are beginning to sing themselves; (iii) Those in which learning can occur at both these stages but is restricted to the first 1-1½ years of life; (iv) Those in which learning can occur throughout life.

(b) Constraints on what is learnt

Within the sensitive period for song learning many factors may influence whether or not a bird learns a song that it hears. How often a particular song is heard may be one of these, although recognizable copying has been reported with remarkably few repetitions. Thielcke-Poltz & Thielcke (1960) found one male European Blackbird (Turdus merula) to produce an element that it had heard only twelve times, while some other Blackbird sounds heard much more frequently were not imitated. Other results suggest that the number of repetitions, beyond some minimum, may be less important than other factors (e.g. Kroodsma 1978b). Even with extensive training at a time when others would learn, some birds persist in singing songs more typical of isolates (Thielcke-Poltz & Thielcke 1960; Marler 1970; personal observation). The importance of daylength and of hormone levels have already been suggested as possible factors here, influencing the timing of the sensitive period. Social factors have also been found to influence preparedness to learn in some species. Zebra finches will learn the songs of their Bengalese Finch (Lonchura striata) foster-father even if members of their own species are singing in the same room (Immelmann 1969); Indigo Buntings learn from males with which they can interact rather than those from which they are visually isolated (Payne 1981b); in Nightingales (Luscinia megarhychos) visual contact with a tutor is required for complete songs to be learnt (Todt et al. 1979). Kroodsma (1978b) found that Sedge Wrens (Cistothorus platensis) would not learn from tape-recordings and that, while Marsh Wrens would do so, they sang only the songs of live males if they heard these later but still within the sensitive period. Thus social factors may lead young birds to select particular models in preference to others in the wild.

Experiments to determine whether or not a bird has learnt a song that it was exposed to depend on whether or not it subsequently produces that song or one based upon it. For this to be possible the bird must be able both to memorize the sound and to produce it, and failure to reproduce a particular song may depend on an incapacity in either or both of these respects. As far as memorization is concerned there is some evidence that birds may learn more sounds than they later produce. Both wild and hand-reared Chaffinches sometimes sing perfect copies of song types during quiet sub-song that they do not produce in full song (Slater & Ince unpublished observations). In the Swamp Sparrow males may perfect many more syllables in plastic song than are retained in full song (Marler & Peters 1981b). It is not known why certain sounds are rejected and others accepted from amongst those that have been learnt.

Considering the motor side of song learning, the syrinxes of passerine birds are all remarkably similar, and it is unlikely that differences in them can account for differences amongst species in what songs birds can be taught to produce (Marler 1970). The idea of a rough template acting as a filter to constrain what is learnt is much more plausible as the major factor limiting what is reproduced. The specificity of this filter varies enormously. At one extreme are the vocal mimics such as Grey Parrots (*Psittacus erithacus*), Indian Hill Mynahs (*Gracula religiosa*) and Mocking Birds (*Mimus polyglottos*) in which constraints appear to be slight (Todt 1975; Bertram 1970; Laskey 1944), so that in some cases even such unbirdlike sounds as human speech can be learnt. A remarkable example of interspecific mimicry in the wild is provided by the Marsh Warbler (*Acrocephalus palustris*) in which Dowsett-Lemaire (1979; Lemaire 1974) has shown each wild individual to mimic an average of 76 other species. Altogether she has recorded 212 different species as mimicked by Marsh Warblers. The learning appears to occur entirely in the first autumn and winter when adult Marsh Warblers are not singing, and it involves copying of birds from both Europe and Africa learnt before, during and after migration. In this case the main constraint may well be a motor one: some of the sounds that they hear may not be copied simply because they are outside the frequency range of the bird's syrinx.

In the great majority of bird species constraints on song learning ensure that they only produce the songs of their own species in the wild, although there are occasional instances of mimicry in species that do not normally mimic (e.g. Baptista 1972; Conrads 1977). Laboratory training can lead a wider variety of species to mimic. Barrington (1773) showed this in several European species; Thorpe (1958) succeeded in training a Chaffinch to sing Tree Pipit (Anthus trivialis) song; Marler et al. (1972) found that Red-winged Blackbirds (Agelaius phoeniceus) would learn Northern Oriole (Icterus galbula) song, but only if they were isolated without females of their own species. Training with songs which have been altered experimentally can indicate some of the rules which constrain learning. Swamp Sparrows will only learn syllables of their own species and not those from Song Sparrows, and will learn them even if they are edited to give Song Sparrow temporal organization (Marler & Peters 1977). The equivalent is not true of Song Sparrows: they will not learn ordinary Swamp Sparrow song, but will learn syllables from it organized like those of a Song Sparrow, or Song Sparrow syllables edited into the Swamp Sparrow pattern (Marler & Peters 1981a). The cues which birds use to exclude particular patterns from learning presumably depend on how likely they would be to be misled in their normal auditory environment. In some cases these rules are very strict and, despite extensive training at appropriate times, young birds will not learn songs of alien species even if these are similar to their own (Marler 1970).

The song of isolated birds gives some indication of the form of the crude template which constrains their learning. In Chaffinches, for example, isolate song is approximately the normal length and in the correct frequency range; it also tends to descend in frequency like normal song although it is grossly aberrant in many other ways (Thorpe 1958; Nottebohm 1968). However, neither isolate song nor the crude template is simply the lowest common denominator of song in a particular species. Isolate songs vary considerably from bird to bird (Nottebohm 1968; Konishi 1978) and birds can be trained with edited tapes to produce songs quite different from those of their species in the wild. Thus the basic whistle followed by trill form of White-crowned Sparrow song does not always appear in isolate song nor in tutored birds (Konishi 1978). Chaffinch song in the wild always consists of a trill followed by a complex end-phrase, yet Thorpe (1958) succeeded in training a bird to learn a song in which the end phrase had been transposed to the middle.

In summary, the main constraint on song learning seems not to be motor, but to be provided by a filter the specificity of which varies considerably from one species to another. Some birds will mimic a wide variety of bird and other sounds, while in others the restrictions are so tight that they are limited to learning a small variety of sounds similar to those normally produced by their own species. In some species there appear to be further limitations within these general constraints, dictating that some individuals are more likely to be copied than others and that some sounds that have been memorized are more likely to be included in full song than are others.

(c) Accuracy

Whether a bird learns only the song of its own species or will mimic a wide range of other sounds, it may copy with a greater or lesser degree of accuracy. In some species learning is normally extremely accurate, as shown by the sharing of songs in more or less identical form between wild individuals, as well as the results of training experiments. Laboratory experiments on White-crowned Sparrows (Marler 1970) and on Chaffinches (Thorpe 1958; Slater & Ince 1982) suggest that in these species the exact details of complete songs can be learnt. That this normally occurs in the field is indicated by the close similarities found between the songs of different individuals in an area (Marler & Tamura 1964; Slater & Ince 1979). Slater et al. (1980) estimate that song learning in wild Chaffinches is precise on at least 85% of occasions, the same song type being passed on without alteration from one individual to another. Many of the song types within an area are similar to each other, suggesting that they have arisen from one another by inaccurate copying (Slater & Ince 1979) and, consistent with this idea, the song types present in an area change with time (Ince, Slater & Weismann 1980). The songs of laboratory reared birds can also differ from those on which they were tutored (Slater & Ince 1982).

The very precise copying of complete songs may be rather unusual. In the Indigo Bunting syllable sequences are passed on from one individual to another both in the wild (Payne et al. 1981) and in the laboratory (Payne 1981b) and this may involve complete songs. Again the sequences present in an area change over time (Payne et al. 1981).

Neighboring Winter Wrens (Troglodytes troglodytes) tend to have many syllables in common and some of these are in the same sequences when they are shared (Kroodsma 1980). Song Sparrows trained on different song types often construct novel types using syllables from various different training models (Marler 1981). In these cases syllables, or sequences of a few syllables, are copied accurately but not complete songs.

Some laboratory studies point to improvisation as being an important source of variety in bird songs. It has been considered a major influence on song development in Oregon Juncos (Junco oreganus) by Marler et al. (1962), and may also be the case in Song and Swamp Sparrows as these species invent syllables even when trained on a variety of models (Marler 1981). This may explain the great individual variation found in the songs of wild Song Sparrows (Harris & Lemon 1972). However, it is not easy to be certain of the role of improvisation in the wild as songs sung by one individual may have been copied from others unknown to the observer. While laboratory experiments do suggest that species differ in the accuracy with which they copy from others and the extent to which they can improvise, here too one must be cautious. Laboratory conditions and training procedures are usually quite different from those the birds would experience in the wild, and this may lead to a greater or lesser degree of accuracy than is found in nature. Because of this it is essential to study the distribution and use of different songs in the wild if the functional significance of song learning is to be understood.

NATURAL VARIATIONS

Variation of song in the wild can be looked at on several different levels. Do neighbors share syllables, phrases or songs ?

Can similarities be found between more distant individuals within a population ? Are there differences between populations ? Are these greater than those between individuals within a population ? Do the differences between populations appear random or can they be related to environmental variations ?

There are substantial differences between species in the variations that are found in the wild. As studies of geographical variation have recently been reviewed by Krebs & Kroodsma (1980), they will only be dealt with briefly here. A number of factors contribute to the exact pattern shown by a particular species, including the variations in song learning reviewed above. By improvisation, reordering and recombining of sub-units birds can develop songs which differ from those to which they have been exposed and this will lead the songs of individuals within a population to differ. If young birds learn songs as fledglings and then disperse some distance to their breeding sites, there may also be differences amongst neighbors even with accurate learning. On the other hand similarities within a population are likely to be found if learning occurred in fledglings, was very accurate and was followed by little movement before breeding. This could also arise if birds learnt accurately from their territorial neighbors after dispersing, in which case the songs of neighbors would be expected to have more in common than those of more distant individuals within the population. The major determinants of song sharing within a population are therefore the accuracy of learning, the distance of dispersal and the timing of dispersal in relation to that of learning.

Generally speaking male birds do not disperse as far as females, and males may often nest on or close to the territory of their birth

(Greenwood 1980). It is also common for adults to nest on the same territory in successive years. Given this pattern of dispersal it is not easy to determine whether similarities between the songs of males nesting near each other arise from learning as fledglings or as young adults. Less close similarity within a population may also arise for two reasons: greater dispersal or lesser accuracy in learning. These considerations indicate that there are several ways in which the individuals in an area might come to sing the way they do, and that the exact schedule of song development and dispersal may be an important factor in the pattern of geographical variation in song found in a particular species (Kroodsma 1974; Krebs & Kroodsma 1980).

In some species there is a very high degree of song sharing amongst individuals on neighboring territories. In Marsh Wrens, for example, Verner (1975) found five males which averaged 112 song types each to have only 127 types amongst them. Such a high degree of sharing appears, however, to be commoner in birds with small repertoires, perhaps because larger ones are more often built up by improvisation. In many species the songs of neighbors are more similar to each other than are those of more distant birds within a population (e.g. Kroodsma 1974; Avery & Oring 1977; Payne 1978; Bitterbaum & Baptista 1979). However, there is sometimes only chance association between the songs of neighbors compared with non-neighbors (Slater & Ince 1982; Payne & Budde 1979). Neighboring White-eyed Vireos (Vireo griseus) actually share less than expected by chance (Bradley 1981), and in both Nightingales (Hultsch & Todt 1981) and Cirl Buntings (Emberiza cirlus) (Kreutzer 1979) sharing is also greater between more distant individuals than it is between neighbors. All these findings involve comparison with chance expectation. In other studies, while this has not been done, strong variation amongst individuals in a population has been reported, suggesting either that birds copy inaccurately or that individuals with similar repertoires show no tendency to nest on adjacent territories (e.g. Konishi 1964b, 1965a).

The ontogeny of song has been examined in some detail in two of the species which share more than expected with neighbors. Interestingly, the reason for the similarity with neighbors appears to differ between them. In the Indigo Bunting young males learn primarily from territorial neighbors when they are starting to sing themselves, and Payne (1981b) has found a tendency for them to learn the songs of individuals with which they are in visual contact and can interact. The similarity of songs is thus because birds learn from their neighbors. In the White-crowned Sparrow, by contrast, the sensitive period for song learning is much earlier, and the fact that neighbors usually have identical songs seems to stem from the very strong tendency of young males to breed in the same area as that in which they hatched. In the White-crowned Sparrow, as in some other species (Grimes 1974; McGregor 1980), similar songs are found in areas with more or less sharp boundaries between them (Baptista 1975; Orejuela & Morton 1975), a mosaic distribution of song types for which the word "dialect" is sometimes reserved. As Payne (1978) suggests, this is most likely to arise where songs are learnt by birds when they settle on their territories, although one would only expect this to lead to sharp boundaries between dialects if there were geographical barriers to copying. These are present at some borders between dialect areas (Baptista 1975), but certainly not in all cases (McGregor 1980). Another possibility is that secondary contact between previously isolated groups has led to sharp divisions (Baker 1975; Jenkins 1978). In species such as the White-crowned Sparrow, where there are sharp boundaries despite learning early in life, the dialect boundary probably acts as a barrier to dispersal (Baker & Mewaldt 1978), though there is conflicting evidence on this (Petrinovich et al. 1981; Baker & Mewaldt 1981).

The mosaic pattern of song distribution seems to correlate with small repertoire size. The Splendid Sunbird and European Redwing have but one song type (Grimes 1974; Bjerke & Bjerke 1981) and the White-crowned Sparrow usually has only one (Marler & Tamura 1964); in the Corn Bunting each male has two, both of which show the same dialect boundaries (McGregor 1980). The Chaffinch has a repertoire which is often as low as this, averaging 2.9 song types (Slater et al. 1980), but the distribution of song in this species is quite different. Neighbors in a group of 42 territories shared no more than would be expected at random (Slater & Ince 1982) and each population contains many song types. Up to half the individuals in a small area may sing the commonest of these; in other woods some distance away this song may be found rarely but another will be very common (Slater & Ince 1979). In other words there is a gradual shift in the frequencies of different song types with distance rather than sharp boundaries. A song type which is rare in a particular area, perhaps being sung by only one bird, may be so for two reasons. It may be a song which is common elsewhere but which is, in this area, on the edge of its distribution, or it may be one which has recently been formed by inaccurate copying. Slater et al. (1980) argue that 15% of the songs sung in the wood they studied have either been inaccurately copied or introduced from elsewhere. The song distribution of Chaffinches seems therefore to arise because birds often learn their songs before they set up territories but, unlike White-crowned Sparrows, learn them inaccurately quite frequently. They also seem not to chooseto settle next to individuals with similar songs. Thus, although the songs of Chaffinches do fall into discrete types, there are no discontinuities which could be used to define dialect areas. The lack of sharp boundaries is also found in some other species despite the sharing of phrases of songs between individuals (e.g. Nottebohm 1969; Bitterbaum & Baptista 1979). The pattern of song distribution and development in Cardinals appears similar to that in Chaffinches (Lemon 1975), although neighbors probably share song types to a greater extent (Lemon 1968).

Perhaps the most important question about variation in song from one area to another is whether it is of any functional significance. It has been argued that natural selection may favor song learning partly because it leads to such variations, and that these in turn are advantageous because they enable individuals to mate assortatively (Nottebohm 1972). Nottebohm (1969) found song to change most with distance in the Rufous-collared Sparrow (Zonotrichia capensis) where there were also sharp habitat changes, and suggested that birds mating within a dialect group might be at an advantage as this would preserve adaptations to that particular habitat. Consistent with this, there is some evidence that birds within a dialect area are more similar genetically than individuals from different areas, both for this species (Nottebohm & Selander 1972) and for the White-crowned Sparrow (Baker 1974, 1975). One interpretation of these results is that the dialect of a male provides a means whereby a female can choose a mate well matched to her. However, it is equally possible that gene flow between populations is restricted for other reasons and that dialects have formed because birds learn song within the population from which they come. An alternative form of assortative mating would be that which ensured outbreeding. Jenkins (1978) suggested this as a reason for dialects in the Saddleback, a species in which the young males which were followed moved to a different area from that in which they hatched and learned the songs of their neighbors on arrival.

Another possibility is that geographical variation in song is a by-product of vocal learning and is of no functional significance in its own right (Andrew 1962). This is unlikely for species where there are sharp dialect boundaries unless these correspond to geographical barriers. However, such sharp boundaries have been described in only a few species: they should not be presumed to be widespread simply because they occur in the White-crowned Sparrow, a species Baptista (1975) refers to as 'the white rat of the ornithological world'. Even in this species sharp boundaries do not occur in all populations (de Wolfe et al. 1974). Where song variation from one area to another is gradual and not obviously correlated with ecological variables, it seems plausible to suggest that it has no functional significance. If features of song are learnt from other individuals, if birds do not move long distances between learning and singing, and if, as seems inevitable with any learning process, the copying is not always exact, some geographical variation would appear to be inevitable. Slater et al. (1980) found that random inaccuracies in copying could have been responsible for the distribution of song types found in a population of Chaffinches, and that a similar rate of inaccurate copying would account for the changes over time described by Ince et al. (1980) in the same species. Changes over time have also been described by Payne et al. (1981), on the basis of a long-term study of Indigo

Buntings. Like changes with distance they would be predicted if song learning is not always totally accurate regardless of whether or not they have any functional significance.

In summary, song learning in some species may have been selected for because it leads to geographical variation, this in turn being advantageous because song is a cue in assortative mating. But in many other species geographical variation, while a consequence of song learning, is not likely to be a reason for it. As we shall see in the next section, the question of why these birds learn their songs is very much an open one.

WHY LEARN ?

The significance of song learning is a fundamental issue which has attracted a good deal of interest because it may be relevant to discussions about why vocal learning arose in our own species (Marler 1970, 1976). Nottebohm (1972) suggested that the development of vocalizations without learning was probably the primitive situation in birds and that learning must have arisen subsequently through natural selection. He suggested several reasons why this change might have been favored in addition to the idea that it would promote mating within populations through the formation of dialects which act as barriers to outbreeding. These and other possibilities will be discussed briefly here. It is important to remember that several selective forces may have been acting simultaneously on the same species and that different species may have been subject to different forces. Especially given the variety of song, no single answer to the question of why it is usually learnt seems likely.

The different explanations for song learning that have been proposed fall into two general classes. First is the suggestion that learning may be required if something as complicated as song is to be passed from one generation to another with any precision. Second is the idea that the young bird may be better able to fit its song to some aspect of its animate or inanimate environment if it is learnt. The first of these is rather more speculative and not easy to put to the scientific test. The most likely reason why song is sometimes very complex is through sexual selection, males with more elaborate songs being more successful in obtaining mates or territories, as shown by Howard (1974) and Yasukawa et al. (1980). Nottebohm (1972) suggests that complexity may be difficult to code beyond a certain point and that selection may therefore have favored learning, and this seems plausible given that selection seems to favor economy of genetic material (Williams 1966). As Marler (1981) puts it, 'The interspecies complexities in bird song exceed what one usually thinks of as limits to the competence of genetic mechanisms'.

If all that selection required was complexity, this could probably be achieved most simply and economically by improvisation, but a striking feature of song learning in many species is its precision, fine details being passed very exactly from one individual to another. It is commonly argued that behaviour which is learnt is likely to be more variable than that which is passed from one generation to the next without learning, but Slater & Ince (1982) have found that variation between individual Chaffinches is most marked in features of song which appear not to be easily modified by learning. They suggest that this may have arisen through high genetic variance being tolerated where precision is not required and that learning, far from leading to differences amongst individuals, may have been selected for because of the precision of copying that it allows. Thus, as well as being necessary for the generation of large and complex repertoires, learning may also enable individuals to achieve songs which match each other more precisely than would be possible without it.

The general idea that learning is necessary if song is to be precisely matched to that of other individuals or to the ideal for the environment in which the bird finds itself has been proposed a number of times. Many simple vocalizations are learnt and it is unlikely that this is because they are too complex to be developed without learning. Instead, theories of this sort propose that the exact form of a particular vocalization that is best for an individual is unpredictable and cannot therefore be programmed without learning. For example, different environments have different sound transmission characteristics (Morton 1975; Wiley & Richards 1978), and there is evidence in the Rufous-collared Sparrow (Nottebohm 1975), the White-throated Sparrow (Zonotrichia albicollis) (Wasserman 1979), and the Great Tit (Hunter & Krebs 1979) that song features correlate with these environmental differences. Hansen (1979) has suggested that song learning may be the means whereby this is brought about, young birds preferentially learning those sounds that reach them through the environment in which they learn. Consistent with this, Gish & Morton (1981) have shown that songs of Carolina Wrens (Thyrothorus ludovicianus) degrade less with distance at their site of recording than at other sites. However, in many species the differences in song from one area or habitat to another do not seem in any way systematic, and the variation in an area approaches that found between distant sites (e.g. Lemon & Harris 1974; Martin 1979). Thus, while the hypothesis that learning matches song to the environment deserves to be examined in more species, the extent of its applicability is doubtful.

An alternative type of matching is not to the physical environment but to other individuals of the same species, and this again may necessitate learning if the songs to be matched cannot be predicted. In some species where learning occurs very early in life young birds are most likely to learn from their fathers (Nicolai 1959; Immelmann 1969). In such cases song may be used as a cue to mate choice to achieve an optimal degree of outbreeding (see Bateson 1978), and learning may have become involved because it leads to more rapid divergence than would be possible with genetic control. Learning also makes it possible for the song of a son to match that of his father despite the fact that only half his genes are from that source. This would ease the discrimination between relatives and non-relatives. These points are, however, purely theoretical: there is at present very little evidence on how song influences mate choice.

Vocalizations learnt at a later stage, at around the time of territory establishment, may be important in relationships between neighboring males (Payne 1978, 1981a). Matched countersinging is common in species where neighbors share songs (e.g. Lemon 1968; Krebs, Ashcroft & van Orsdol 1981), and is likely to be important in their relations with each other (Kroodsma 1979; Smith & Norman 1979). If young birds cannot predict where they will settle, learning from neighbors is the best way of ensuring that their songs match. The learning of particular songs in this way may enable birds to address their songs to specific neighbors (Armstrong 1963; Lemon 1968), to provide a graded signal, the gradation being based on the amount of matching they show (Krebs, Ashcroft & van Orsdol 1981), or to take over territories more easily by matching songs that had been sung by the previous occupant (Payne 1978; Slater 1981). Learnt songs may therefore facilitate communication between neighbors and thus help in territory maintenance. Learnt signals may also assist in communication by identifying an individual or the group to which it belongs. Several species of cardueline finches have call notes which are pair specific and are learnt from each other within the pair (Mundinger 1979): the role of learning here is most likely to be that it facilitates partner recognition. Sharing of songs or calls more widely within a group of individuals (e.g. Bertram 1970) may enable members of the group to identify each other and so exclude intruders more easily, as suggested by Feekes (1977).

There are thus many reasons why natural selection may have favored a role for learning in the development of bird vocalizations. Two of these perhaps deserve some stress because they may go some way towards explaining the variety both of song itself and of its patterns of development and, within that variety, to account for the correlation between continuity and versatility first described by Hartshorne (1956). Where song is primarily a mate attractant signal sexual selection may have led to learning as a means of achieving an elaborate repertoire. Continuous singing is possible here because the individual is not listening for a reply. On the other hand, where song is mainly used as a signal between territorial males, less variety is required, but learning may have arisen to allow individuals to match their songs accurately to those of their neighbors. The gaps between songs which accompany low variety and give rise to Hartshorne's correlation may arise simply because countersinging males, having sung, must pause and listen for a reply (Slater 1981). Similar ideas have been independently elaborated by Catchpole (in press) with a view to accounting for differences in song complexity among Acrocephalus warblers.

These arguments suggest that there may be a continuum of species between those with relatively simple and stereotyped songs which are copied precisely and sung discontinuously and those with elaborate and varied songs produced more continuously and copied less precisely, and that the position of a species on this continuum depends on the relative importance of mate attraction and territory maintenance in shaping its song. This may account for some of the variety of song, but there are undoubtedly species in which it also serves other functions (see, for example, West, King & Eastzer 1981; Brenowitz 1981) and in which the form and ontogeny of song are best viewed as compromises shaped by several different selective forces pulling in different directions. With this in mind, it is perhaps less surprising that song varies so much between species and that efforts at making simple generalizations tend to be accompanied by long lists of exceptions.

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SEQUENCES OF SONG IN CHAFFINCHES

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Abstract: Male chaffinches (*Fringilla coelebs*) have between one and six different song types in their repertoire. Individuals with more than one sing a series of each type before switching to another. Individuals with more than two tend to cycle through their repertoire singing a series of each in turn. Some first-order transitions are much commoner than expected by chance. However, the tendency to cycle through the repertoire is so strong that the occurrence of a rare sequence can be predicted when a particular song has not been sung for some time. It is suggested that competition between song types for expression is a more important influence on their sequence than direct effects between successive songs. Two birds with unusual patterning, involving the occurrence of the same song type more than once in the cycle, are discussed. It is suggested that, in these cases, a single type may be controlled by two separate systems. The possibility is raised that it may also have been learnt from two separate sources.

Introduction

While individuals of some songbird species usually possess only a single type of song, repeats of which are more or less identical in form (e.g. white-crowned sparrow, *Zonotrichia leucophrys*, Marler 1970), in most species individuals possess a repertoire of different types ranging in size from two up to many hundreds (see Krebs & Kroodsma 1980). In a few cases it has been found that types differ in their context, suggesting that they convey different messages (e.g. in several *Dendroica* warblers, Morse 1966, 1967; yellow-throated vireo, *Vireo flavifrons*, Smith et al 1978). In most, however, this is clearly not so and the different songs appear in the same context as each other, the song produced being dependent on rules intrinsic to song organisation rather than on wider aspects of motivation or on the external situation.

The rules of song organisation vary enormously from species to species. In some the same song type is repeated a number of times before the individual switches to a second type (e.g. cardinal, *Richmondena cardinalis*, Lemon & Chatfield 1971; western meadowlark, *Sturnella neglecta*, Falls & Krebs 1975; dark-eyed junco, *Junco hyemalis*, Williams & MacRoberts 1977), while other species show immediate variety, the same type seldom, if ever, being sung twice in a row (e.g. rock wren, *Salpinctes obsoletus*, Kroodsma 1975; canary, *Serinus canarius*, Wolffgramm 1973; blackbird, *Turdus merula*, Todt 1975). When a switch between song types occurs, the rules governing which type is sung next can sometimes be deterministic (e.g. nightingale, *Luscinia megarhynchos*, Todt 1971; Swainson's thrush, *Hylocichla ustulata*, Dobson & Lemon 1977), but are more often probabilistic. Attempts to fit stochastic models to these more complex sequences have suggested that a first-order Markov chain provides an adequate description in some cases (cardinal, Lemon & Chatfield 1971; blackbird, Morgan 1976), but that higher order models are required for other species (e.g. wood pewee, Contopus virens, Chatfield & Lemon 1970; western meadowlark, Falls & Krebs 1975; wood thrush, Catharus mustelina, Dobson & Lemon 1979). If a bird has more than two song types it is common for occurrences of each type to be spread out in time so that, after switching away from a particular type, the bird is unlikely to return to it until several further switches have occurred (Todt 1975). Birds sometimes maximise the interval between bouts of the same type so that all other types are often sung before a return to the first (Falls & Krebs 1975); this is most obvious where the bird cycles through its repertoire singing each song in turn in a deterministic fashion (Todt 1971; Dobson & Lemon 1977).

Although the organisation of song varies a lot from species to species, as the above examples indicate, in many cases it has been possible to discover fairly precise rules determining which type is sung. Song is an ideal subject for studies of sequential organisation, for many of the difficulties of interpretation which arise in studies of more heterogeneous categories of behaviour are not present when the categories are both similar and equivalent to one another like song types (Slater 1973). The standard techniques of sequence analysis are thus both more appropriate and more illuminating than in many other studies, and the structure of song can be examined in detail. In species where it does not prove too complicated, this structure may give clues as to the sort of underlying mechanisms that must be involved.

The chaffinch (Fringilla coelebs) is an excellent species for such studies. Repertoire size varies between one and six song types, and the majority of birds have more than two. Although song types are often not used equally, each is usually sung a number of times before the bird switches to another (Slater 1981). Hinde (1958) provides a great deal of information on the organisation of song in this species, but he did not consider sequences, presumably because most of the hand-reared birds on which he worked had repertoires which were too small. This paper deals only with the sequential organisation of song; other aspects of its patterning will be considered elsewhere (Slater & Lester in preparation).

Methods

Data were collected in Orkney in 1978 and in Sussex in 1979-1981. The males to be recorded were selected as individuals which sang frequently and whose singing did not appear to involve a great deal of interaction with neighbours. As male chaffinches differ enormously in their song output, it is possible to find birds which sing a lot but have neighbours which sing very little. Because chaffinches show some tendency to match songs played to them (Hinde 1958; Slater 1981), song sequencing is better studied in birds that are not greatly influenced by neighbours.

The majority of data were collected in the field using either a Uher 4000 tape-recorder or a Marantz C-205 cassette-recorder with parabolic reflector. Sequences were then transcribed from the tape, played at slow speed if necessary to distinguish between similar song types, either by ear or using a Unigon continuous spectrum analyser. Where sequences were transcribed by ear a sample of songs from each bird were first sonagrammed, using a Kay 6061A Sonagraph with wide band setting, to familiarise the observer with all the song types in the bird's repertoire and ensure that no different but very similar songs had escaped detection. A few of the birds in Orkney, which had song types that could be distinguished reliably by ear, were recorded initially to prepare sonagrams of their songs, but their song sequences were subsequently noted down by hand in the field. A sample of between 500 and 2200 songs was collected from each individual. Only results from birds with more than two song types will be discussed here, as sequences in birds with two types can only be deterministic.

To study the temporal aspects of song organisation, data from several individuals were transcribed onto floppy disc for computer analysis. The results of this analysis will not be described here but showed the probability of singing to drop to a low level rather sharply 25-30 s after the last song; the probability of singing the same song as before also dropped to a chance level at around this point. In view of these results, transitions between songs separated by greater than 30 s have been excluded from the analysis described here: these are in any case unusual, as a singing bird most often sings at a rate of one song every 5-15 s and can do this for many songs in succession.

The analysis of sequences excluded consideration of repetitions of the same song type in calculating expected values (see Slater 1973). Observed and expected first-order transition frequencies were compared for each bird's matrix using χ^2 with degrees of freedom as given by Lemon & Chatfield (1971, p 16). Whether particular transitions were more common than expected was tested by condensing the matrix about the cell of interest and then using a 2 x 2 χ^2. Higher-order effects were examined by testing whether the frequencies of longer sequences differed significantly from those predicted from the first-order transition matrix. The frequencies of different recurrence intervals were also calculated for each song type. The recurrence interval of a song is the number of switches in song type occurring between two bouts of the same type (Falls & Krebs 1975). Thus the recurrence interval of the sequence ABA is two and that of ABCA is three. If a bird is maximising the return time to a particular song, tending to cycle through its repertoire, the commonest recurrence interval should be the same as its repertoire size. If, on the other hand, birds switch between songs at random, recurrence intervals should follow a negative exponential distribution, although with a minimum of two as we are only considering switches between different song types. The recurrence intervals for the different song types in each bird's repertoire were tested against each other using the Kolmogorov-Smirnov two-sample test and, where this did not reveal a significant difference, the results were combined for plotting (see Figure 1).

Results

The results for each bird will be presented separately, first for four individuals in which all song types occurred at about equal frequencies, then for three in which one or more song types were much rarer than the others, and finally for two in which one song type was disproportionately common. Tables I, II and IV are first-order transition matrices for a representative sample of the birds to illustrate how these were analysed; Figure 2 shows flow diagrams based upon both these and the equivalent tables for the other birds.

Sequencing with all songs at similar frequencies

Racecourse bird. 1018 songs were recorded, and these fell into three types: A (35.4%), B (30.6%), C (33.9%). First-order transitions diverged significantly from randomness (Table I). On the basis of the transition frequencies shown in Table I, 55.6 out of 94 triplets would have been expected to include all three song types (i.e. to be of the general form XYZ rather than XYX), whereas 91 were of this form ($\chi^2 = 55.2$, $\underline{df} = 1$, $p < .001$). Thus higher-order dependencies were also

Table I. First-order song sequences in the Racecourse bird*

	A	B	C
A	325	26 (18.2)	10 (17.8)
B	9 (16.8)	273	28 (20.2)
C	24 (16.2)	12 (19.8)	305

$\chi^2 = 20.2$, $\underline{df} = 1$, $p < .001$

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*In this and subsequent tables expected values, shown in brackets, are calculated only for transitions between different song types. The figures show the number of times the song at the left was followed by that at the top.

in existence, the bird tending to sing triplets in which all three songs were different. This tendency was very strong so that the recurrence interval histogram peaks very sharply at three (Figure 1). As might be expected from Table I, the most usual sequence was ABCAB... (see Figure 2).

Stenaday top bird. 950 songs were recorded, belonging to four different types: A (26.3%), B (28.6%), C (20.0%), D (25.1%). First-order sequences were non-random, but not as strongly so as in the last bird (see Table IVa of Slater 1981: $\chi^2 = 20.3$, $df = 5$, $p < .01$). Higher-order influences were also important: of 181 quadruplets, 42.2 would have been expected to include all four song types on the basis of the first-order transition frequencies, but 121 did so ($\chi^2 = 191.9$, $df = 1$, $p < .001$). As the flow diagram in Figure 2 suggests, the commonest of the quadruplets were the four drawn from the sequence ABDCABD... and the next commonest were the four included in the sequence ABCDABC... However, 57 quadruplets contained all four song types but were not drawn from these sequences, while 17.7 would have been expected. The tendency to cycle through the repertoire is so strong that first-order dependencies may be overshadowed: for example, if the bird sings the rare sequence CBA the most likely next song is D despite the fact that AD is a very unusual transition (CBAD occurred on five occasions compared with an expectation of 0.67). As these results might predict, the recurrence interval histogram peaks strongly at four (Figure 1).

Arboretum bird. 641 songs were recorded, and these belonged to four types: A (12.3%), C (35.6%), L (27.3%), S (24.8%). This bird is included here because the variation in frequencies between song types is largely due to differences in bout length: the number of bouts of the commonest was only slightly greater than that of the rarest (27.7% were C, 21.4% were A). This bird provides a particularly good example of sequences which are organised in a predictable manner within a recording session

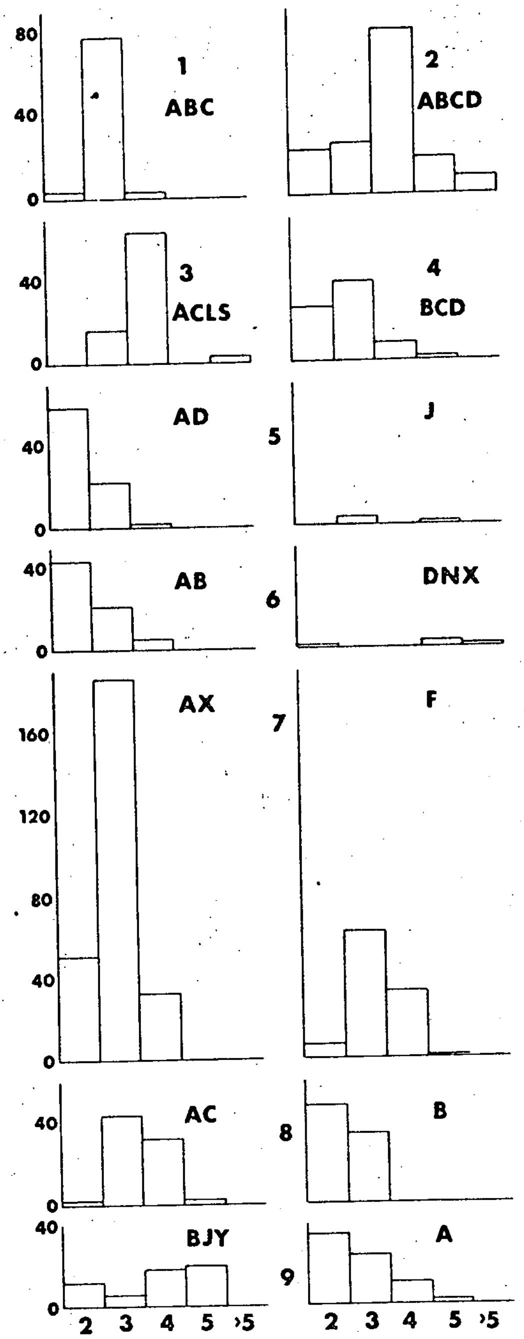

Figure 1. Recurrence interval histograms for the songs of all the nine birds studied. The recurrence interval of a song type is the number of switches between song types which occur between two bouts of that type. Song types in the repertoire of a bird which are not significantly different in recurrence interval distribution have been massed for plotting; the letters indicate the song types covered by each plot. The numbers refer to the different birds as follows: 1. Racecourse bird; 2. Stenaday top bird; 3. Arboretum bird; 4. Wasdale bird; 5. Waterfall bird; 6. Lower conifer bird; 7. North monument bird; 8. Middle hedgerow bird; 9. Quarry garden bird.

but which can vary from session to session. First-order transitions diverged significantly from randomness ($\chi^2 = 45.7$, $\underline{df} = 5$, $p < .001$), but not in such a way as to suggest a single most common ordering of the four types (Figure 2). As with previous birds, quadruplets including all four song types were very much more common than expected: of 90 quadruplets, 74 were heterogeneous against an expectation of 35.9 from the first-order transition matrix ($\chi^2 = 67.4$, $\underline{df} = 1$, $p < .001$). The recurrence interval histogram also peaked at an interval equivalent to the repertoire size (Figure 1). However, the quadruplets which were commonest varied from day to day, explaining the heterogeneity in the first-order transition matrix. For example, on 22nd May 1981 all 35 quadruplets recorded were in the sequence ...ASCLASC..., while three days later the 11 recorded were all in the order ...LSACLSA...

Wasdale bird. 718 songs were recorded, and these fell into three types: B (36.4%), C (31.9%), D (31.8%). Again, the first-order transitions were non-random ($\chi^2 = 22.7$, $\underline{df} = 1$, $p < .001$), and triplets involving all three song types were commoner than expected (69 observed, 55.5 expected: $\chi^2 = 7.9$, $\underline{df} = 1$, $p < .01$), as were recurrence intervals involving three switches (Figure 1). The bird tended to sing in the sequence BDCBD...

Conclusions. The results of these four birds suggest certain basic rules which male chaffinches follow when singing. Each song is repeated several times before the bird switches to another and a bout of each song type tends to be sung in turn. Variation in the number of each type sung is therefore primarily in bout length rather than in the number of bouts. Two main factors govern sequencing. First, some first-order transitions are very much more common than others. The extent to which this is the case varies from bird to bird, the sequences of some being near deterministic, while in others they can approach randomness. The Racecourse bird was especially predictable, while the first-order

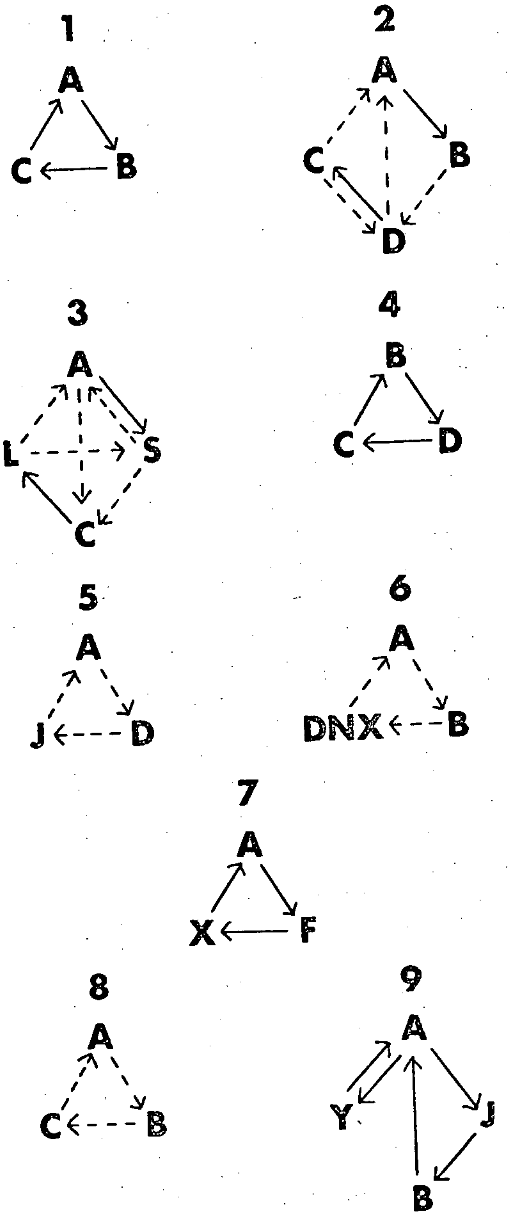

Figure 2. Flow diagrams indicating the commonest sequences between song types in all the birds studied. Arrows indicate all sequences that were commoner than expected. The arrows are broken where the relationship is not significant on a 2 x 2 χ^2 test, and complete where it is significant at $p < .05$. The numbering of the birds is the same as for Figure 1.

transitions of the Arboretum bird varied substantially from day to day. The second influence on sequencing is the tendency to maximise return time to the same song type. This was a strong effect in all four birds: they tended to sing a bout of each song in turn before returning to the first. In some cases this higher-order effect is stronger than the first-order one, so that it can be predicted that a rare transition will occur simply to comply with this rule. It can also be a strong influence even where there is no evidence for first-order effects: thus, in a bird with song types X, Y and Z, it may not be possible to predict after X whether Y or Z will occur, but YX nearly always leads to Z and ZX to Y.

In general, therefore, these four birds follow similar rules in the organisation of their singing. The sequencing of the others to be discussed is most easily explained in relation to this basic pattern.

Sequencing with some rare songs

North monument bird. 2178 songs were recorded and these belonged to three types: A (41.7%), F (23.7%), X (34.6%). First-order transitions showed a significant departure from randomness ($\chi^2 = 7.06$, df = 1, $p < .01$), although the effect was not very strong, partly perhaps because this bird countersang with a neighbour quite frequently. From the frequency of first-order transitions, 187.3 triplets would have been expected to include all three song types, whereas 323 did so, giving a highly significant result ($\chi^2 = 196.6$, df = 1, $p < .001$). The most usual sequence sung was FXAFX... (Figure 2), but the bird also sang FAXFA... quite frequently. The recurrence interval distribution for song type F was significantly different from that of the other two types (Figure 1), primarily because this song was somewhat rarer so that the distribution was skewed towards longer intervals. Apart from this, the pattern of singing in this bird was similar to that of those with equally common songs described above.

Waterfall bird. 858 songs were recorded and these belonged to three types: A (48.8%), D (45.3%), J (5.8%). Given the rarity of type J, it is perhaps not surprising that first-order transitions do not differ significantly from random (Table II). Type J being infrequent, few triplets involving all three song types were expected, but significantly more were found than this expectation ($\chi^2 = 8.5$, df = 1, $p < .01$). Here therefore higher-order influences can be detected without a significant first-order effect. The recurrence interval distribution differed significantly between J and the other two song types, showing that A and D tended to alternate with each other while J occurred at less frequent intervals (Figure 1).

Lower conifer bird. The 1041 songs recorded fell into five song types, but with two of these comprising the great majority of the bird's output. Frequencies were: A (53.3%), B (39.3%), D (0.5%), N (1.6%), X (5.3%). The last three types were combined to test for first-order influences and none were found ($\chi^2 = 0.1$, df = 1, NS). As with the previous bird, however, series of three song bouts all of which were of a different type were commoner than expected ($\chi^2 = 9.2$, df = 1, $p < .01$). The bird tended to alternate between types A and B (see Figure 1) but, where it did introduce one of its rarer types, it switched to a different song after it to that which it had been singing before (Figure 2).

Conclusion. In these three birds one or more song types were rarer than the others and yielded significantly different recurrence interval histograms. The basic rules of sequencing are similar to those in earlier birds except that, where two songs are much commoner than the others, near random sequencing is more prevalent because the scope for departure from randomness is slight. The birds tend to sing bouts of each song in turn, but with the rarer songs only occurring intermittently rather than in every cycle.

Table II. First-order song sequences in the Waterfall bird*

	A	D	J
A	333	56 (54.6)	9 (10.9)
D	44 (45.4)	308	9 (7.6)
J	10 (8.6)	6 (7.4)	31

$\chi^2 = 1.0$, _df_ = 1, NS

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*See footnote to Table I

Sequencing with one very common song

Quarry garden bird. 1839 songs were analysed. These fell into four types: A (68.7%), B (5.2%), J (14.1%), Y (12.1%). First-order transitions were non-random (See Table IVb in Slater 1981: $\chi^2 = 89.3$, *df* = 5, $p < .001$). As with earlier birds, quadruplets involving all four song types were commoner than expected ($\chi^2 = 32.4$, *df* = 1, $p < .001$). However, certain other quadruplets occurred considerably more frequently than some of these. The five possible ones in the sequence AJBAYAJBA... accounted for 72 of the 153 quadruplets recorded, and it was noticeable in the field that the bird spent long periods singing in this sequence. Thus the five quintuplets which can be drawn from this series accounted for 51 of the 120 quintuplets in the data, whereas the expectation was only 18.2 ($\chi^2 = 70.1$, *df* = 1, $p < .001$). Although this sequencing cannot be deduced directly from the first-order transition matrix, the transitions involved in it are all significantly commoner than expected (Figure 2). The recurrence interval histograms show that song A tended to occur after only one or two other song types had been sung, as this sequence would suggest. The other three song types showed similar patterns to each other, the commonest recurrence interval being five (see Figure 1).

A possible explanation for the unusual results of this bird would be if the songs labelled as A belonged to two song types and not one, one of them occurring after Y and the other after B. However, careful examination of the sonagrams of this song in these two contexts showed the elements comprising the song to be identical in form between them. An alternative possibility is that the same song type appeared at two positions in the sequence because it was being treated by the bird as if it were two separate song types. Thus, although the bird appeared to have only four songs in its repertoire, and these seemed to follow a complex temporal pattern, it might have had five songs with rules of

Table III. Number of elements in the different phrases of two songs which occurred in two different contexts, analysed according to context. Ranges given are standard deviations.

(a) Song type A of the Quarry garden bird

	Phrase 1	Phrase 2	Phrase 3	N
After B or J	3.20 ± 0.77	5.07 ± 0.70	6.13 ± 0.52	15
After Y	3.25 ± 0.45	5.22 ± 0.65	6.50 ± 0.89	16

(b) Song type B or the Middle hedgerow bird

	Phrase 1*	Phrase 2	Phrase 3	N
After C		3.45 ± 0.62	6.66 ± 1.03	47
After A		3.49 ± 0.61	6.50 ± 0.80	84

*Phrase 1 was omitted here as it sometimes commenced so quietly that it was impossible to gain an accurate assessment of the number of elements in it. All the songs analysed were from sequences when the bird sang ABCBABCB...

sequencing similar to those of other birds. When sung by different individuals, the same song type can show divergences in the number of elements in a phrase (Slater & Ince 1978). A sample of type A songs from this bird was analysed to see if equivalent differences were present between the two contexts. None were found (Table IIIa). There is thus no evidence that this song had been learnt from two separate sources, although it is still possible that it might have been, as individuals do not always differ in this respect. The only way in which this song type was found to differ between the two contexts was in bout length. As most of the data from this bird were collected by ear, this was assessed as the number of songs in a bout rather than with a criterion based on duration. The mean length was 13.1 songs following Y and 7.7 following B or J ($p < .001$, Mann-Whitney U-test). Such differences are common between different song types and this finding suggests that A in this bird may have been used as if it were two types.

Middle hedgerow bird. 2166 songs were recorded. These were of three song types: A (28.5%), B (49.1%), C (22.4%). Despite the fact that all three songs were common, first order transitions did not differ from independence (Table IV). Of 212 triplets, 157 involved all three song types while 94.6 were expected to ($\chi^2 = 74.3$, df = 1, $p < .001$). However, as with the last bird, it was noticeable that sequences fell into particular categories. The bird would spend periods of time singing in the sequences ABCAB... and CBACB..., but it also frequently sang ABCBAB... Although, when combined in a transition matrix, these different patterns did not give a significant result, after a few bouts of song had been heard during a particular recording session its singing was relatively predictable.

These differences in sequencing from one time to another suggested that the bird may have had two song type Bs in its sequence, which were

Table IV. First-order song sequences in the Middle hedgerow bird*

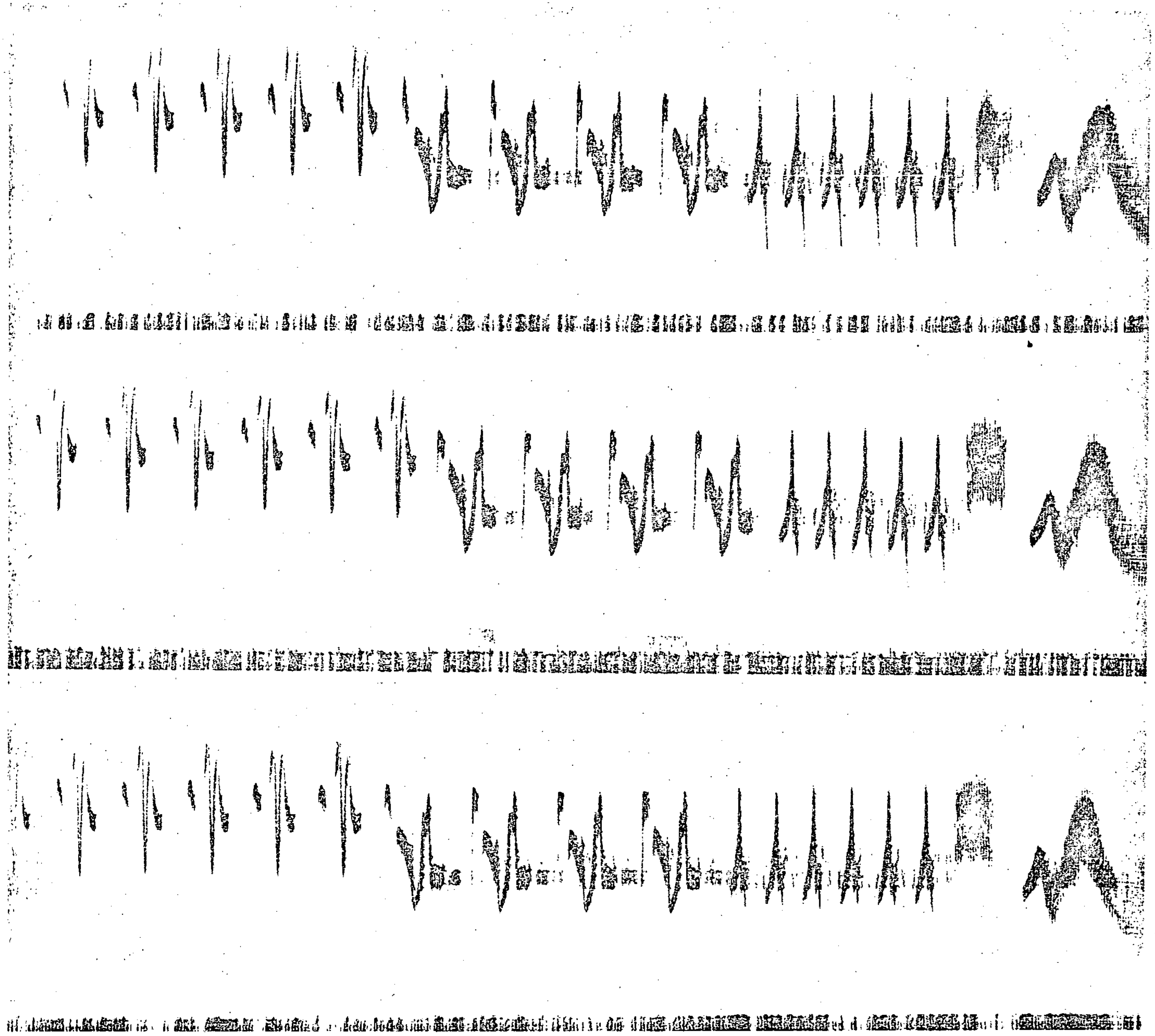
	A	B	C
A	516	67 (63.3)	21 (24.7)
B	60 (63.7)	904	65 (63.3)
C	28 (24.3)	60 (61.7)	384

$\chi^2 = 1.6$, $\underline{df} = 1$, NS

*See footnote to Table I

sometimes separated and sometimes sung consecutively. Although they cannot be distinguished by ear, we can call them B and B' and suggest that the bird sometimes sings ABB'CABB'..., which is heard as ABCAB..., and sometimes ABCB'ABCB'..., giving ABCBABCB... to the ear. If this was the case, its patterning would be similar to that of other birds: for example, Stenaday top, which sometimes sang ABDCABD... and sometimes ABCDABC... As with the Quarry garden bird, no distinction could be found between examples of this song type in the two different contexts of its occurrence, either by comparison of sonagrams (Figure 3) or by analysis of the number of elements in a phrase (Table IIIb). However, bout length did differ according to whether the song occurred at one or two points in the sequence. But length was, in this case, analysed as the time between the start of the first song in a bout of one type and the end of the last. As singing rate varies independently of the time of switches between song types, this is a better criterion of bout length than number of songs in a bout (Hinde 1958; Slater & Lester in preparation). Bouts of B which were both preceded and followed by bouts of both A and C averaged 1131 s in length, whereas those with only one other song type before and after them (as in the sequence BABCB) averaged 497 s in length (Mann-Whitney U-test, $p < .002$). This fits in with the suggestion that B occurs twice in the sequence as, in the former context, a bout would be B and B' combined, whereas it would either be B or B' in the latter. Bouts in the sequence ABCABC... should therefore be twice the length on average of those when the bird is singing ABCBABC... Thus, as with the Quarry garden bird, the apparently complex sequencing of song in this bird comes much more into line with the patterning shown by other individuals if it is suggested that the bird has one more song in its repertoire than it appears to have by ear, but that that song type is indistinguishable from another in the repertoire.

Figure 3. Sonagrams of three examples of song type B from the Middle hedgerow bird. One was taken from each of three successive bouts of B when the bird was singing ABCBABC..., so that the centre sonagram should be different from the other two if B is really two different song types.



Conclusion. Unlike the previous birds, these two both sang with more complex sequences in which, instead of singing each song in the repertoire in turn, they frequently sang the same song type at two different positions in the sequence. In both cases, however, the sequences were similar to those of other birds if this song type was taken to be used by the bird as two types, one for each of the two contexts in which it occurred. While there was no evidence from its form in the two different contexts that it was separable into two different types, bout length differences between the two situations fitted in with the idea that it was being used as such. This, and alternative hypotheses, will be discussed below.

Discussion

Some aspects of the organisation of song in chaffinches could be accounted for in Markovian terms, by suggesting that the song produced at a particular moment depends on the sequence of songs that preceded it. Transition analysis demonstrated first-order influences in all the four birds with songs which were nearly equal in frequency, but not in the two (Waterfall and Lower conifer) in which two song types comprised the great majority of the output. It was decided not to search for higher-order influences, by looking at progressively longer sequences, as has been done in a number of other studies of bird song (e.g. Lemon & Chatfield 1971; Dobson & Lemon 1979), because inspection made it clear that the order of chain which would be necessary to account for the organisation would be highly dependent on repertoire size. Furthermore, even if it were possible to state that song sequencing followed an nth order Markov chain, this would say little about the exact principles involved and be of little help in building a model of song organisation.

Whatever systems underlie the production of different song types must have certain properties: they must vary from song to song in the time for which they are activated, so leading to differences in bout length; they must have connections with other systems which account for the non-random first-order effects found; over and above these connections, which could be constructed to lead each song to be sung in turn, there must be a mechanism leading songs to occur out of sequence when they have not been sung for some time. This last property requires something more than simple connections between systems. It suggests that, in addition to such connections leading some sequences to be commoner than others, songs may compete for the output pathway, causal factors being expended during performance and building up during non-performance. This seems the most economical way to account for the tendency to maximise return time between songs which, while it could be described as a Markov effect of high order, would be hard to model using only sequential connections between systems.

It may not seem parsimonious to suggest that both Markovian and competitive influences are involved in the sequencing of song. How necessary is this? The need for a model involving competition is clear from the fact that songs often occur totally out of sequence when they have not been sung for some time, and that the sequential patterning of some birds can vary from day to day. This is reminiscent of the competitive model proposed by Slater (1978), though not specifically for bird song, in which the priority of an act diminished during performance and rose during non-performance. Such a model would produce cycling through the repertoire, and it does also generate non-random transitions between acts, although primarily where these occur at very different frequencies. Some of the first-order relationships described here could have arisen for this reason, without it being necessary to postulate facilitatory connections between successive song types. Some could also have arisen through biassed sampling. As some birds adhere to the same sequence for long periods, but sing other sequences at other times, extensive recording on one day could suggest a particular pattern even if sampling on many other days showed all other patterns to be equally common.

These arguments suggest that competitive mechanisms are essential to account for the pattern of singing, but that the need for sequential influences is more questionable. However, in most birds a large number of transitions were recorded over several days of observations so that significant first-order influences were unlikely to be due to biassed sampling; where song types occur at about equal frequencies they are also unlikely to be a side-effect of competition. In such birds some direct sequential effects seem likely. A model might for example propose that some of the excitation in a system controlling a song type spreads to other systems depending on how closely connected they are to one another. A possible model here would be similar to that proposed by Whitney (1981) for the varied thrush (Zoothera naevia), except that he had to cope with the added complication that these birds tend not to sing similar songs close together in a sequence.

At first sight, the last two birds considered would require a more complex model than the others to account for the sequential organisation of their song. In both cases, instead of habitually singing each song in turn before returning to the first, these birds tended to sing one of their song types at two different positions in the sequence. Two main hypotheses may be suggested to account for this. The first is that which was put forward earlier: the singing of these birds becomes less complex and follows a similar pattern to that of the other birds if the song type in question is assumed to be treated by the bird as two song types, one for each of its contexts. This could arise because each of these two songs has a separate system underlying its occurrence in each context. If so, then the mechanisms which need to be proposed to account for the singing of these birds are identical with those required for the birds showing simpler sequences. The only difference between the two groups would be that the repertoire size of one is actually one song larger than it appears to be because the same song is included in it twice. The alternative hypothesis is that there is only one system controlling the occurrence of this song type but that it is normally activated twice in each song cycle. The fact that the song did not differ at all in form or in number of syllables between the two contexts might argue in favour of this idea; however, in both birds, bout lengths differed between the contexts. It is not easy to see how this could arise from a simple competitive model without two separate systems being involved in controlling this song type. However, a more detailed consideration of the mechanisms underlying song must await inclusion of information on other aspects of temporal patterning (Slater & Lester in preparation), together with computer simulations aimed at examining the output of different models in detail and comparing between their output and that of the birds.

If these two birds do have two systems responsible for production of one of their song types, an ontogenetic question also arises. Has the bird learnt the same song twice, once into each of the two repertoire slots that it occupies, or is it just that two song producing systems have access to the same output form? The data do not allow distinction between these possibilities. Evidence for the former would be if the number of elements in a phrase showed differences between the two contexts, as it can do between examples of the same song type sung by different individuals. There was no evidence of this in either case. But the song could be learnt twice without necessarily being learnt from two different individuals.

A commonly heard song might be copied into one slot until a precise match was achieved and then copied into another if one was available. Both the song types concerned were amongst the most common in the populations from which these two birds came.

How frequently might one expect the same song to be learnt twice if birds drew their models at random from the population without the constraint that each could only be learnt once? Slater, Ince & Colgan (1980) argued, on the basis of computer simulations, that the observed mean repertoire size of 2.9 song types in a population of 42 birds would represent an actual size of 3.3 if double copying occurred. Thus about two birds in five would have the same song in two different slots. However, the existence of double copying could only be detected in birds with an apparent repertoire size of three or more songs as sequential organisation cannot be studied in the others. As 62% of birds have repertoire sizes of three or more, the possibility of detecting an extra slot should exist in 40% of these, or 25% of the population as a whole.

The idea that chaffinches may have a limited number of slots into which songs can be copied has an interesting parallel with the work of Nottebohm, Kasparian & Pandazis (1981) on canaries. They found that the size of two of the brain nuclei involved in singing (HVc and RA) correlated positively with song repertoire size. In what he refers to as the 'library principle', by analogy with the numbers of books on library shelves, he suggests that birds with large nuclei can have large or small repertoires, but that birds with small nuclei cannot have other than small repertoires (Nottebohm 1981). The idea put forward here is that, just as a commonly used book may appear in two positions on the shelves of a library, so a commonly heard song may be copied into two slots in the brain of a chaffinch and used as if it were two songs.

Although the evidence in favour of it is not strong, the hypothesis that male chaffinches can learn the same song type more than once has been discussed here in some detail in the hope that the phenomenon may be examined in other species. The ideal way of testing such an hypothesis would be with hand-reared birds trained on differing amounts of different song types. As chaffinches are hard to hand-rear (Slater & Ince 1982), studies of this sort would be most easily carried out on other species with relatively small repertoires. Another species in which the phenomenon might exist is the veery (_Hylocichla fuscescens_). Dobson & Lemon (1979) interpreted the singing of one which they studied as following a second-order Markov chain. However, the data they present show that it frequently sang its four song types in the sequence 4312143121... In Markovian terms one cannot tell after 1 whether 2 or 4 will occur so that a first order model is inadequate. After the arguments presented here, however, it seems more fruitful to think in terms of a competitive model with the possibility that song type 1 occupies two different slots.

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