PAIR BONDING IN THE ZEBRA FINCH

by

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ABSTRACT

The overall aim of this thesis is to provide a clear descriptive account of pair formation and bond maintenance in the Zebra Finch. Factors important in the processes involved are assessed and the hope, explained at the outset, is to provide a clear grounding upon which future work can be based. The first three sections of the work review and analyse the background to this bird species. Types of pair bonding in birds are discussed and the general biology of the Zebra Finch is explained in detail. Section 3 deals with the behavioural displays observed during the course of the present study and reviews such observations as have been made in the light of the literature. One display, described probably for the first time, is an 'intense head-forward threat' posture which was previously thought to be absent from the behavioural repertoire of this species.

The pair formation process is assessed in two situations; pairs of males and females in isolation in individual cages and in small groups (two males and two females). In both cases behavioural changes are found to occur which are indicative of pair formation in this species. Courtship is initially high but declines after the first watch. It is directed at the mate from the outset which shows that mate selection, in the groups, is rapidly concluded. Aggression between mates is never obvious and that between non-mates shows an interesting difference between males and females. In the former, levels are high from the outset, the first day of introduction, but the females only show aggression after the bonding relationship has been initiated for at least a day. The result of this aggression in the groups is to provide a mobile 'mate territory' which, in many cases, both male and female will defend. Other behaviour increases

in its frequency of occurrence as pair bonds are formed and is presumably important in the maintenance of bonds. This includes the number of bouts of undirected song and the length of time spent allopreening and in clumps. This contact behaviour (allopreening and clumping) is confined to mates only. The behaviour of the mates tends to become synchronised and this change is more marked in the groups than it is in the isolated situation.

The birds used in the pair formation situations described above had not met prior to the experiments and in some cases pairs failed to form. This suggests that incompatibility is a real possibility in this species and also indicates that both the male and the female have preferences for particular individuals which they express during mate selection.

As an addition to the work on pair formation, experiments described in Section 5 deal with changes in courtship due to the possession of a pair bond. Males who are separated from a female for a period of time will court that female on introduction and it is shown that pair formation between the two individuals reduces this tendency and, although courtship still occurs on introduction, there are far fewer bouts involved. In addition, males are found to remain sexually active towards non-mate females even after the establishment of a presumably strong pair bond. This so-called promiscuous behaviour is not observed in mated females who tend to react aggressively towards a courting non-mate. The possibility is thus proposed that the bond could be 'stronger' in the case of females than it is in males of this species.

Contact between the mates will be important during pair maintenance and Sections 6 and 7 are devoted to an examination of the role of vocalizations in this process. In Section 6, it is

clearly demonstrated that the calls of both males and females provide ample individual characteristics on which identification of the mate can be based. These are accurately reproduced in successive calls and appear to provide a predictable and recognisable form of communication. Of the calls assessed, the male 'loud' calls emerge as a long-distance vocalization which is highly variable between individuals, far more so than female loud calls, and one which shows marked individual distinctiveness. Male song is also described and was found to be similarly individually distinct. There are some cases where two males sing almost the same song but the loud calls of the males concerned are measurably different. This is taken as indicative of the importance of a long range vocalization which is individually distinct (male song is of low volume compared to the loud calls).

Evidence for individual recognition of the calls of the mate is provided by the work described in Section 7. Males and females do call more to one another when they are mated but the relationship between the rate of calling and pair formation is not a simple one. Females are found to show more significant recognition of the mate and this could be linked with the greater individual distinctiveness of male vocalizations. In addition, females show that they can alter their calling rates far more readily than can males which supports the suggestion from Section 5, that the bonding relationship may be stronger, or at least more evident, in the female of the species.

The last two sections of the thesis deal with pair maintenance activities. The relative importance of vocal and visual factors in bond maintenance is assessed. A male and female cannot form a bond in situations where physical contact is prevented, either by a solid or transparent partition. Complete contact is essential which suggests

that activities such as copulation, clumping and allopreening are necessary before a bond can be fully established. Separation of mates on the other hand, does not disrupt an established bond, the bond is still evident after the period of separation even if the bird re-pairs with another individual (see below). However, behaviour common to a pair formation situation reappears on the reunion of mates indicating that the responses of the male and female have altered as a result of the lack of reinforcement of the bonding relationship during the period of separation.

The importance of auditory and visual reinforcement is assessed in a situation in which mates are separated and provided with a new partner. Pair bonds result with the new partner only in the situation in which no contact is allowed with the former mate. If established mates can hear or see one another then the established bond is retained and the new partner rejected. It is interesting to note that on reunion with the established mate, both males and females choose to re-establish their former bonds and, even after having formed a 'new' bond, the new partner is rejected in all cases. This raises the possibility that more than one bond can be present at any one time but, at least in the case of the Zebra Finch, only one (that with the mate) is ever expressed.

Finally, in Section 10, pair formation is reviewed in the light of the experimental findings. It is divided into two processes, mate selection and bond maintenance or reinforcement, which are discussed separately. Comparisons with imprinting responses seen in parent/offspring relationships are made and the thesis ends with a few proposals as to the direction future research could take.

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CONTENTS

INTRODUCTION

The courtship displays performed by birds during pair formation are some of the most beautiful and complex behavioural acts seen in the animal world. In a paper published in 1940 Lack wrote that there was probably more ignorance concerning pair formation than any other aspect of bird behaviour and since that date few researchers have shed any light on the features of the processes involved. It is true to say, however, that the role of pair formation activities in reducing aggression and promoting copulation between potential partners has been well established in a number of species and a considerable amount of literature concerning the motivation and derivation of the displays concerned has built up over the years. Yet little has been done to trace systematically the behavioural modifications that manifest themselves during the pair formation period or to assess the actual nature of the pair bond that results. Indeed the term 'pair bond' itself is vague and ill-defined implying some form of physical tie or link between two individuals.

This thesis can be divided into two broad sections: the first deals with an examination of the changes in behaviour that occur during the pair formation of a species within the laboratory environment and an assessment of the length of time before such a process is complete, i.e. a pair is formed. This includes an analysis of the role played by vocalizations in the process and forms the bulk of the written work. The second section involves an experimental approach into the importance of various factors in the formation and maintenance of pair bonds. The main aim of the work is to provide a clearer picture of pair formation and the pair bond which could form the basis for future work.

INTRODUCTION

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The species chosen for this study, the Zebra Finch, Taeniopygia guttata (Vieillot 1817), is ideal for the experimental work described. It is an Australian member of the Grassfinches or Estrildididae, a family well noted for the formation of prolonged pair bonds (Kunkel 1974) and their suitability for laboratory studies (e.g. Morris 1954, 1958; Goodwin 1959, 1960, 1962; Immelmann 1965, 1967, 1969; Butterfield 1970; Evans 1972; Zann 1972; Caryl 1975). The Zebra finch has been domesticated in this country since before the turn of the century and has the admirable advantages of being cheap, easily obtainable in large numbers, and possessing several well-established colour mutants. The excellent field studies carried out by Immelmann on this species (e.g. 1968), indicate that the pair bonds formed between individuals are maintained for life. Breeding is geared to the aperiodic environmental conditions encountered in its natural semi-arid habitat; the stimulus of rainfall appears all important and is apparently responsible for pair formation and maintenance activities being prolonged throughout any non-breeding periods. Thus it is possible to study pair formation in this species outside of the actual breeding situation, when endocrinal complications may arise, and at any time of the year providing laboratory conditions are kept approximately constant throughout. This offers considerable advantages over those species with periodic breeding cycles where for much of the year pair formation and bonding is not a likely occurrence. Finally, in this extolation of the virtues of the Zebra Finch as a laboratory subject, it remains to mention that it has formed the basis for some previous studies which in turn provide a starting point for the present work. Morris (1954, 1958) and Butterfield (1970) have examined pair formation and bond maintenance, and Caryl (1970, 1975) considered the effect of pair bonds on the aggression between conspecifics.

Other types of bonds, or relationships, between individuals occur in the social organization of the higher vertebrates. These are notably the parent/offspring relationship and the social tendency or bond between members of the same species (the 'social group'). Of these the latter, aside from some admirable work by Crook (1961), has suffered from a similar lack of experimental analysis as has the pair bond. The possibility that the pair bond and social bond may be similar processes, differing only in a matter of degree, has received scant attention. In contrast the experimental investigation of the parent/offspring relationship has proved remarkably rewarding and our knowledge of at least the initial stages of the imprinting process and its profound long term effects are considerably advanced. The study of the interactions between parents and offspring has been extended to the primates and much is now becoming known of the nature of this attachment in man. In view of this development it is surprising that so little time has been devoted to the other major bonding process in man, the pair bond. Man is one of the few monogamous primates who expends considerable time and effort in the procuring and retention of a mate for life.

It is unwise to draw direct comparisons between birds and mammals. There are for example large differences in brain structure and the respective evolutionary lines have diverged since at least the Permian era. Yet striking similarities have been found in the nature of their parent-offspring bonds. It therefore seems likely that an understanding of factors involved in the pair bonding of birds will be useful when extending studies into the realm of man himself.

An investigation of pair bonding would be incomplete without some knowledge of the ultimate and proximate factors which determine the type and nature of the bond under consideration. A bond may be monogamous or polygamous, prolonged or merely last long enough to enable copulation to occur, and this will be dependent on the way in which environmental and physiological factors interact and affect the social processes involved. Thus in Section I some time is devoted to a discussion of the types of pair bonds found in birds and the ways in which these may be adapted to the needs of a particular species. This is followed by sections dealing with the general biology and behaviour of the Zebra Finch.

Changes in behaviour occurring during pair formation of Zebra Finches are examined in Sections 4 and 5. The actual behavioural changes are noted including such features as courtship, aggression and proximity changes. Section 6 is devoted to vocalizations; a sonographic description of calls and song, their possible functions in different contexts, and, Section 7, the possibility of individual recognition of the partner by calls. The discussions at the ends of these sections formulate ideas on what is meant by a pair bond in the Zebra Finch and the behaviour that is essential in its formation and maintenance.

The question of the relative importance of these behavioural changes in bond formation is investigated in Section 8. For example, is the experience of auditory and visual signals enough to develop a relationship between potential partners or is contact behaviour (i.e. tactile) essential to the process? This question is carried one stage further in Section 9 where the importance of auditory and visual cues in maintaining already established bonds is determined which makes possible a comparison of behavioural factors important in the early stages of a bond with those prevalent in its maturity.

Section 10 is in the form of a general discussion where information gleaned from the preceeding work can be assessed and interpreted in the light of vertebrate behaviour in general.

SECTION I. PAIR BONDS IN BIRDS

1.1 Types of Pair Bond

Lack's 1940 publication contained what is still probably the best and certainly the most quoted classification of pair bond types. Drawing up such a classification is not a simple process as the number of categories can vary depending on the criteria chosen, but following Lack's lead, bonds can be placed into one of five groups on the basis of their duration prior to and succeeding copulation.

(a) The sexes meet solely for copulations. Two groups can be distinguished. The so-called lek species in which the males perform a communal display which attracts females to a display ground where copulation may take place and the sexes then separate e.g. Blackcock, European Ruff and, among passerines, the Cock-of-the-rock. In other species the male displays singly, not at a lek, and associates with the female only until copulation has taken place e.g. Ruffed Grouse, Spruce Grouse and probably most Bower birds.

(b) A pair bond is formed for a few days at the time of copulation. This is the case in the North American Humming birds in which the pairings remain intact for a few days but the males play no part in nesting activities. Other examples are the Red-necked Phalarope and the Tinamous, in these cases it is the female that departs after she has laid the eggs and the male continues with their incubation and rearing of the young.

(c) A pair bond is formed some time before copulation but breaks down shortly afterwards. This type is exemplified by many of the Waterfowl (Anatidae). As in (b), the male leaves shortly after egg-laying, but the bond is formed in these birds several weeks prior to copulation often in the preceeding autumn or early spring.

(d) The pair bond lasts for the raising of the brood or for the duration of the breeding season. This is the largest of the categories including the majority of the passerines and almost all the wading species. In many cases the bond is formed several weeks or months before nesting e.g. the Chaffinch and European Robin, and may be retained for successive broods. In addition the same bond may be renewed annually as in the Robin (Lack 1939) and the Kittiwake (Coulson 1966).

(e) The pair bond lasts for life. The pair bond is maintained throughout the non-breeding season in these species without the sexes separating e.g. Great Tit, many grassfinches, parrots, some swans and geese, and corvids. It could be argued that those birds in category (d) which renew the same bond annually also pair for life. The distinction made here is that in these species the pairs separate during the non-breeding season and the bond is not maintained throughout the year.

An assumption made in this classification is that the pairbond is the same in each of the categories. Clearly, birds exhibiting types (d) and (e) will emphasise behaviour important in the maintenance of their bonds to a much greater extent than in those cases where the pairing is far more transitory. Indeed it could be argued that no bond is formed at all in those species where the sexes meet solely for copulation though the difference lies mainly in the lack of pair maintenance, pair formation can remain essentially the same.

The majority of bird species fall into either groups (d) or (e) and, with the exception of a few polygynous species, these are all monogamous bonds. Lack 1968 calculated that over 90% of all bird species are monogamous and explained his results in that if the sex ratio is not badly distorted, and there are few cases reported of wild bird populations in which it is, then a pair will produce on average most offspring if both the male and female help in the raising of the young. This help may be in the form of the provision of food and/or protection of the mate and offspring. Promiscuous, polygynous and polyandrous bonds are characteristically of short duration and occur in those species in which one individual is capable of rearing the young alone without any risk of decreased chances of reproductive success. Interestingly the ploceid *Quelea quelea* may exhibit both types of bonding, the male often remains and assists in the rearing of offspring from the first brood of the season and then shows successive polygyny with a number of females thereafter. This suggests that the bonding process underlying both monogamous and multi-individual relationships may be essentially the same.

1.2 The prolonged or permanent pair bond

The Zebra Finch possesses a permanent pair bond and thus the factors, both hormonal and behavioural, which are correlated with the appearance of this bond type deserve consideration. Kunkel (1974) has recently drawn attention to the fact that the majority of species with prolonged bonds occur in the tropics and presumably therefore selective pressures common to these regions must have been important in their development. Instances of permanent bonds in species of higher lattitudes cannot be ignored, however, and in these cases different selective pressures may be operating.

(i) Factors affecting the duration of pair bonds

There are three main factors which appear important in deciding the length of a pairing relationship.

a) The environment and its effect on the timing and length of the breeding season

Every bird species is apparently adapted to breed at the time of year at which conditions are most favourable for rearing its offspring. The ultimate control of breeding efficiency is thought to be the availability of an adequate food supply and the most critical time will be from the beginning of the nesting period until the young are fledged by which time the species will be present in its largest numbers (Lack 1968).

In temperate zones favourable conditions last for only three to four months and cover the same predictable period each year. The onset of the breeding season can thus be accurately timed such that rearing of the young will coincide with the most favourable months. Pair formation will occur at the same time each year, usually early spring, and all individuals in a given population will come into reproductive conditions at the same time. In these species one can argue that the main selective pressure influencing breeding success will come from conspecifics of the same sex and this will favour the setting up of territories. The function of territories in the life of birds is a disputed topic but this may indicate one of the reasons why it may be adaptive in these species.

Different conditions exist in the tropics. Here the dominant factor deciding when favourable conditions will ensue is the onset of the rainy season. Kunkel (l.c.) describes how close to the equator there are two rainy and two dry seasons per year but, with increasing distance away from the equator one of these cycles is reduced until the outer tropics are reached where the season becomes biphasic and the single rainy season is more prolonged. It is important to note, however, that local conditions may alter this basic scheme considerably. For example, in the equatorial forests conditions remain favourable for breeding throughout the year, whereas in other areas the time available may be restricted to a few unpredictable months. It is this unpredictability of the onset of the breeding season, coupled with the tendency towards a more prolonged subsequent period of favourable conditions, which is probably one of the most important selective pressures leading to the development of permanent pair bonds.

In arid regions, such as those found in Northern Australia and coastal Equador and Peru, the breeding season, heralded by the onset of the rainy season is frequently of short duration. Bird species living in these regions (the Zebra Finch is common in Northern Australia) must react to the very first signs of improving conditions if they are to rear their young when food will be most plentiful. Pair formation may take a considerable length of time and following this the nest has to be built and ovulation and copulation completed. It is in order to reduce the time lost to breeding that birds of these regions are thought to have developed a permanent pair bond which must be maintained throughout the unfavourable, non-breeding periods. There is little experimental evidence to support this suggestion but Coulson (1966) has shown that in the Kittiwake, a species of the temperate zone, breeding success is increased in those pairs returning to the nesting colony at an earlier date. They produce their eggs more quickly than the later arrivals who are usually unmated birds and who lose even more breeding time through the necessity of pair formation. Presumably a similar effect on breeding success would be found in birds living in arid conditions who responded slowly to the onset of the favourable season.

The effect of a prolonged breeding season is somewhat different. After the onset, environmental fluctuations are not strong enough to synchronise the breeding cycles of all the individuals within a population. This means that any two potential breeding partners who meet cannot guarantee with any certainty that they will be at the same stage of the breeding cycle and hence pair formation may not be possible. Kunkel (1974) believes that this risk of non-synchronisation between breeding individuals is a major factor governing the development of prolonged bonds in these regions. Once synchronisation of a pair has been achieved it will be advantageous if that pair remain together for successive breeding cycles, the need for an early response to a new breeding season will ensure that the same bond is retained throughout non-breeding periods.

Thus the unpredictability of environmental fluctuations has almost certainly played a major part in the evolution of permanent pair bonds. That similar selective pressures may sometimes operate in temporate regions has been suggested by Simmons' (1970) study of the nesting behaviour of the Great Crested Grebe. Here the pair bond is apparently maintained so that nest building can begin as soon as the cover (usually reeds) becomes sufficiently high to provide protection for the nest and young. The exact timing of cover availability appears to fluctuate in different years and cannot be accurately predicted.

b) The length of parental care

There is a clear relationship here, the longer the period of parental care of the young then the longer the pair bond must be maintained. In cases where this period lasts from one breeding season to the next it will enforce a permanent pair bond on the parents if they share responsibilities for the care of the young. This is thought to explain the permanent pair bonds of the larger Anatidae such as swans and geese and would suggest the pairs unsuccessful in a breeding season would, without the need for parental care, be expected to split up. Minton (1968) found evidence of quite high rates of 'divorce' amongst British swans but he was unable to determine the reasons behind these cases of bond breakdown.

c) The effect of breeding success or lack of it

This relies on the assumption that in bird populations all individuals are not capable of achieving the same breeding success. This means in practice that mating with one particular conspecific may result in a reduced breeding success when compared with the rate that could be obtained with a more 'compatible' or 'hard-working' partner. Where such fitness or compatibility could be accurately predicted from the appearance or behaviour of an individual at the time of mate selection one could predict that pair formation might involve competition for mates. In addition, selection would favour the elaboration of those cues used in making the predictions, i.e. sexual selection. In those species with prolonged periods of parental care by both sexes this fitness will not merely involve a genetic compatibility but also the more physical attributes of nest building, incubation and rearing and feeding of the young.

There is evidence accumulating that some bird species are not capable of making predictions accurately at the time of pair formation and thus the pair subsequently breaks down, in other words, the pair are divorced. Coulson's (1966, 1968) excellent long term field studies on the breeding behaviour of the Kittiwake in North East England unearthed the surprisingly high figure of 25% of a ringed breeding population changing their mates in any one year. This occurred in spite of the fact that their previous mates were still alive and had been observed within the colony. Poor breeding success in the preceeding year was found to correlate with this change in mates, in those cases where a high number of offspring were fledged the individual pair bond was apparently reinforced and retained the following year. In addition, paired birds had the advantage of nesting earlier in the colony and thus a greater chance that their offspring would survive.

Mills (1973) found that essentially the same situation occurred in the Red-billed Gull though in this case the link with breeding success was more tenuous in that pairs retaining their bonds produced a larger clutch size but this did not necessarily mean that more offspring were fledged. However, earlier breeding by mated birds was similarly well established and as Coulson had also found, Mills suggested that any incompatibility between mates probably occurred during incubation. The amount of feeding of the female by the male varied and in some cases the female was forced to leave the eggs in order to forage for food herself. Erickson and Morris (1972) attempted to show that incompatibility and bond breakage could be demonstrated in the laboratory with captive Ringdoves. However, they were unsuccessful and blamed the controlled conditions which did not punish inefficient breeding as strongly as it might be punished in more natural surroundings.

This work indicates considerable variation in the potential fitness and compatibility of partners in a breeding population and, providing the species is long-lived, successful bonds will be retained in future years and probably for life. The fact that in the Kittiwake the incidence of bond breakages is highest in young birds supports this view. Le Resche and Sladen (1970) found that in the long-lived Adelie Penguin mate changes were common only in the first few years of life. In small birds, with high annual mortality rates (at least 50% in the Chaffinch), the effect of choosing a poor partner on overall breeding success will carry the same penalties but fewer cases of bond breakage can be expected. This is because incompatibility will only affect at most one or two breeding cycles though multiple broods in a season may increase this number. Selection will still favour an accurate choice during mate selection, however. Only in those tropical species, such as the Zebra Finch, with extended breeding seasons and rapid succession of broods could we expect appreciable rates of bond breakdown.

(ii) Reproductive rhythms and endocrinal modifications of species with prolonged bonds

Before considering those species with prolonged pair bonds it is worth outlining the situation occurring in more temperate regions where a restricted breeding season leads to short annual bonds (bond-type (d)). The ultimate factors controlling breeding success operate towards the end of the breeding season and therefore many species must begin egg-laying in what are at best, sub-optimal conditions. They need to react to those environmental factors which predict the advent of the new season; Immelmann (1971) has termed such factors releasers or 'Zeitgebers'.

In the temperate climate, where the optimal season occurs with regularity each year, a fixed annual event can be chosen as the Zeitgeber. The particular phenomenon used by the majority of species is the increase in day length at the onset of spring. An endogenous reproductive cycle is brought into phase by means of the Zeitgeber stimulating the production of gonadotropins by the pituitary which leads to testis or ovary development and the consequent production of higher levels of androgens or oestrogens. Changes in behaviour occur as a result of these hormones circulating in the blood stream, notably an increase in the amounts of courtship and aggression amongst conspecifics, which lead to pair formation and the establishment of the breeding bond. It is known that males are stimulated more fully than females by the external Zeitgeber and complete spermatogenesis can be induced by the light stimulus alone. Ovarian development appears to halt at an advanced stage at which rapid follicle development can ensue. The stimulus for this development, and hence the timing of ovulation, is determined by signals and displays incident during male courtship and nest building activities (c.f. Lehrman (1965) and Hinde (1966) for general reviews and Hutchi son (1974) for a recent paper).

The end of the breeding season is distinguished by gonadial regression due to cessation of gonadotropin production and without the influence of the sex hormones, the pair bond breaks down. Courtship no longer occurs and aggression becomes more prevalent between mated birds and thus the total length of the pair bond bears a direct relationship to the length of the reproductive cycle, and the occurrence of bond maintenance activities are dependent on the circulation of the gonadial hormones. The birds now enter a refractory period during which temporarily favourable conditions, at the wrong time of the year, will not result in atypical breeding behaviour.

Less is known about the reproductive rhythms and timing mechanisms of species living in tropical regions with extended breeding seasons. A response to photostimulation has been demonstrated in the laboratory (Immelmann 1971) but fluctuations in day length in the wild would be very small and this could be at the most a subsiduary Zeitgeber. It may in fact demonstrate the primitive origins of the photoperiodic response. A totally endogenous rhythm has been suggested to explain the breeding cycles of some of the tropical seabirds. An example is the Wideawake or Sooty Tern (Sterna fuscata) which nests on Ascension Island and breeds at intervals of 9.6 months. In terrestrial birds the Andean Sparrow (Zonotrichia capensis) has been extensively studied by Miller (1959 , 1962) who found that they breed throughout the year; the males have a gonadic cycle lasting six months, their gonads are active for four of these months and in a refractory state for two. The females on the other hand maintain a state of readiness at all times and can enter gonadic activity within a few days of stimulation by the males. Both these cases resemble the temperate species in that their breeding cycles involve a refractory period during which, however short it may actually be, one could expect pair bonds to breakdown.

Endocrinal modifications which subserve a permanent pair bond are clearly demonstrated by the oppurtunist breeders of arid regions and in these species no refractory period has been found. The breeding seasons are of irregular occurrence and length with suitable rearing conditions frequently lasting only for a matter of weeks. The Zeitgeber in these cases is thought to be the actual sight of rainfall (Immelmann 1971) but both sexes maintain a continual state of reproductive readiness and will breed at any time of the year and will continue breeding as long as the favourable conditions last. These so-called oppurtunist breeders include the Australian Zebra Finch and Budgerigar. Males of both species are not known to enter a refractory period of gonadial regression and Brockway (1964b) has shown that in the Budgerigar this is dependent on the continual stimulation of male vocalizations. She found that in the absence of male "loud warbles" both the male and female showed significant regression of the gonads. Farner and Follett (1966) suggested a hypothetical endocrinal controlling system to explain the cycle of the Zebra Finch. In this they proposed that the hypothalamus maintained a tonic state of gonadotropin secretion and the negative feedback effects of increasing levels of gonadial hormones was minimised (in temperate species high levels of gonadial hormones suppress gonadotropin secretion). In species like the Zebra Finch therefore, the absence of a refractory period presumably means that gonadotropin is continuously produced, even during unfavourable conditions, and bond maintenance behaviour can be prolonged through the non-breeding periods.

A similar system could be operating in those tropical species with a permanent pair bond living under conditions of extended breeding seasons. In general refractory periods of tropical species are known to be short and have been shown to be absent in at least two species, the Baya Weaver, Ploceus philippinus (Thapliyal and Saxona, 1964) and the Moorhen, Gallinula chloropus (Siegfried and Frost, 1975). In the latter breeding was found to be continuous in the two pairs observed, successful hatchings being recorded at remarkable forty-two day intervals over a period of two years. They noted that breeding success was reduced in the winter periods but there was no obvious seasonal alteration in the intervals between clutches. A refractory period, if one was present must have been extremely short.

(iii) Behavioural modifications of species with prolonged bonds

A number of behavioural adaptations have been proposed as important mechanisms involved in the prolongation of pair bonds. These were extensively reviewed by Kunkel (1974) and a brief summary will suffice here. It is worth noting at the outset that the maintenance behaviour discussed is not necessarily unique to species with permanent bonds but it may reach what is possibly its most advanced and elaborate form in such species.

The behaviour patterns of importance include:

(a) Contact behaviour (clumping and mutual preening of allopreening) which involves body contact between mates during resting periods. Whilst in contact individuals may preen the head or neck regions of their partners. Though such allopreening will no doubt result in cleaning of the feathers in these otherwise inaccessible regions, Sparks (1963) demonstrated that this was not its primary function (at least in Amandava) as the intensity of allopreening did not alter with the degree of dirtiness of the feathers. It seems that its primary role is in the reduction of aggressive tendencies between mates (Harrison 1965), and this will be particularly important during the non-breeding season when sexual tendencies will be presumably lowered.

(b) The song given by birds with permanent bonds is invariably of low volume which would be audible only over short distances ("Short distance song" Kunkel l.c.). No advertising functions at the time of pair formation have been ascribed to such song and it does not appear to elicit aggression from potentially rival males. Such song is a feature of both the Estrildines and the Carduelines and it is thought to be important in maintaining contact between mates.

(c) A further development of (b) is duetting in which a particular song (or calls) are exchanged between the members of a pair, often with an individualised temporal pattern. Such duetting occurs throughout the year in, for example the Laniarus shrikes (Thorpe 1972), and must be of importance in maintaining contact between individual pairs. In addition the more complex exchanges involve learning and perfection of the duet which must result in considerable fixation on the mate.

(d) Many species with a prolonged pair bond remain on the same well-defined territory throughout the year. The maintenance of such a permanent territory by a pair could clearly assist in the retention of a bond between them.

(e) In many cases, fidelity by the pair is to a particular nest site. Immelmann (1963) describes many Estridines which roost during the non-breeding season in the same nest they used to raise their young. This will have a similar advantage to that described in (d) above.

(iv) The interaction between endocrinal and behavioural factors

Butterfield (1970) drew attention to an interesting evolutionary problem concerning the effect of the reproductive physiology of a species on the duration of the pair bond. It could be that due to ecological selective pressures modifications of the reproductive rhythm was favoured and this then had a secondary effect on the length of the resulting pair bond. Continuous gonadotropin and gonadial hormone output, as postulated for the Zebra Finch, would result in sexual activities (including courtship and nest building) throughout the non-breeding season and this in turn would maintain the bond. On the other hand it could be argued that the long term pair bond, with its attendant maintenance activities, evolved directly and that it is the interaction between the sexes which affects gonadial secretion. As yet this remains unresolved but the evidence quoted earlier that male courtship and vocalizations may accelerate ovarian development possibly favours the second suggestion. In addition, Arnold (1975) has recently published his results on the affects of castration on the behaviour of the Zebra Finch. He found that behaviour described as bond-maintenance activities, allopreening, clumping and the production of short distance song, continued in the males in spite of the absence of androgens in the blood stream.

More evidence is required to completely resolve this evolutionary dichotomy but it raises fundamental questions as to the nature of pair bonds in birds. Are they entirely dependent for their maintenance on endogenous hormonal factors or is the bond to any extent independent of such control? No conclusions can be drawn until far more is known about the reproductive rhythms of birds with permanent pair bonds but Arnold's findings suggest that at least some aspects of the bond's manifestations is outside of the gonadial hormone's control.

SECTION 2. THE GENERAL BIOLOGY OF THE ZEBRA FINCH

Introduction

It is essential in laboratory studies of behavioural phenomena not to lose sight of the natural setting in which the particular behaviour has arisen and to which it has been adapted. The discovery that it is not possible to teach chimpanzees to speak more than a few simple words of the human language is not so surprising when the nature of their vocalizations in the wild is examined and the fact that they never imitate another chimpanzee's calls, let alone a human's, becomes clear (Nottebohm 1972). In an attempt to avoid such misapprehensions this section deals with the systematics, habitat and specialized ecological adaptations of the Zebra Finch. In addition work concerning the effects of captivity on the Zebra Finch's behaviour is reviewed.

(a) The Family Estrildidae, order Passeriformes

The classification of the estrildids as a separate family has been disputed for a number of years and remains to this date unsettled. Delacour(1943) originally considered them a sub-family, Estrildinae, of the Ploceidae which suggested a close affinity to the true-weavers, the Ploceinae. On anatomical grounds Tordoff (1954) proposed that they were related to the Carduelinae and Stallcup (1954) went so far as to place them in the same family grouping. Though it is clear that they share the same ecological range, they are both small, often social, seed-eaters, and will thus be subject to similar selective pressures, most authors believe they should be placed in separate families. Sibley (1970), however, has again suggested a close relationship between the true weavers and the estrildids as a result of an analysis of their egg-white proteins. The value of these findings is not fully understood and, at least for the time being, the Estrididae retain their family status, though a possible relationship with the Plooeidae and/or the Carduelinae cannot be over-looked.

Confusion also stemmed from the popular title for the estrildids, the weaver-finches, as none of the 108 - 125 species recognised in Africa, Southern Asia and Australia are known to utilise a weaving action in their nest building. For this reason Immelmann (1965) proposed that they be known exclusively as Grassfinches. It is thought that Africa was the likely evolutionary centre of the family and they are the only seed-eating passerine to have reached Australia in their dispersion. The African and Australian species share similar habitats and the marked parallel of adaptations which has resulted has been the topic of a comparison of the two continental groups by Immelmann (1966).

(b) The habitat of the Zebra Finch

The Zebra Finch is the most widely distributed of all the Australian estrildids and its range extends throughout the continent. It is primarily considered a species of the semi-arid interior (some 70% of Australia is described as "arid land") where prolonged droughts occur frequently which may force nomadic migrations of the indigenous bird populations (Immelmann 1965). One essential requirement appears to be the presence of surface water and the range has extended over the years into previously inhospitable areas due to human settlements.

Although often described as a nomadic species, the Zebra Finch appears to be sedentary over the majority of its range except under extreme circumstances (Serventy 1971). Birds visit the same water hole or pool each day which often involves travelling considerable distances. Enforced movements are similar to those described for 'true' nomads in that they are irregular in their occurrence and may result in huge congregations of birds around available water.

Their food is mainly half-ripe and ripened grass seeds and some insects are taken at all times. Unlike some African estrildids, there is no evidence that insects form an essential part of the diet during the breeding season in Australia, nor do they appear to use insects to obtain water as has been shown for some of the desert bird species. There have been no specialised feeding methods described, Zebra Finches spend much of their time on the ground picking up fallen seed or jumping to reach seeds in standing grass-heads.

The nests are built usually in small bushes and trees and this is a further restricting factor to their range within arid regions. More than one nest per tree or bush has been observed where potential sites are limited and Serventy (l.c.) describes an extreme example of 21 nests in a single Acacia tree. The average distance between nests measured for two sample colonies by Immelmann (1962) was 14 metres, this distance was defended by the resident pairs.

(c) Social activities

The Zebra Finch is a highly gregarious species forming flocks of from 50 - 100 individuals in the non-breeding season. The breeding colony is made up from 5 to 25 pairs and Immelmann (1965) found that they form tight, compact groups in which all members are known and strangers are met with a speedy repulsion. Social activities occur each day with pairs gathering to bathe, drink, preen or fly off together in search of food. Where the species is resident during the non-breeding season the same nest sites are often retained for roosting and thus the integrity of the social group is probably maintained. In some of the other Australian estrildids, e.g. Poephila species, the social groups are more intensely organised with the evolution of greeting ceremonies and the extension of bond-maintenance activities to include all members of the social group (Zann 1972).

Courtship by Zebra Finches occurs often within the groups at a social gathering site near to the nesting colony. It is assumed that pair formation is initiated on these occasions. The dispersion of nests is in the form of a loose colony and the distances between them, as mentioned above, is maintained by the pair in the form of a small territory. Immelmann (1965) suggests that neighbours visit each other at the nest but the stage of the breeding cycle to which he is referring is not clear. Frith and Tilt (1959) found that defence of the nest was very intense to all comers, the attacks frequently being launched with such alacrity that eggs were damaged within the nest. Both the male and the female incubate the eggs and share the duties of rearing and protecting the young.

(d) Drought adaptations

Much of the behaviour exhibited by the Zebra Finch can be viewed in terms of their adaptability to the unpredictable nature of their arid environments. That these ecological selective pressures were of major importance was highlighted by Immelmann (1965) and the way in which they are related to the general tropical adaptations of birds was described in Section 2.

i) The breeding season.

In the arid regions conditions are conducive to breeding only after rainfall. The effects of sudden downpours includes rapid growth of green vegetation which may appear as little as 48 hours after the onset of rain. However, such bursts of growth are often transitory with the flora flowering and producing seeds within a few weeks. As already stressed, the rains occur at unpredictable intervals and drought conditions may be prolonged for many months.

McGilp (1923) noted that in bad drought years few bird species attempted to nest whereas after good rains there was often an influx of birds and the nomads and residents would begin nesting very promptly. A correlation between egg-laying and rainfall was found by Carnaby (1954) and it now appears almost certain that the chief Zeitgeber for breeding is the occurrence of rain.

Thus the Zebra Finch, and other inhabitants of the arid regions, have broken free from regular breeding seasons and will respond to rainfall in whatever month it may occur. Immelmann (1963) has even suggested that the stimulus is the actual sight of falling rain rather than the appearance of green vegetation, the latter is known to be important in triggering the breeding response of the ploceid _Quelea quelea_. To argue his case Immelmann sites examples of rainfall occurring at night and thunderstorms, when humidity increased dramatically without any rainfall, neither of which appeared to stimulate breeding behaviour. Results were unfortunately not quantified and there remains some doubt as to the exact identity of the Zeitgeber. In Northern and Eastern regions of Australia rainfall is more regular and favourable breeding conditions exist for a considerable part of the year. Zebra Finches in these localities have been reported by Frith and Tilt (l.c.) to breed in all but the coldest months of the year, irrespective of the months in which the rains actually fell. Under European captive conditions the Zebra Finch will similarly breed continuously throughout the year.

ii) The permanent pair bond.

The Zebra Finch, in common with many Australian birds that inhabit the arid regions, maintains a pair bond for life. The major selective pressure, as already outlined, is almost certainly the irregular breeding season of these areas. The pair bond is maintained so that whenever favourable conditions ensue a rapid response will take place and little time will be wasted in the preliminaries of pair formation.

A state of reproductive readiness is apparently maintained at all times. Farner and Serventy (1960) carried out an extensive survey of Zebra Finches and found no instances of birds with completely inactive gonads at any time of the year. One effect of this is a reduction of the time taken before ovulation occurs at the start of the season as the female ovaries will already be in an advanced state of development. As a possible consequence of continuous gonadial secretions some sexual activity can be observed even in the non-breeding season and Immelmann (1963) reports that nest building is similarly extended.

iii) Breeding potential.

During very prolonged droughts populations of Zebra Finches can be drastically reduced and the species has developed the ability to rapidly increase in numbers once the rains arrive. Breeding is continuous as long as conditions last and broods can follow each other with remarkable regularity. As an example of breeding ability in captivity Serventy (1971) describes a pair that raised 23 broods in succession over a period of 3 years 4 months! Moulting does not affect the breeding cycle (Keast, 1968) as it is a continuous process that can easily overlap with it. Serventy (1971) suggests that this modification is unique to Australian birds but the Crossbill (Newton 1972) and Moorhen (Siegfried and Frost 1975) are examples of at least two European birds with this adaptation.

Zebra finches begin breeding at a very early age, in captivity Serventy claims that males started nesting at 6½ weeks post-hatching, females at 9½ weeks, and clutches were hatched and reared when 11-12 weeks old. This will assist in increasing numbers in the population rapidly and can be considered an adaptation to the drought conditions.

(e) The Zebra Finch in captivity

Captivity can have a marked effect on the behaviour of all animals. This is immediately obvious to anyone visiting a zoo or pet shop where animals are kept in small, restrictive cages. The repetitive stereotyped behaviour of small mammals in such conditions, often involving the meticulous tracing of an unvarying route around the cage coupled with a variety of head-shakes and scratching movements, must engender a sympathetic reaction in all but the most hard-hearted or ignorant of observers. Hediger (1950) first drew attention to the problems involved in keeping zoo animals and Morris (1964) elaborated on the effects of restricted environments on behaviour. In addition domestication can affect behaviour in that artificial selection may take place such has occurred in the canary resulting in bizarre plumage types and peculiar song varieties.

Domestication of the Zebra Finch has been popular in this country since the turn of the century and there has been a flourishing Zebra Finch Society since 1952. The ease with which the species settles and its extreme readiness to breed has lead to an increase in its numbers until today they are only surpassed by the budgerigar and canary. A comparison of wild-caught and domestic stock was first made by Morris (1954), and then by Immelmann (1962a) and Sossinka (1970). They all found that differences appeared slight, domestic birds tended to be larger, had different plumage markings and slower gonadial development in juveniles. Display behaviour did not appear to have been altered by domesticity though Sossinka notes a reduction in the amounts of sexual activity given by domestic males. Thus any effects of artificial selection in this species appear negligible.

The restricted cage environment is more likely to result in atypical behaviour. The reduction in the amount of incoming stimuli is thought to produce smaller demands on the central nervous system with the result that the arousal system is generally dampened (Immelmann 1962a). This may lead to a reduction in the endogenous stimulation of certain drive actions which Morris (1966) suggests will cause a loss of appetitive behaviour. This could explain the reduced amounts of sexual activity Sossinka reported. However, Immelmann (l.c.) writes that the sexual drive shows strong hypertrophy in captivity and the situation is not entirely clear.

Repetitive stereotypes have been described for the canary by Keiper (1969) and these appear as repetitive route-tracing through the cage and spot picking, repeated placing of the bill on the perch or a region of the body. These were seen not only in domestic birds but also with wild-caught individuals in captivity. Route-tracing was found to be a result of restriction as it disappeared when birds were placed in larger aviaries. Spot picking on the other hand appeared to be a feature of sensory deprivation as it declined when birds were required to work for their food. Neither of these stereotypes was seen in any of the birds used in this study nor have they been reported by any previous workers and it is hoped that any effects of restriction are minimal in this species.

Thus the use of domestic stock can be justified at least until the Australian Government changes its views on the exportation of live birds and wild-caught individuals can be obtained once more. Comparisons between behaviour in experimental situations will be made with that seen in the wild though with some reservations in mind (q.v. Hinde 1956).

(f) The colouration of the Zebra Finch

The Zebra Finch is sexually dimorphic throughout the year and its colour markings may be divided into those common to both sexes, the species markings (Morris 1954), and those peculiar only to the male, the male markings. The descriptions given are of the domestic wild-type or "grey" which closely resembles actual wild-caught individuals.

i) Species markings.

The crown, neck, back and wings are grey; the ventral surface is white, often appearing more cream-like and this tendency is even more marked in wild-caught specimens. The cheeks are white with a short vertical black bar whilst the rump region is white with the upper tail coverts banded black and white, the tail black. The legs and feet are orange with the bill red, in the males the red of the bill is deeper in colour.

The red beak is thought to be an important releaser in the displays of the Zebra Finch. Immelman (1959) found that when using models of females male courtship could be elicited from a female-shaped object with a red beak and no plumage markings. This is also reflected in the fact that juvenile plumage in this species closely resembles that of the adult female except that the beak remains black until sexual maturity is reached. In addition Immelmann (1962 .) suggests that beak colour may be important in the formation of mixed species flocks in the wild; he notes separate flocks forming from those estrildids with red beaks compared to those species with yellow bills.

ii) Male markings.

In the males the sides of the face and ear coverts are chestnut-brown and the flanks are a similar hue but speckled with white spots. The throat and breast are finely barred with black and white terminated by a broad black band below which the belly is a similar white to that of the females.

Considerable plumage variations occur within the domestic wild-types such that it is possible to recognise individuals. The broad black band on the male's neck region often appears in an incomplete form for example.

iii) Colour varieties or mutants.

In the course of domestication several colour varieties have been established. These are quite recent developments, the first recorded is that for a pure white in Australia in 1921. In this mutant all the plumage markings are absent though invariably traces of grey patches remain. The only colour difference between male and female in this case is the depth of red of the bill.

The other varieties include, fawn, in which the grey areas are replaced with pale brown, chestnut flanks, where individuals are white except for male markings and tail and cheek bars, and pied in which fawns or greys have irregular patches of white plumage. Other 'diluted' forms exist, such as Silver (diluted grey), Cream (diluted fawn) and there is a white-fronted "Penguin" type. In the present study greys, fawns, and chestnut flanks were used with one or two pied individuals.

The only evidence of colour mutants occurring in the wild is quoted by Immelmann (1965); the chestnut flanks are thought to have been first obtained from the natural habitat in 1937.

SECTION 3. THE BEHAVIOUR OF THE ZEBRA FINCH

Introduction

The following section deals with the displays and behaviour of the Zebra Finch both in the wild and in captivity. It is a descriptive survey of the activities seen during courtship, agonism, nesting and contact behaviour with an attempt to make comparisons with other bird species. During the course of the experimental work many personal observations were made as to the form and nature of particular displays and frequently these differed from those accepted in the literature. Such observations fall outside of the main scope of this thesis but can be included in this general review.

The descriptions that follow are based largely on subjective unquantified interpretations and any attempts to outline the derivations of display components are speculative and unproved. Work on the derivation of displays must be speculative, no fossil record exists for behaviour, but providing this is born in mind discussions can still prove very interesting as Tinbergen (1952) and Andrew (1961) have clearly shown. In view of this, the first discussion deals with a short review of the origins and ritualization of displays. In later descriptions many questions are raised which remain unanswered. This is unsatisfactory but reflects the difficulties involved in interpreting the kind of subjective data that must be dealt with in such studies.

Thus, whilst accepting the speculative nature of the following section, it is still considered a worthwhile endeavour. The descriptions of behaviour here will form a useful reference for those unfamiliar with the displays of small passerines and will therefore preclude lengthy descriptions in later experimental sections.

(a) The origin and ritualization of display components

A display given in an agonistic or courtship context usually involves numerous components which, when combined, make up a particular pattern in which it is performed. Whenever a particular display is elicited in birds it is usually given in its entirety, the components following one another in the prescribed temporal pattern. Andrew (1961) listed the possible origins of such display components and included:

i) Movements which are not given as part of the display but which occur within it either incompletely (e.g. intention movements) or redirected in a new direction.

ii) Displacement activities are patterns of behaviour other than those immediately evoked by the context of the display and therefore appear to be out of context (also called irrelevant behaviour), e.g. pecking at food or wiping the bill during a courtship display. Reasons why such behaviour should occur in these seemingly unlikely situations is not clear at present, but Delius (1967, 1973) has proposed that they are important in regulating the arousal system of the organism.

iii) Autonomic responses such as raising of the feathers or dilation of blood vessels (probably more common in mammals), appear to have been incorporated into displays.

iv) Finally, there is what Andrew calls compromise behaviour. These are actions which arise when two tendencies conflict and are, in effect a partial expression of both of them, e.g. tail-flicking in birds which is thought to indicate simultaneous tendencies to fly both towards and away from another individual.

This is not presented as an exhaustive list but one which will serve for the purposes of the present discussion.

It has been proposed that during the course of evolution the components of displays have changed, certain elements may be exaggerated, and that the sequence in which they are given has become fixed and stereotyped. This process was termed ritualization of the display (Tinbergen 1952 ; Morris 1957). The selection of components to be incorporated in the display is influenced by environmental factors as Crook (1962) clearly demonstrated in the ploceids, but once the display is elicited it is given with the same intensity on every occasion, what Morris (1957) called the 'typical intensity'. This stereotypy must involve a reduction in the amount of information given in the display that is indicative of the signaller's motivational state but in contrast the signal is less likely to be viewed with any resulting ambiguity by the receiver. As Morris (l.c.) aptly states "a signal that is constant cannot be mistaken".

The informational content of animal displays was considered by Smith (1969) and he suggested that two main factors or 'modifiers' were operating. The display provided an 'identification' message, e.g. the sex, maturity and characteristics of an individual, and a 'probability' message indicating to what extent a behaviour was likely to occur. The latter could be achieved by altering the rate and repetition of the display or certain components within it. In this way, in spite of the rigid ritualization of the display, information as to the signallers likely motivational state could be transmitted. Simpson (1972) gives some indication of how subtle this transfer may become in his work on the Siamese Fighting Fish, Betta splendens.

Thus in the performance of displays there are two conflicting tendencies. Ritualization places the emphasis on a rigid, easily understood signal whereas the motivational state of the signaller affects the actual outcome in a particular context.

(b) Courtship displays and Copulation of the Zebra Finch

The courtship displays of the Zebra Finch, in common with those of many other bird species, cannot be easily divided in to those given by the male and those by the female. There is considerable overlap and Hinde (1956) and Andrew (1961) have both pointed out in many passerines nearly all the components of the male's sexual display have been recorded, at one time or another, in the female's repertoire. The difference between the sexes lies in the frequency with which the different displays tend to be given and clearly there will be occasions when a display cannot be rigidly assigned to one or other of the sexes. These tendencies were quite marked in the displays of the Zebra Finches observed in the present study and form the basis for the following personal descriptions. Attempts will be made to relate these observations to behaviour described in the literature.

1) Behaviour immediately prior to courtship activities.

On many occasions birds were seen to collect and mandibulate nesting material immediately before a courtship display began. It appeared that such behaviour was often incidental in eliciting courtship in that the partner would approach the mandibulating bird and attempt, sometimes successfully, to remove the material from the bill. Much hopping about the perches then ensued with beak mandibulations by both birds and often this lead into a courtship situation. Both sexes were seen to initiate such exchanges and in some cases males were clearly seen to give courtship song even whilst retaining the nesting material firmly in the bill.

This type of pre-courtship behaviour has been described in other estrildids, though not the Zebra Finch. Moynihan and Hall (1954) describe in the Spice Finch (Lonchura punctulata) both individuals of a pair flying and hopping about the cage with nesting material until close proximity was attained whereupon courtship began. As in the Zebra Finch, there were many occasions when courtship began without such activities and thus the collection of nesting material appears to be unritualized as far as the courtship display is concerned.

Unritualized collection of nesting material is widespread amongst the displays of Passerines (Andrew 1961) but it is particularly interesting in the estrildids as some species in the family have ritualized this behaviour. Goodwin (1960) and Harrison (1962) described the courtship display of the African waxbills (Estrilda spp.) in which the male bows to the female whilst holding a long piece of grass in the bill. This ritualized component of the display may well have arisen from the tendency to mandibulate material noted in the Zebra Finch. This seems even more likely when one includes Morris' (1958) description of courtship in the Painted finch (Emblema picta) where he saw the bowing, straw display degenerate into picking up and dropping material when it was given on the ground. His findings were confirmed by Immelmann (1965) who noted similar behaviour in the Pictorella Finch, Heteromunia petoralis.

The importance of unritualized handling of nesting material in eliciting courtship of the Zebra Finch, or indeed of stimulating it, is unclear. However, in many passerines copulation only occurs when the female is ready to begin, or has completed, building the nest (e.g. the Snow Bunting, Tinbergen 1939; the Chaffinch, Hinde 1970) and in these cases the sight of nesting material and its mandibulation presumably has a stimulatory effect on the female. This could explain its incorporation into the courtship displays of the estrildids where it has become a ritualized component in some species.

ii) The courtship display - a general description

Typically the courtship dance occurs above ground in the branches of a bush or tree (Immelmann 1965) and involves an introductory phase during which both male and female hop too and fro giving frequent beak wiping. This is followed by the female stopping on the perch and the male advancing towards her with characteristic pivoting movements and beak wipes whilst delivering bouts of courtship song. As the male nears her the female may solicit copulation, by rapid lateral movements of the tail, and the male mounts her. The exact form of this display varies, however, and is affected by the arrangement of available perches and may show individual variations. Morris (1954) goes so far as to describe it as a 'semi-ritualized' display in that the components are stylized but not, as yet, entirely emancipated (or divorced from their origins) and are thus susceptible to changes in underlying motivations. This description appears unnecessary in the light of current postulates of display origins (see above).

In the present study it was noticeable that the courtship dance depending on the situation in which it occurred. When only one horizontal perch was offered, the male pivoted up to the female, though she rarely remained stationary. Where two horizontal perches were available with a gap between them, both individuals hopped too and fro and there was little evidence of the male 'pivoting towards the female' as such. Finally on the ground the male's dance consisted of short diagonal runs to either side of the female and no beak wiping was seen. Courtship on the floor of the cages was rare but it has been noted in the wild (Immelmann 1965) where it appeared basically simpler.

In all these cases the dance of the male ensures that his flanks are presented which Morris(1954) concluded, means that the species and male markings are displayed clearly to the female. This is not always the case in established pairs. Males were seen to begin courtship song on occasions without any accompanying movements and if the females did not respond, the bout ceased as abruptly as it had begun. This may be a feature of courtship between birds with established pair bonds though no data was collected to establish its incidence amongst newly paired individuals.

The components of the male's courtship display, whatever actual form they take, are probably derived from the conflicting tendencies incident in the male. Hinde (1970) reviews the evidence that in birds the components originate from a composite of aggressive, sexual and fear responses which are elicited by the sight and close proximity of the female.

iii) Features of the pivoting dance

This was first described in the Zebra Finch by Morris (1954) in the rather restrictive conditions of a male moving towards a female along a single horizontal perch. The whole body of the bird was swung from side to side with each hop, the head and tail being pointed in the direction of the female. Beak wipings, in which the male bent and scraped the bill across the perch, frequently occurred between each hop in an unritualised fashion. Morris concluded that the pivoting movements were the outcome of alternating tendencies to first flee from, and then approach and behave sexually towards, the female. Each pivot first carried the male away and then swung him back towards the female.

It would appear, however, that the nature of the pivoting action is not as clear cut as this suggests. In this study, two parallel perches were provided and it was soon evident that in the introductory phase of the display both the male and the female indulged in pivoting movements. They both hopped from one perch to the other with the head and tail inclined towards the partner and pivoted with each turn. No approach tendency was in evidence, the birds remained from 10 to 20 cm. apart, and they tended to move asynchronously with one bird vacating a perch as the other landed on it. Kunkel (1959) has described similar behaviour in the waxbills and notes pivoting as a spiral or semi-circular display during which the flank of the male is presented to the front of the female thus preventing her from departing. Immelmann (1965) does mention that in the Zebra Finch the female may incline her tail whilst hopping but he does not emphasise that her movements appear essentially the same as those of the male.

Female pivoting in this introductory phase of courtship may be important in initiating the actual display. On some occasions females were observed pivoting towards males before they showed any advances in their direction; in the newly established pairs of Section 4. 24% of the courtship bouts observed were begun by the female in this way. These bouts appeared no more likely to lead to copulation than did male-initiated ones though Hinde (1954) suggested such a relationship might hold in the Greenfinch as far as copulatory success was concerned.

Mutual pivoting by both sexes is reported for the Cardelines, the Goldfinch and the Bullfinch (Newton 1972) and, at least in the latter, tail inclination also occurs. In these species pivoting has been linked with aggressive tendencies as it is often seen outside of courtship during boundary disputes between rival males. Andrew (1957) noted pivoting during the mobbing behaviour of the Emberizinae (Buntings) and suggested a similar aggressive motivation, pivoting often degenerated in these cases into actual approach and retreating movements.

Aggressive tendencies could play a part in the motivation of pivoting in the Zebra Finch though it was never recorded during actual fighting bouts. Morris described two forms of pivoting and suggested that they showed variations in the intensity with which they were performed. In the first, low intensity display, the body and head were held more horizontally and the pivots were irregular. The high intensity display involved a more vertical posture with wide and strong pivots. It is not clear whether Morris refers to differences between individuals or those within a single individual but it is possible that the more horizontal display could indicate greater aggressive tendencies in that the body is held in a 'forward threat-like' posture. The more vertical dance, on the other hand, could indicate a greater likelihood of flight on the part of the male. Both types of dance were noted in this study but links with either fear or aggressive responses were not established.

A final note, pivoting is seen in the locomotory movements of small birds along perches (Kilham 1972) and appears to be a common form of progress. Such unstylised movements were seen in Zebra Finches of both sexes and tail inclination was also noted when hopping near to a stationary bird. The latter seemed to involve a balancing movement to counteract asymmetry in the hopping movement due to a tendency to lean away from the stationary bird. Thus both of the main features of the pivoting dance occur during normal movements around the cage, in one case fear may play a part in its production, and this has lead Kunkel (1967) to suggest that in the waxbills weak ritualization of these 'locomotory' movements has occurred in their courtship displays. Aggressive tendencies are generally less pronounced in estrildid courtship displays (Hinde 1955, Andrew 1961) and the part they play in eliciting the ambivalent pivoting may be subsiduary at the most with fleeing tendencies affecting the form of ritualized locomotory movements.

iv) Beak wiping during courtship

Displacement beak wiping is common during the courtship displays of passerines, e.g. Hinde (1954) describes its occurrence in the Fringillids and Carduelines. Both male and female Zebra Finches were seen to give beak wipes during pivoting movements and these resembled beak wipes given outside of courtship in that they were always orientated towards the perch. Invariably the beak was actually wiped across the perch but in some cases only the tip of the bill made contact. Morris (1954) recorded a similar distinction and added that displacement wipes were faster and "less complete" than normal ones.

There is no evidence of ritualization of beak wiping in Zebra Finch courtship as has been noted in the related Spice Finch (Moynihan and Hall 1954). In this species beak wipes are no longer orientated to the perch but are given in a lateral direction as a "low twist". In addition Kunkel (1967) has proposed that displacement beak wiping led to the ritualized bowing or curtseying displays which are used by males in greeting conspecifics as well as between pair members.

Displacement acts were classically considered irrelevant behaviour and non-functional when given outside of their normal context. However, recent work has suggested that they play an important causal role in motivational adjustment systems (e.g. Wilz 1970). Delius (1967) suggests they could serve a dearousal function preventing the overloading, and consequent inefficiency, of the handling of information by the central nervous system. Displacement beak wiping in the Zebra Finch was seen by Morris (1954) to be due to sexual frustration acting as an outlet for aggressive and fleeing tendencies and thus prolonging a courtship bout. Attractive as this theory is, one would expect displacement beak wiping to increase in frequency the longer a bout proceeded and to be more common in newly established pairs, but this is not the case. Beak wiping was often most marked at the beginning of courtship and was given just as frequently by established pairs of birds.

This appears to rule out sexual frustration as an underlying causal factor but assuming beak wiping may play a part in regulating the arousal system it could play a direct function in eliciting the courtship display itself. Hailman and Dzelzkahns (1974) carried out a computor analysis of sequences of behaviour in the social displays of Mallards. They noted that tail wagging, said by them to be a displacement activity, tended to occur most often inbetween different bouts of behaviour and suggested that they might act rather as punctuation marks. In this way they could denote the end of one display element and the beginning of the next. Beak wiping occurs throughout the courtship dance of the Zebra Finch but it appears particularly marked in the early stages of the 'introductory phase' and may serve to draw attention to the bird about to display; a 'capital letter' as Hailman and Dzelzkahns might put it.

Clearly the nature of beak wiping deserves further attention and it will be considered later in this study (Section 4.).

v) Feather postures during courtship

During his courtship display the male Zebra Finch assumes a characteristic feather posture. The body, flank and neck feathers are raised and fluffed out, the crown feathers are strongly depressed whilst those of the back and sides of the head are raised resulting in a triangular head profile. Such triangular head outlines are common in displaying estrildids (Immelmann 1965) and Morris (1954) has suggested that the function of the feather raising is to ensure that the male and species markings are clearly displayed.

The females were seen to assume a similar fluffed appearance during courtship but on only one occasion was the triangular outline recorded. Fluffed feather postures are common amongst passerines in reproductive condition (Hinde, 1954) and often they are associated with wing lowering during courtship. This was not noted in the Zebra Finches but was seen in females about to lay eggs and in sickly birds (both male and female). The fluffed appearance of the birds contrasted markedly with the feather posture of aggressive or fleeing individuals where all feathers tended to be sleeked. This was seen in courtship where the female was unreceptive and fled from the advancing male. Mild alarm situations apparently caused sleeking of the head feathers only.

vi) Courtship song

Singing by the male formed an integral part of the courtship display. It was given during the pivoting dance though on some occasions it preceeded any movement by the male. When given by a stationary male it is accompanied by rapid pivoting of the head only which is also a feature of song given out of courtship. Morris (1954) reported that song always accompanied pivoting but this was not found in the present work. Courtship can occur in virtual silence, both birds pivoting with a few soft calls given, and this may even lead up to successful copulation without a single song phase being given. Whether such silent bouts are more common in established pairs was not recorded in this study but one would suspect that the courtship song might be most important during pair formation when the female must be sure that the male is in fact a Zebra Finch and giving the correct species song-type. The female gives no song at any time but may call during the bout.

vii) Aggression during courtship

Aggressive components of courtship in the form of threat displays, are largely absent in the Zebra Finch (this was noted earlier with a possible exception, see Section 3 (b) iii). Direct aggression was noted amongst some pairs where the male was seen to jab at the female's head at the end of a courtship bout. This has been seen even amongst well-established pairs and may be a feature of the behaviour of particular individuals. Females rarely attacked courting males, their usual response, if unreceptive, was to flee.

Aggressive tendencies are marked in the courtship of other birds e.g. the head forward threats of the Paridae (Hinde, 1952) and Laridae (Moynihan, 1955). Interestingly, the Bullfinch is a notable exception to this trend amongst the Carduelines (Hinde 1966) with no threat postures involved in courtship; it is the Bullfinch alone amongst the Carduelines that maintains a permanent pair bond similar to that of the Zebra Finch. Thus the absence of aggressive threats in courtship may be correllated with the permanent pair bond type.

viii) Soliciting

This is considered to be a behaviour predominant in the female and indicative of her readiness to accept male copulation attempts (Morris, 1954 and Immelmann, 1965). The female assumes a horizontal position at right angles to the perch, she then quivers the tail rapidly so that its actual movements are lost in a blur, and the male mounts her back. Since the females' feathers are sleeked, unlike during the earlier stages of courtship, Morris proposed that soliciting was derived from a flight intention movement due to the close proximity of the male.

The soliciting act of females is apparently fully ritualized as little individual variation was noted in its performance in this study. Copulation did not appear to be entirely dependent on the female soliciting; on some occasions males mounted females as soon as they became stationary. It was noticeable that unsolicited mountings were common in birds that had just been introduced when, presumably, the sexual tendency of the male was enhanced. In addition, soliciting did not always result in copulation attempts and on only one occasion a female solicited before male courtship started. This happened in a group situation, with newly introduced birds, which suggests that the mutual courtship display is important in eliciting, or stimulating, this behaviour in the female.

Soliciting displays are also given by male Zebra Finches and this behaviour was quite frequently observed. Morris (1954 and 1955) first described this and termed it pseudofemale behaviour. This is a rather unsatisfactory title as it apparently forms part of the behavioural repertoire in the wild (Immelmann 1965) and male soliciting has been recorded in other bird groups, e.g. the Carduelines (Hinde 1955) and the Emberizines (Andrew 1957). It also seems to be a more persistent part of the male's behaviour in other estrildid species. In the Masked Finch Immelmann describes social groups greeting one another with tail quivering and such behaviour is clearly recorded for both the sexes in the greeting ceremonies of the Poephila species (Zann 1972).

The form of the male's display was exactly as that of the female with the exception that on some occasions it degenerated into tail fanning movements which was never noted in female soliciting. Tail fanning is given by both male and female in nesting and aggressive behaviour and its appearance in male soliciting may suggest a similar underlying motivation.

Males tended to solicit after unsuccessful copulation attempts or prolonged courtship bouts during which the female did not solicit. Morris also noted this tendency and considered that "sexual thwarting" was a "fundamental causal factor" in its elicitation leading to a "displacement-like spark over to dormant female behaviour". As Hinde (1955) points out, this is not really a causal factor and it seems more likely that it is linked with a strong tendency to flee from the female. Andrew (1957) agrees with this suggestion in that it represents compromise behaviour on the part of the male which allows the expression of his sexual tendencies. It is a stationary display which, as Andrew argues, enables the male to avoid the female and indicates that he has a strong fear of her. It seems plausible that a motivation based on a tendency to flee whilst at the same time expressing a sexual tendency, could explain the use of tail quivering as a greeting ceremony amongst some Estrildids. It does not appear to be used to any extent as a submissive act during aggressive encounters, as has been reported for primates; it was only observed on one occasion in this context.

Adkins and Adler (1972) found that in the Japanese Quail castration and subsequent treatment with gonadal hormones affected the sexes differently. The males were apparently more "bisexual" in that female behaviour could be obtained from either sex whereas male behaviour was exclusive to that sex. Support for these findings came from embryological differences between the sexes and, if the same tendency holds for other species, may help to explain the frequent observations of female displays given by male Zebra Finches.

Finally, Morris observed reversed mountings (the female mounting a soliciting male) in the Zebra Finch and on some occasions these included the full copulatory movements. In the present study females were seen to place one or both feet on the male's back, but never simulated actual copulation. Immelmann (1965) has never seen complete reversed mountings, either in the wild or in captivity and it seems that such behaviour is extremely rare.

In conclusion, soliciting in estrildids of both sexes, appears to involve strong tendencies to flee from a conspecific and functions in preventing such flight whilst expressing the individual's sexual tendencies. In the Zebra Finch such behaviour is usually elicited by the mate only but, in some estrildids, it has been extended to include the members of a social group.

ix) Copulation

This involves a stereotyped behaviour pattern during which the male climbs onto the female's back, spreads his tail and then twists it round and below that of the female and makes cloacal contact. Balance is made by flapping the wings and the movements are accompanied by the copulation call (described in detail later). On some occasions the male jabs at the female's head whilst mounted and this is also seen in reversed mounting. Copulation is not repeated as in the House Sparrow (Danje 1941) and marks the end of any courtship bout.

Not all copulatory attempts are successful, birds were frequently seen to fall from the perch for example, and even in established pairs, a long courtship bout did not necessarily lead to copulation. There was no obvious refusal by the female, i.e. she did not attack the male or fly away as he approached, as has been described by Hinde (1953, 1954) in the dominance relationships of European finches. Wilson and Bermant (1972) have suggested that copulation in the Japanese Quail originates from a different site in the central nervous system to that of the courtship displays. If this holds for other bird groups it might help to explain how courtship can so frequently occur without any attempts at copulation.

x) Summary of male and female courtship display components

The table below (Table 1) summarises the display components of courtship by male and female Zebra Finches. The terms 'frequent', 'occasional' and 'never' are a subjective indication of the number of times the behaviour was observed during this study.

COMPONENT	GIVEN BY MALE	GIVEN BY FEMALE
(1) Pivoting	Frequent	Frequent
(2) Tail twisting	Frequent	Frequent
(3) Displacement beak wiping	Frequent	Frequent
(4) Fluffed feathers	Frequent	Frequent
(5) Triangular head shape	Frequent	Frequent
(6) Courtship song	Frequent	Never
(7) Soliciting	Frequent	Frequent
(8) Mounting	Frequent	Occasional
(9) Cloacal contact	Frequent	Never

(c) Agonistic behaviour of the Zebra Finch

The term agonistic is used here in reference to all attacking, threatening, fleeing and submissive behaviour on the part of individuals. Although these acts involve quite different motor patterns and have different functions Hinde (1955) believed such a grouping was justified as they share common causal factors and are clearly interrelated.

Aggressive behaviour, i.e. fighting, is nearly always concerned with the possession of some object or situation. It may be subdivided into reproductive fighting (Tinbergen 1939, Hinde 1952) which occurs in disputes over mate or territory, and fighting over food or roosting sites. Fighting over food is elicited by the feeding tendency whereas reproductive fighting is motivated by the sexual tendency and this dichotomy has been shown to exist in the hormones that influence fighting in different contexts (see Crook and Butterfield,1968 (a) and (b); Lazarus and Crook,1973, and Dunbar and Crook,1975 in Quelea quelea).

The Zebra Finch is a particularly pugnacious species at all times but the agonism described dwells on reproductive situations in which fighting will be important in the establishment and maintenance of the pair bond. Aggression is very noticeable in group situations and in those in which nest sites are limited it can even lead to fatalities. Fighting over food could be differently motivated to reproductive fighting in this species because birds clearly dominant over an individual on the perches were not necessarily dominant in a feeding situation. However, one could argue that the subordinate bird had a territory which included the feeding site and was thus more aggressive close to home but the widespread occurrance of this dominance reversal, plus the fact that it was still seen in birds with territories on the perches, or even nest boxes, suggests that the dichotomy does exist.

i) Bill pointing and head forward threats

Morris (1954) has proposed that the use of threats is relatively unimportant in the Zebra Finch where disputes are settled by actual aggression. He suggests that this is because the beaks can do little damage to the opponent. In view of the highly aggressive nature of the Zebra Finch and the fact that ritualized threats have been found in other comparatively small passerines (e.g. the Carduelines, Newton 1972) this ommission seems surprising. However, Moynihan and Hall (1954) reach a similar conclusion to Morris' in the related Spice Finch. They found no evidence of ritualized threats and suggested that the role of threats was filled by unritualized intention movements and that this situation might be linked with the highly gregarious social habit which requires no long-distance hostile displays. The situation in the Zebra Finch is not clear, and personal observations suggest that a review of threatening behaviour would be rewarding.

Morris notes the occasional use of bill pointing as a threat. It involves sleeking of the feathers and a horizontal attitude with the bill directed at the opponent. A possibly less intense form was frequently seen in which sleeking and pointing occurred without the horizontal posture, or with only a slight inclination of the body. This behaviour was not considered by Andrew (1961) to be a full <u>head forward threat</u> because in other passerines it includes opening or gaping of the bill. However, Caryl (1975) describes it as a head forward threat and it appears to have a similar derivation in that it consists of attempts to bite the opponent. Whether it can be considered a ritualized display or not seems largely a matter of choice.

The Spice Finch has been shown to bill mandibulate (rapidly open and close the beak) in hostile situations (Moynihan and Hall, l.c.). Caryl (1970) did not report such behaviour in the Zebra Finch whereas it has been seen in this study accompanying bill pointing on many occasions. Such bill mandibulation (BM for convenience) also accompanies nesting behaviour and is described fully in 3 (d), iii). BM in aggressive encounters seems to occur in situations where fear predominates and is directed at the approaching opponent. Andrew (1957) described BM in the threats of the Gosling Bunting and proposed a similar link with fear and that it was derived from attempts to bite the opponent (other possible derivations will be considered with nesting behaviour).

Where rivals were evenly matched an intense threat was observed which fulfilled all of Andrew's (1961) criteria for true head forward threat in passerines. The description which follows has not figured in any of the literature and it would appear that this is the first time it has been observed. The threatening bird assumes a sleeked horizontal posture with the head in line with the body and directed at the opponent; the bill is opened and then gaped and the whole head shaken slowly from side to side. Slow, rhythmic tail-fanning accompanies the bill gaping and this threat often resulted in an attack if it went unheeded by the rival. This threat was not used as frequently as bill pointing, it appeared particularly when two opponents were evenly matched and often when they were rivals for the same potential mate, but it still must be included in the behavioural repertoire of both males and females. Interestingly, rapid tail fanning occurs when an individual lands on the perch between successive supplanting attacks and thus may be derived from a balancing action.

The above head forward threat display has figured in the literature but in a completely different context. Morris (1958) called it nest invitation behaviour and noted its occurrence between mates at a potential nest site. This confusion could possibly have arisen because both tail fanning and BM are also features of nesting activities. One clear distinctive feature of the head forward threat, however, is that it occurs in silence whereas calls accompany nesting behaviour. In addition, head shaking is not seen during nesting and BM rather than gaping occurs. The head forward threat shows in fact more similarities with juvenile food begging behaviour than with nest invitation, particularly the shaking of the head which will be described later. The tail fanning in aggressive encounters figures in other estrildids, the Crimson Finch (Morris 1958) and Waxbills (Harrison 1962), and it has also been seen in carduelines such as the Hawfinch (Hinde 1955).

Crook (1960) has described a very similar head forward threat display in the Ploceid Quelea quelea. It involves a head forward posture with depression and fanning of the tail. It is given by a male in defence of his territory and appears to be derived from conflicting tendencies to attack, flee and behave sexually. He suggests a link between tail fanning and copulation movements though this seems unlikely. It could be significant, however, that the threat occurs in the Zebra Finch in situations in which defence of the sexual partner, and possibly the nest site, are involved, and thus may represent a further relationship between the Estrildidae and Ploceidae groups.

Thus, it appears that the Zebra Finch does possess a head forward threat posture but that this display is only seen occasionally in situations where tendencies to attack and to flee are in conflict. A less intense display, the bill point, which lacks tail fanning and bill gaping though it may include bill mandibulating, is more frequently seen in such situations.

ii) Bill fencing attacks

Threats may lead to avoidance behaviour on the part of a subordinate bird but in cases where this fails the encounter may be resolved by actual physical contact. This is usually confined to the bills, vigorous jabs are countered and returned, with only infrequent attempts to deliver blows to the belly and flanks. The two opponents rarely trade blows in a strictly one to one ratio and dominance is indicated by a horizontal posture, the subordinate bird's stance is more vertical whilst leaning away from the opponent (Morris 1954).

Bill fencing may occur during courtship bouts as was noted earlier, and Caryl (1970) found a sequential link between these two activities. Andrew (1957) noted the converse in the emberizines, song was given by males when fighting with females. This represented a weak sexual tendency as song was notably absent in encounters between males but in the Zebra Finch no courtship tendencies were seen in agonistic bouts.

iii) Supplanting attacks

Supplanting attacks occur when an opponent vacates the perch as the attacker arrives thus avoiding physical contact. These often develop into continuous chases with the attacker repeatedly landing in the position the subordinate bird has just vacated. Actual contact may well occur, as in bill fencing, the head is usually the target but the horizontal attitude of the initial lunge may result in biting of the flank of the opponent. Many feathers may be removed in such encounters, particularly in captivity where chances of escape are fewer, and areas particularly vulnerable seem to be the back of the head and tail region. As Morris (1954) also described, birds seem reluctant to let go of a rival if they have made contact and where the wing has been grasped both birds may end up hanging upside down from the perch, the attacker tenaciously holding onto the wing with his bill, the perch with his feet!

It was found that supplanting attacks occurred rarely between mates in the Zebra Finch and there was no evidence of sexual chases during pair formation. Hinde (1952) has recorded how, in the Great Tit (Parus major), the male 'drove' the female from the flock by a series of supplanting attacks which resulted in the privacy from intervention he required for courtship. This has also been seen in the Carduelines (Newton 1972) but was notably absent at all times in the present work.

iv) Submissive displays

The only submissive display, aside from actual avoidance of attack, described for the Zebra Finch is one common in many captive birds. It involves a general fluffing of all the body feathers and the bird becomes largely inactive as Morris (1954) described; Hinde (1954) notes a similar display in the Greenfinch. In neither of these cases has the behaviour been seen in the wild and thus it is thought to be associated with an inability to make a complete escape from an attacker. It was observed on rare occasions in this study, birds presenting the feathers in this attitude were usually found to be sickly rather than healthy individuals. It may, as

Morris suggests, prevent outright attacks by other birds but it certainly did not prevent plucking of feathers from the unfortunate individual.

Harrison (1962) proposed that bill mandibulation seen in agonistic encounters of Waxbills could be an "appeasement gesture" and this may be its function in the Zebra Finch, particularly between mates. This will be discussed further below as will also tendencies to bend away, or to offer allopreening which may similarly reduce aggressive tendencies.

A case of an individual using actual begging in aggressive encounters was recorded on one occasion only. A young male (6 months post-hatch) was persistently attacked by a rival male and, unlike the examples quoted by Morris (l.c.), gave distinctive begging calls. It should be remembered that these birds become sexually active by 3 months post-hatch and thus this behaviour was surprising when it first appeared. What it may indicate, however, is that other possible appeasement behaviour, described under nesting activity, may share a similar derivation from begging behaviour. The use of juvenile behaviour as appeasement gestures in humans has been well documented by Eibl-Eibesfeldt (1970).

In conclusion one could say that, apart from possible appeasement displays between mates, submissive displays are rare in the captive Zebra Finch.

v) Plucking of feathers

This does not really fall into the agonistic category but is closely related with the actual acts of aggression. Subordinate and ill birds may be severely plucked; feathers were frequently removed without aggression and it seems likely that this activity is linked with nest building. Goodwin (1960) cites the case of a female

Amandava sp . removing feathers from her male when ready to re-nest and Hinde and Steele (1972) noted an increase in plucking amongst canaries when nesting material was not available.

(d) Nesting displays and breeding in the Zebra Finch

The nest advertisement display has been linked with pair formation in the past and will therefore be described in detail. The juvenile begging display is also included as some adult display components may be derived from it.

The term nest advertisement is preferred to that of nest-soliciting (used by Caryl 1975) in that, as I will attempt to show, it invariably occurs in relation to a potential, or actual, nest site and involves attraction of the mate. It was used by Crook (1962) in a similar sense to describe the pair formation behaviour of the closely related Ploceids and has the added advantage of clearly distinguishing the display from the dissimilar soliciting seen during courtship.

i) Nest advertisement; the "pairing ceremony" of Morris (1954,1958)

The display has been described by both Morris and Immelmann (1965), and consists of twisting and turning movements during which bill mandibulation (BM) occurs with tail fanning and, on some occasions, wing drooping. The body is lowered to the perch with the head hunched in and the tail raised whilst turning (the tail is depressed whilst fanning). The display may also include short runs or hops as well as brief vertical flights and is accompanied by low "mewing", "chattering" and "whining" calls. These are the nesting calls of Immelmann, and he notes that they resemble the crying of a small child.

Similar displays have been described in other estrildids and other families; Goodwin (1960) notes crouching displays accompanied by nesting call and directed at the female in Amandava spp.; Andrew (1957) observed the emberizine, Gosling Bunting, giving head forward threats with BM at an approaching female; in the carduelines Hinde (1955) and Newton (1972) noted horizontal twisting from side to side in the potential nest site with BM for at least the Goldfinch, Bullfinch and Hawfinch. Apparently tail fanning does not figure in any of these displays.

The Zebra Finch nest advertisement occurs on and around a potential nest site and also the completed nest. Morris (1958) found that it was given away from nest sites and, suggesting it was important in pair formation, called it the "pairing ceremony". No differences between the two displays were evident and it seems unnecessary to perpetuate this dichotomy. In the present work, birds did give the display in the absence of nest boxes but it was never given in the centre of the perches but always close to the side walls or occasionally in the corners on the floor of the cage, i.e. in situations where nests could most likely be constructed.

A final point arises from Immelmann's (1965) suggestion that males probably use the display to attract females to the nest site. At least in the captive birds used in this study, females were also seen to give the nest advertisement display in an identical form.

The components of nest advertisement have not been described in detail before and are discussed further below.

ii) Bending away (twisting and turning)

A displaying bird was found to alternate between bill pointing at the approaching mate and then, after turning, bill pointing away. The horizontal posture of an aggressive bill point was usually maintained and this behaviour accounts for the various descriptions of "twisting and turning" which have appeared in the literature. The bill point away from the mate was termed 'bending' away here, as when the body was held more vertically it was clearly inclined or bent away.

The bending away appears to be the same ritualized movement as the bill pointing towards the mate with the exception that BM, commonly directed at the mate, is usually absent. Once in close proximity, both birds were seen to BM and bend away, either alternately or simultaneously, whilst still edging closer until in many cases actual body contact resulted. The bending away only became apparent after the mate approached indicating that proximity may be important in its elicitation. It must be stressed that these observations were not quantified.

It seems likely that this is an appeasement gesture in that aggressive tendencies indicated by bill pointing and BM are removed by turning away from the mate, as in the well cited case of head flagging in the Black headed Gull (Moynihan 1954). Even in well established pairs sudden turning of the head in the direction of the mate can result in rapid fleeing hops on the part of the latter. In this sense it may be similar to allopreening invitation postures (see §3.(e)) in which the head and beak are directed away from the bird approaching to begin preening. Presumably the same conflicting tendencies are present in both cases, namely those leading to approach and flight whilst being attracted sexually to the incoming bird (Sparks 1963). The tendencies to approach and flee are clearly seen on occasions where the turning movements break into actual running and hopping towards, and then away from, the mate. In addition the body feathers are usually sleeked which is thought to be indicative of flight intention.

Bending away did not appear to be used in aggressive encounters where it could have figured as a ritualized appeasement gesture. It appears to be restricted to members of a pair which is also the case in the Zebra Finch, for allopreening. The normal response to attack, as noted above, is counterattack or flight.

Zumpe and Michael (1970) have outlined an alternative explanation for similar behaviour occurring in primates which they termed "threatening away". This is seen in Rhesus monkey encounters when the male gives threats in directions other than towards the female, i.e. away from her. These threats are apparently not related to environmental stimuli, such as potential rivals, and are apparently related to the sexual attractiveness of the female as they are given most frequently when she is reproductively receptive. In the Zebra Finch, bending away resembles bill pointing and tail fanning and is a feature of intense aggressive threats which suggests that agonistic tendencies are involved; the sexual tendency will presumably increase as the mate approaches.

Thus threatening away may be a better descriptive term than bending away but, whatever its derivation, it is clear that this display component is important in promoting the close proximity of mates, particularly around a potential nest site.

iii) Bill mandibulation (BM)

BM accompanies bill pointing as the mate approaches the bird giving nest advertisement. It has also been observed in aggressive encounters when the tendency to flee is apparently high and presumably denotes a decreased likelihood of an attack being launched. It would seem from Morris' (1954) account that BM is audible up to a range of about 2 metres, however the display described here were not audible over this range.

It is possible that BM is derived from mandibulation of nest material (Moynihan and Hall, 1954, Morris, 1958) and occurs in nest advertisement presumably as displacement behaviour. Hinde and Steel (1972) found that, in the canary, early nest building consisted of pecks and mandibulation without any material in the bill. However, mandibulation-like bill movements also occur after feeding, drinking and frequently at the end of preening bouts, though in the last two, movements of the chin accompany those of the bill. Morris (1954) remained undecided as to whether the derivation was from nest building or feeding.

BM occurs in the related Waxbills (Harrison 1962) and it appears similar to billing occurring in the courtship feeding of the Carduelines. In these species BM is directed towards the mate and often both birds stretch towards each other until the bills touch and "caressing" occurs (Hinde 1955, Newton 1972). This billing leads into courtship feeding in the Carduelines and also in the Budgerigar (Brockway 1964b), an activity not seen in any of the Estrildids. Harrison (l.c.) noted "kissing" in his waxbills but this was not observed in the Zebra Finch and bending away would seem to make it highly unlikely that it could. A link with courtship feeding in the Carduelines would suggest a derivation for BM from feeding movements although the possibility of juvenile begging being the source of this component has been suggested by Andrew(1961).

The derivation of BM must remain unclear, at least for the present, but the contexts in which it is given suggest fear, with resulting tendencies to flee, is involved. In addition, its use in the bill pointing threat suggest that agonistic tendencies are also present. A derivation from either feeding or nest material mandibulation can be justified whereas a decision between the two cannot.

iv) Tail fanning

Rhythmic tail fanning occurs throughout nest advertisement and displays the vivid black and white species markings of the tail and this probably aids in attracting the attention of the mate. Wing drooping has been connected with tail fanning in the Zebra Finch (Morris, 1958) but did not appear, at least not obviously, in the present study. Tail fanning is a common component of displays of birds and it is thought to be derived in this case from the sun bathing posture described by Morris (1958). This was not observed here but appears to involve similar rhythmic movements and is accompanied by wing drooping. Andrew (1961) has described its occurrence in other species and suggested that it may be linked with thermo-regulatory behaviour. That it may also occur during antagonistic encounters has been described earlier suggesting the likelihood of aggressive tendencies in the display, which leads to a similar situation to that described for BM.

Crook (1961) has described tail depression and fanning in the threatening behaviour of male Quelea on the approach of conspecifics to the nesting territory. Tail depression is a feature of copulation and thus Crook suggests a conflict between the sexual response and attack tendencies is indicated; the tail fanning is indicative of the former tendency, the head forward threat that of the latter. A similar suggestion may hold for the Zebra Finch but it must be remembered that copulatory movements are thought to be independently determined from the rest of the courtship display (see earlier discussion) and its appearance in these contexts is unprecedented. A sexual tendency is usually expressed as a component of the courtship display.

Tail fanning is seen on two other occasions, during preening and, commonly amongst birds, to assist in balance on landing. As noted in the discussion of threats, a single rapid tail fan is often seen on landing between successive supplanting attacks. Balance will also be important during copulation and this may represent yet another possible derivation of this display component.

Further consideration of the derivation of these display components would be fruitless in the terms of the present thesis. The main points which emerge are that the nest advertisement display as a whole contains components which indicate that a conflict of tendencies is occurring, namely those of an approach, flight and sexual nature. Some or all of these tendencies are also present in the elicitation of the head forward threat and courtship displays.

v) Juvenile food begging

This behaviour is described here as the performance of begging displays by adults is known to be a source of many display components (Andrew 1961). Young Zebra Finches adopt a horizontal position, with the body held close to the perch, and the head is kept low and then twisted to one side so that the open bill is directed upwards. This twisting of the neck is unique to the Estrildids and Immelmann (1965) considers it is an adaptation to the domed shape of their nests. However, it must be noted that other species with similarly shaped nests lack this feature in their begging displays. During food begging the head is shaken vigorously from side to side and a loud insistent begging call is given until feeding begins. Similarities between components of the head forward threat and the begging display are quite marked in this species.

(e) Contact behaviour of the Zebra Finch

Hediger (1950) was the first to divide social animals on the basis of whether they showed contact behaviour or not. He suggested two groups: the contact species, in which individuals maintain bodily contact, particularly during rest periods; the distance species avoid such proximity and defend an individual distance which is an area around themselves into which other members of the species are not allowed to enter. In the latter, spacing of the population occurs and distances are maintained by aggression, e.g. the roosting behaviour of Starlings during winter months when they form huge communal roosts with individuals clearly space out along a ledge or frontage (pers. obs.). Contact species such as the Red Avadavat roost in long rows with each individual pressing up against its neighbours (Sparks 1963).

This division is undoubtably useful but cannot be used too indiscriminately. In the case of the Zebra Finch, and some other estrildids, individual distances are maintained between conspecifics at all times but clumping, or physical contact, is allowed between mates, indeed it appears to be actively sort after. Close proximity with other members of the species is prevented by aggressive tendencies. In other estrildids, such as the Poephila spp. (Zann 1972) the clumping response is shown towards all members of the social group but not strangers, and whilst the birds are active, individual distances are maintained. This leads one to view with some trepidation the statement made by Moynihan and Hall (1954) to the effect that the Spice Finch shows no individual distances. To be sure they clump in long rows, but when active, distances are in evidence and if the term contact species is to mean anything then the context in which it occurs must be referred to.

Immelmann (1965) considers the Zebra Finch a contact species yet, as outlined above, contact and mutual preening is only allowed between mates and is very rarely shown towards other conspecifics. Hediger's division is therefore not all that useful in discussing this species and perhaps, if there needs to be a classification, it is time the situation was reviewed. For the purposes of this thesis behaviour seen commonly amongst recognised 'contact' species, mutual preening (or allopreening) and clumping (individuals pressing together), will be referred to as contact behaviour and no further labels are necessary.

i) Allopreening

This term was first introduced by Cullen (1965) to describe preening by one individual of the plumage of another, in contrast to autopreening where the individual preens himself. It has been of popular usage amongst researchers of bird species whereas in the primates analogous behaviour is referred to as social grooming.

The nibbling of feathers of other individuals has often been noted in species forced into close contact e.g. Guillemots and Domestic hens (Sparks 1963) and it seems that birds possess an innate response to the sight of feathers. In many contact species this tendency takes the form of prolonged allopreening bouts and ritualized allopreening invitation postures have been developed. Sparks (l.c.) concluded that this behaviour has probably reached its highest development in the estrildids.

Sparks (1963, 1964, 1965) and Harrison (1965) have examined allopreening closely. Harrison lists three criteria by which a preening attempt can be classed as allopreening and these are; (1) the actions normally resemble those of autopreening; (2) the main areas allopreened (usually the head) are those normally inaccessible to the preened bird; (3) often a characteristic posture is adopted by the preened bird. In this discussion Sparks' (1965) terminology will be used; 'actor' refers to the preening bird, 'reactor' to the individual that is preened.

It is thought (Goodwin 1960, Harrison 1965) that allopreening is primarily caused by aggressive tendencies on the part of the actor which are "sublimed" or "cut-off" by the stimulus of the offered head and plumage of the reactor. These presentation postures are in turn expressions of submissive tendencies and, by this argument, one would expect the actor to invariably be the dominant bird, the reactor the subordinate. However, this is not the case in many tropical species in which Kunkel (1974) found that allopreening alternated between mates. In the Domestic hen (Wood-Gush and Rowland, 1973) the incidence of "allopecking", a behaviour fulfilling all of Harrison's criteria, had apparently no direct relationship with aggressive dominance. Harrison explained such phenomena in that allopreening may be primarily aggressive with a shift of its motivation to sexual tendencies as a pairing relationship develops. This might suggest that the form of allopreening may vary as the pair bond progresses, it could be expected to become less aggressive, and this will be examined in the experimental data.

Kunkel (l.c.) has attempted to provide a 'simpler' explanation. Aggressive tendencies towards the mate, he believes, wane as the acquaintance proceeds and this is accompanied by habituation to the partner as an outlet for any low aggressive tendencies which may remain. These take the form of allopreening and this is facilitated by low fleeing tendencies which may also still exist. In this way, he argues, the outlet as allopreening is appetitively sort and coherence of the pair is actively maintained. Again, as in Harrison's argument, one may suggest that if this theory holds then allopreening between birds in the process of pair formation will contain more aggressive components than that between well established mates. In addition, in the early stages of the pair, when aggressive tendencies will be high, there should be much more time spent in allopreening than in later periods. This too will be examined in the data.

Whatever the outcome, it seems likely that the primary function of allopreening will involve the lessening of aggressive tendencies between mates whilst promoting close proximity. In this way the likelihood of the pair disbanding should be reduced. A second function, omitted thus far, is the possibility that the cleaning of the feathers by the actor is of value to the reactor. This is largely ruled out by Sparks (1964) findings that the intensity of allopreening did not increase with the dirtiness of the plumage, although his findings hold for one species, Amandava, only.

ii) Allopreening invitation postures

At least three such postures were seen in the allopreening behaviour of Zebra Finches and these do not appear to have been described in detail elsewhere. The term invitation is not meant to imply that the reactor always attempted to incite allopreening by assuming a particular posture, but refers to the attitude assumed after allopreening was initiated and because of which the preening bout was prolonged. Fluffing of the head feathers is a feature common to nearly all allopreening behaviour of birds (Sparks 1963) and was seen in all of the Zebra Finch postures described.

Initiation of allopreening invariably consisted of the actor delivering a jab with the bill to the reactor's head or neck region. This peck, for such it appeared to be, was delivered with the mandibles closed and was described in Amandava as an "aggressive thrust" by Sparks (1963). The reactor responded by offering the head feathers for preening in one of the following ways, assuming that he/she did not repel the actor and terminate the allopreening bout with an aggressive act or flight.

(1) The head was turned through 180^{o} so that the bill was pointed away from the actor. The bill could be slightly raised, in which case the actor tended to concentrate on the cheek coverts, or depressed which ruffled the feathers of the back of the head and led to allopreening of this region.

(2) The legs were flexed and the body of the reactor was lowered in relation to the perch, and usually at right angles to it. The actor assumed a vertical pose and allopreened the top and back of the reactors head.

(3) On less frequent occasions, the bill of the reactor remained pointing at the actor throughout the allopreening bout and was held in a slightly raised position. The actor allopreened the short feathers around the base of the bill.

Sparks (1965) has described similar invitation postures in the estrildid *Amandava amandava* though he did not note any cases of type (3).

The approach of the actor was usually slow, appeared guarded and was apparently correlated with autopreening, a suggestion Sparks also noted. The actor was seen to take advantage of the reactor's lack of attention, the first jab might be delivered when the head was turned away or whilst the reactor was engaged in autopreening. On some occasions the invitation postures were given as the mate approached before contact was made, particularly types (1) and (3) and these were also given by females of established pairs to their singing mates. In the latter cases the aggressive jabs of the male, common in courtship (see earlier), soon turned into the softer allopreening movements. When regions other than the head were jabbed at no invitation postures were seen, e.g. the flanks or rump; a similar observation was noted in the Domestic hen (Wood-Gush and Rowland 1974).

As in bending away, discussed under nesting activities, pointing the bill away from a bird in close proximity seems important to these allopreening invitation postures. It is thought that turning the head away removes the potential opponent from the field of view thus cutting off any aggressive tendencies that might otherwise be elicited. A tendency to flee is also indicated, type (2) is very like a flight intention movement, but rarely did the reactor actually take flight (Wood-Gush and Rowland (l.c.) found that invitations graded into fleeing in the domestic fowl). It was clear that allopreening was facilitated by this turning of the bill away as unresponsive reactors repulsed an allopreening jab by bill fencing, i.e. they did not turn the bill away but returned jab for jab. In established pairs the observation of type (3) invitation gives a subjective impression that the need for turning away becomes less prevalent once the pair bond is formed. However, it must be remembered that types (2) and (3) are still the most commonly given invitation, even in established pairs.

iii) Clumping

Bodily contact is frequently maintained between mates in the Zebra Finch and this has been termed clumping behaviour in other estrildids (e.g. Sparks, 1964; Evans 1970). The activity involves actually pushing up against each other rather than merely sitting next to one another. Allopreening, though correlated with the occurrence of clumping, is not essential to it, birds spend considerable lengths of time sleeping or autopreening whilst in this position. A considerable part of the day is spent in clumping particularly during the longer rest periods of the late afternoon and evening.

Clumping is commonly seen in other estrildid species. Long rows of clumping individuals are reported in the Spice Finch (Moynihan and Hall, 1954) and clumping in more than pairs has been seen in the Poephila spp., i.e. the Masked, Long-tailed and Parson Finches (Immelmann 1965). Clumping with the mate only is seen in the Star Finch and Crimson Finch during the breeding season, larger clumping groups are formed at other times, and throughout the year in the Zebra Finch (Immelmann, l.c.).

Sparks (1963) has shown that the separation into exclusive clumping pairs is associated with sexual dimorphism in at least one estrildid species. The Red avadavat, (Amandava) which he studied, is the only member of the family known to enter eclipse plumage in the non-breeding season, and during this time clumping consists of rows of several individuals. With the advent of the breeding season males don the nuptual plumage, and females begin to show a distinct preference for males in nuptual plumage as clumping partners. The males will no longer clump with each other and the social group breaks down into individual breeding pairs. A relationship with sexual dimorphism is supported to some extent when a review is made of clumping in those estrildid species already mentioned: the Spice Finch and Poephila group are all monomorphic whereas the Star Finch, Crimson Finch and Zebra Finch are dimorphic.

In this study, male-male clumps were never observed when in mixed flocks, whereas female-female clumping was more common. In mono-sexual captive flocks males will readily clump but only with one particular partner. Immelmann (pers. comm.) has seen group clumping in the wild on exceptionally cold occasions but a thermoregulatory function, along the lines of the Emperor Penguin huddles, is not thought to be a major causative factor. Sparks (1964) demonstrated that in Avadavats there was no increased incidence of clumping as the temperature was decreased, though it must be said, his lowest temperature of 10°C would be frequently surpassed in the Zebra Finch's habitat. The only time that group clumps could be obtained, in this work or in previous studies (see Evans 1970), is when birds were transferred into strange surroundings. This is thought to be due to a general reduction of activity and, in particular, aggressive tendencies and may indicate that, in the Zebra Finch, the function of clumping is to reduce such tendencies between paired individuals.

It is thought that clumping is facilitated by allopreening (Sparks 1965) and the majority of clumping species exhibit prolonged allopreening bouts. However, as Kunkel (1974) points out, there are tropical species that clump without allopreening and, conversely, those that allopreen without clumping! Ultimately it is believed that the two behaviours serve the same function, i.e. the reduction of aggression and the maintenance of close proximity between pair (or flock) members.

SECTION 4. CHANGES IN BEHAVIOUR ASSOCIATED WITH PAIR FORMATION

Introduction

Courtship behaviour in birds is often highly complex, consisting of a series of auditory and visual signals, which are believed to function in reducing tendencies to attack or flee as two individuals come into close proximity. This is, however, only one part of the behaviour that is involved in breeding. Processes, such as pair formation, which has been called by many authors the period in the breeding cycle from the first meeting of the sexes until copulation has taken place and the nesting phase started (e.g., Hinde, 1955, Moynihan, 1955 and Stokes, 1963) are also evident in a number of species. Changes in behaviour are also associated with this process. In the case of the Chaffinch (Hinde, 1955, 1956), the early stages of this pair formation period are marked by much aggression between the sexes; the male usually dominates. This is followed by a gradual reduction in aggression and an increase in sexual tendencies culminating, often several weeks later, in copulation. The aggressive superiority is reversed at this final stage, the female assuming dominance and this sequence is a feature of the larids, Moynihan (1955), the emberizines, Andrew (1957), and the carduelines, Newton (1972).

In the experiments described in this section the pair formation period of the Zebra Finch was observed in two situations. In the first, pairs of birds (i.e., one male and one female) were isolated in cages and their behaviour contrasted with that occurring in mixed-sex groups of birds. The aim at the outset was to discover and to describe the behavioural changes that may take place during bond formation and the temporal characteristics of the process. It is a common avicultural practice to pair birds straight from monosexual flocks in individual cages and this technique was utilised here to examine the formation of pairs in the absence of any possible interference from conspecifics. In contrast, the group situation provides evidence as to the effects this interference may have and thus should prove a useful comparison. Previous workers on the Zebra Finch have analysed pair formation in group situations but none have compared their results with the process as it occurs in isolation. For example, Butterfield (1970) and Caryl (1975) independently considered the group situation and found several behavioural changes occurring over a relatively short period. However, both used unbalanced groups, more females than males in each case, and this tended to complicate the issue in that bigamy is quite common amongst captive estrildids (it was noted by both Butterfield and Caryl in the Zebra Finch and by Goodwin (1960) in the Avadavat). In the present study, therefore, balanced groups consisting of two males and two females were preferred.

Nest building, as a component of pair formation, was not considered and neither a nest site nor nesting material was provided. Morris (1954) thought that repeated entry of the nest by the male was an important source of stimulation to the female in the Zebra Finch. However, as Collias and Collias (1970) pointed out in the case of the Village Weaverbird, this stimulation is probably more important in inducing ovulation by the female rather than actual pair formation. In addition the advantage of excluding nesting behaviour is that hormonal complications, due to releasers other than those provided by the two individuals, were largely ruled out. Such factors as the sight of the nest, handling and the manipulation of materials have been shown to influence the timing of ovulation (e.g. Warren and Hinde, 1961 and Murton et al. 1969), but it is unlikely that they play a major part in the formation of pair bonds in the Zebra Finch. Intensification of nest building has occurred (Immelmann, 1963) but this is looked on as an adaptation to the prolonged breeding season, rather than pair formation, as such intensification is also found in the successively polygynous ploceids.

A number of behavioural changes were expected and in view of this an attempt was made to quantify as large a spectrum of behaviour as possible. Erickson (1973) found such an approach fruitful in a study of the Ring Dove and as he stressed in his report; "pair bond establishment in birds may be manifested through a variety of behaviour patterns."

Methods

(a) Subjects

Birds were obtained from breeders via a local pet store. There is no evidence of behavioural differences between different colour mutants, and consequently greys (wild-type), fawns, pied and chestnut flanked were all used. The different varieties rendered rapid identification possible in group situations (the use of coloured rings for identification was not found to be successful as at rest, birds invariably sit with their feathers covering their legs).

Observations were made on 12 isolated pairs and 10 groups, each consisting of two males and two females. Care was taken in all cases to ensure that males and females were obtained from different breeding stocks to preclude, as far as was possible, any of the birds having formed bonds prior to the experiments. Whilst in stock cages birds were maintained in small monosexual flocks for a period of between seven and fourteen days before they were tested. This reduced the likelihood of any previous bonds influencing the formation of new ones. The prior experience of the birds was not easy to assess but as far as was known they were in their first or second years and had never bred.

(b) Housing

Stock cages consisted of multiple units each measuring 60 x 50 x 38 cm. and individual cages were separated off by wooden partitions. The wire cage fronts were of standard design. The room was large, well ventilated and equipped with a humidifier. Feeding consisted of pannicum and white millet mixture with cuttle-bone and occasional green material (usually chickweed or groundsel) available. Mortalities, in these conditions, were very rare indeed throughout the study although breeding attempts, in order to increase stock numbers, resulted in a few female losses. Supplementary illumination was provided in the winter to ensure that the light regime was never less than 12 hours light, 12 hours dark.

The experimental cages were the same in both isolated and group situations. A wooden frame measuring 124 x 90 x 39 cm., was covered with ½ inch wire mesh, front and top, and ½ inch plywood on the floor, sides and back. The wire mesh on the top allowed more light to enter the cage which led to clearer and therefore more accurate observations. There were two horizontal perches available to the birds; they were set 20 cm. apart with one, the rear-most, 10 cm. higher than the other. Only four cages could be accommodated in the experimental room at one time and this meant that repetition of the experiments, to complete the sample size (10 , for the isolated pairs), was unavoidable. However, birds in any one cage were in auditory, but not visual, contact with a number of other conspecifics. Conditions prevalent in different trials were kept as constant as possible; small changes in day length might have occurred but would not have affected the Zebra Finches unduly.

(c) Terminology

It is essential to explain clearly some of the terms used in this section of the thesis.

Two birds who have formed a bond, or are in the process of establishing such a bond, are referred to as a pair. Any other birds which showed no tendency to form a bond are, conversely, termed a non-pair. There are two kinds of non-pair; a heterosexual non-pair is one between a male and a female; a homosexual non-pair could either refer to a relationship between two males or two females.

The two experimental situations considered are that for isolated pairs, in which only one male and one female occupy the experimental cage, and group pairs in which two males and two females are present. Non-pairs, as defined above, can only be found in the group situation; the behaviour of an individual towards its mate can be compared with that directed towards the two other birds in the group, the hetero- and homosexual non-mates.

Analysis of the data required that the outcome of the study be pre-judged to some extent in order to determine which birds could be considered to have formed pairs. A subjective measure of overall behaviour was used by Caryl (1975) in a similar situation but herein a specific behaviour was chosen. The occurrence of clumping extensively, and exclusively, with one individual was chosen as a precise criterion. Immelmann (1962), Butterfield (1970) and Caryl (l.c.) have all stressed the importance of exclusive clumping with the mate in the pair maintenance behaviour of Zebra Finches and, in practice, this criterion was quite easily adhered to. Amongst the isolated pairs there was only one case in which birds, which might have been considered to have paired, failed to clump. They were thus treated separately as a non-pair. In seven groups, two pairs were formed (making 14 in all) but this was not the case in the remaining three groups; data for these latter was considered separately.

(d) Procedure

On the day of introduction (i.e., day 1) females were taken from a stock cage and placed in the experimental cages in a separate room. A carrying box was used for transportation, to minimise the effects of handling. The males were introduced after a period of approximately one hour. The males did not appear to be unduly affected by the lack of an acclimitisation period; immobilization and reduced calling rates, commonly seen in frightened birds in new cages, were not observed in any of these cases.

The birds remained in the experimental cages for a period of 10 days during which observations were made on days 1, 2, 3, 4, 5, and 10. Watches comprised 30 minutes each day with the exception of day 1, when a second period, immediately succeeding the 30 minutes after introduction, was observed. This watch was designated day 1b (after Caryl, 1975) and was included in an attempt to capture any rapid changes of behaviour that might occur on the first day.

Observations were made at approximately the same time each day and were confined to the morning period (between 9.00am and 1.00pm) as a pronounced diurnal cycle of activity has been recorded for the Zebra Finch. Ollason and Slater (1972) found that males tended to become less active and to sing less frequently as the evening approached and thus, by confining observations to the morning only this potential source of experimental bias was avoided.

(e) Behavioural measures and recording techniques

Use was made of both live and recorded observations. The experimenter was seated approximately 3m from the cages at a distance unlikely to disturb and unsettle the birds and from which it was possible to tabulate courtship, agonism, vocalisations and allo-preening bouts from direct observations. Video tape recordings were also made of the observation periods using a Shibaden FP100 camera attached to a Shibaden SV-6100E(K) ½ inch VTR (recorder). These recordings were easily obtained, without any sophisticated lighting requirements, and were immediately available for playback. From them measures of activity and proximity were obtained.

The behavioural measures taken were:

i) Courtship A courtship bout was defined as a display in which song accompanied pivoting movements by a male in the presence of a female. Bouts in which components of the courtship dance occurred without directed song were recorded in the remarks column only as they graded into general locomotory activity and were difficult to distinguish clearly. Such incomplete courtship behaviour was discussed in Section 3.

Soliciting and copulation occurred too infrequently to be examined stringently but notes were made on all sitings including those occurring outside of an actual observation period.

ii) Agonism The number of beak fencing encounters were observed (i.e. all occasions on which a bird made contact with anothers head and/or beak). The identity of the initiator and the recipient of the attack was recorded.

Total numbers of supplanting attacks were similarly counted. Those which occurred as repeated supplanting chases were still recorded as individual attacks and both victor (supplanter) and loser of the exchange were noted.

In discussing agonism in the Zebra Finch, Caryl (1975) noted that actual numbers of encounters and the length of time spent in fighting was highly correlated in both beak fencing and supplanting attacks. He presented his results in terms of this total time measure, but here the number of encounters was chosen as it is more readily available and has been used quite extensively in other bird studies.

iii) Vocalizations The number of song bouts in which the male was not obviously orientating himself towards another individual, in the form of a courtship display, was taken as a measure of undirected singing. The position of the female mate, when the song began, was also noted. In practice there were very few occasions on which courtship song and undirected song could have been confused.

Loud calls were given by all individuals and the total number heard in each watch was counted. In the groups this involved distinguishing the calls of 4 separate birds and in these cases the results are approximated and only gross differences between groups can be compared with any certainty.

iv) Allopreening No measure of time spent in allopreening was taken, but the number of allopreening bouts and the identity of the reactor and actor birds was recorded. This provided information on the frequency with which different individuals allopreened.

v) Clumping and Proximity (Settled distance) The distances between individuals were measured at 60 second intervals from the video tape recordings. Measures were only taken for birds on the same perch and were accurate to within ± 3cm. Thus the maintenance of close proximity was indicated by a small average distance score and a high number of recordings. Measures across perches or to the floor of the cage introduced too high a level of inaccuracy to prove useful.

The average distance apart, as measured here, corresponds to Crook's (1961) 'settled distance' measure. In addition, this data provided evidence of the frequency and length of clumping bouts.

vi) Activity and Synchrony The activity which individuals were engaged in was sampled at 60 second intervals, again from the video recordings. Those recognised were;

Sitting alert (SA) - including hopping about, short flights and sitting with the legs and neck stretched and the eyes open.

Sitting drowsily (SD) - this involved sitting with the feathers generally fluffed and covering the feet and legs. Activities such as preening, clumping and sleeping were common.

Feeding (F) - of necessity this occurred on the floor of the cage where the food was made available and included activities such as walking about, pecking or cuttlebone, etc.

Crook (1961) was able to differentiate between activities such as hopping about, flying about and preening. It was found, in this study, difficult to decide when a hop could be considered a short flight and vice versa. It is interesting to note that in a recent paper Crook uses a reduced number of behavioural categories similar to those noted here (Dunbar and Crook 1975).

A measure of synchrony was obtained from the data. The number of times two birds were engaged in the same activity was taken as indicative of the tendency for these birds to perform the same act at the same time. It must be noted that this method does not provide an ideal measure of synchrony. The interval between observations (60 seconds) is too short to prevent bouts of behavioural activity overlapping from one trial to the next. This criticism is accepted and justified in the present context as it is a comparison of changes in relative synchrony which is required rather than an accurate measure of synchronisation itself.

(f) Statistics

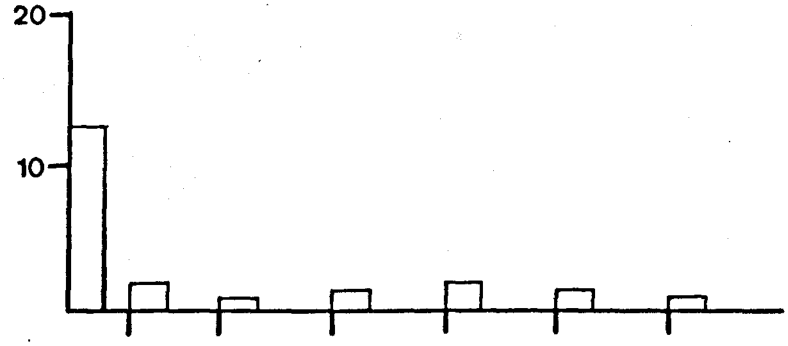
Non-parametric statistics were used extensively (after Siegel, 1956). Individual variability has been avoided wherever possible by the use of the Wilcoxon Matched pairs test (WMP) for related samples. Independent samples were usually compared with the Mann-Whitney U-test (MWU).

Results and Discussions

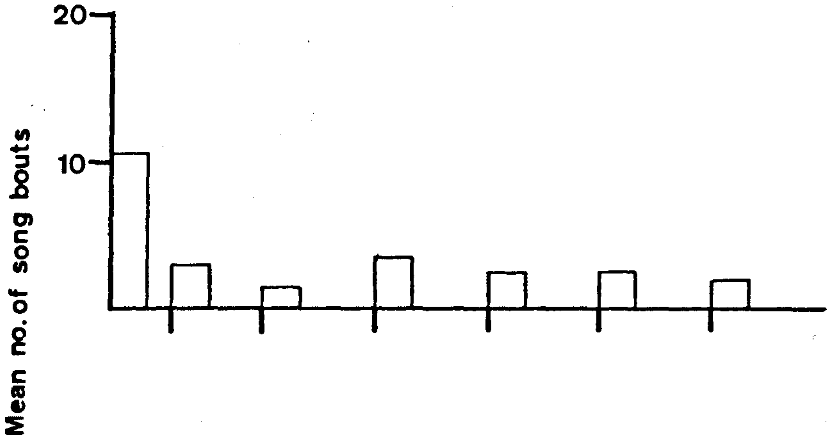
Courtship

(i) The number of courtship bouts (Fig. 1)

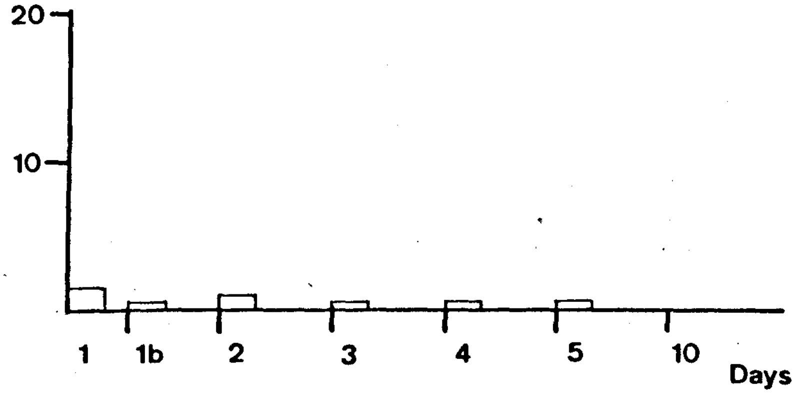
Isolated pairs (Fig. 1(a)). Most courtship involving directed



(a) Isolated pairs



(b) Group pairs



(c) Heterosexual non-pairs

Fig. I. The mean number of courtship bouts given by males on different days.

song clearly occurred on Day 1 immediately after the introduction of the males. 60% of all the courtship bouts recorded were observed in this watch and the decrease to the amounts shown on Day 1b, and thereafter, is significant ($p < 0.005$, WMP). The level on subsequent days remains low and roughly constant.

Group pairs (Fig. 1(b)). Courtship between birds forming pair bonds in the group situation showed a similar emphasis on Day 1 and the fall off to the amounts recorded on Day 1b is again significant ($p < 0.005$, WMP). 91.3% of all the courtship bouts recorded were directed at the eventual mate and the difference between the amount that was directed at the mate compared to that directed at the heterosexual non-mate (Fig. 1(c)) is significant on all days ($p < 0.005$, WMP).

The levels of courtship between pairs on days after Day 1 was slightly higher than that seen in the isolated pairs but the total number of bouts, summed for all watches, did not differ significantly (MWU).

Heterosexual non-pairs (Fig. 1(c)). Courtship of the non-mate female was rare in the group situation on all days. Highest amounts were recorded on Day 1 (5 males were involved) and again on Day 2 but the difference, compared to later days, is not significant (WMP).

Homosexual non-pairs (Not figured). In two groups males were observed courting other males on Day 1. In Group 2 male A and male B courted one another and in Group 6, A courted B once. These bouts were of short duration.

(ii) Soliciting by females during courtship bouts (Table 2(a))

Isolated pairs There was no peak in the amounts of female soliciting corresponding to that recorded for number of courtship

TABLE 2 The incidence of soliciting, copulation and nesting behaviour

	1	1b	2	3	4	5	10
(a) Soliciting (Mean No. of Observations)							
Isolated pairs	0.7	0.3	0.3	0.6	0.6	0.2	0.3
Group pairs	0.7	0	0.4	0.2	0.4	0.4	0.2
(b) Copulation (Mean No. of Observations)							
Isolated pairs	2.1	0.3	0.1	0.2	0	0.2	0.3
Group pairs	0.7	0	0.2	0.1	0.1	0.1	0.4
(c) Nesting behaviour (No. of Observations)							
Isolated pairs (Maxm. 11)	5	9	9	6	9	11	10
Groups (Maxm. 7)	1	0	3	2	4	4	2

bouts. Its occurrence was infrequent on all days but by Day 10 it had been recorded, at least once, in 9 of the 11 isolated pairs.

Group pairs Soliciting was again rare and, if anything, less frequent. By the end of the experiment it had been seen in only 8 of the possible 14 pairs. No soliciting was recorded for courtship bouts between heterosexual non-pairs.

(iii) Copulation (Table 2(b))

Isolated pairs The number of times copulation was recorded did not follow the same pattern as female soliciting. It was most frequent on Day 1, suggesting at most a weak link between the two activities during pair formation. Significantly more cases were recorded on Day 1 when compared with all other watches ($p < 0.01$, Sign Test). On days other than Day 1 soliciting may play a more important role as the two pairs which showed no copulation similarly showed a lack of soliciting.

Group pairs Copulation was rare in the group situation and by Day 10 had only been seen in 7 of the 14 pairs. A link with soliciting by the female was suggested in that copulation was only recorded on one occasion without this accompanying display. Overall copulation was more frequent in the isolated pairs than in the groups and this was largely due to differences on Day 1 when significantly more pairs copulated in isolation ($p < 0.025$, Fisher Exact Probability Test).

(iv) Nesting behaviour (Table 2(c))

Isolated pairs Nesting behaviour occurred early on Day 1 in some cases and thereafter it was observed frequently and was recorded for all 11 pairs. Both male and female were involved in these nesting activities which occurred exclusively on the perches close to the side walls (i.e. in a 'corner').

Group pairs Rough notes in the remarks column of the data indicate that nesting behaviour occurred less frequently in this situation than in isolated pairs. Further study is, however, needed to confirm this point.

Discussion of courtship behaviour

Courtship behaviour is traditionally associated with the first stages of pair formation (Lack, 1940) and it was clear that in both the isolated and group pair situations it occurred most frequently immediately after introduction of the birds. The high level of courtship was not maintained and quickly fell off by the second watch (Day 1b). Courtship occurred between future mates from the beginning in the group pairs which suggests that any preferences for particular individuals must have been very rapidly expressed. Copulation was apparently more frequent in the isolated pairs on Day 1 and this supports Butterfield's (1969) suggestion that males will frequently interfere with the copulation attempts of others. Indeed males were observed to break off their own courtship attempts in order to launch an attack on a copulating pair. Whether this interference was due to the enforced proximity of pairs in captivity cannot be assessed but it would presumably be an important factor. The incidence of female soliciting in different watches did not show the same tendency as courtship song in that there was no emphasis on Day 1. This suggests that soliciting is unlikely to play an important role in the initial selection of mates during pair formation.

These findings are in accord with those reported by Caryl (1976) who found a similar decline in Zebra Finch courtship after introduction. He went on to suggest that this early courtship phase is replaced by nest building activities and this is supported by the data in this study. The smaller amounts of nesting activities in the groups is probably again due to interference as in some cases a subordinate pair was prevented from remaining in the corners of the cage where such behaviour took place. It is important to bear in mind that this replacement of courtship by nesting is not a total one, courtship and copulation continued throughout the later "nesting phase".

The carduelines appear similar to the estrildids in that pair formation is initiated by male courtship before a territory or nest site is established (Newton, 1972). This is a fairly unique feature; the situation is different in many passerines in which the male isolates himself in a territory and attracts the female to him by means of advertising song. The male courts the female on her arrival at the territory and there is then some evidence of nest building activities. No further courtship occurs until the nest building phase nears completion when courtship, female soliciting and copulation take place. The whole process may last for several weeks in, for example, the Snow Bunting (Tinbergen, 1939), other emberizines (Andrew, 1957) and the Chaffinch (Newton, 1972), during which there is little or no courtship.

The functions of courtship are probably complex. It is likely that the following ones are of importance in the Zebra Finch:

(1) It may facilitate invasion of the individual distance in these highly aggressive birds, enabling activities such as copulation and nest-building to occur. The high initial rate of courtship in the Zebra Finch is probably due, at least in part, to the male's sexual tendencies outweighing those likely to promote aggression

towards the female. Summers-Smith (1965) has intimated that sexual activity is important in the pair formation of the House Sparrow as he found no pairs were formed during the coldest months of the year when there is little courting activity.

(2) Courtship may stimulate ovarian development in the female. Erickson and Lehrman (1964) found that this was the case in the Ring Dove and this probably explains the onset of nesting activities by the female in both isolated and group pairs. This suggests that introductory courtship is important in (a) reducing aggression, (b) promoting proximity, and (c) stimulating the hormonal system of the female. The function of courtship between mates later in their relationship is probably similar suggesting a bond maintenance function for this behaviour (i.e., it will promote and prolong the pair bond). This later courtship is presumably linked with the Zebra Finch's continual maintenance of breeding readiness which allows nest-building to begin at any time of the year. Newton (1972) reports that amongst the carduelines, the Bullfinch is similar in that courtship can be seen between mates throughout the year. A smaller amount of courtship is required in these later stages of the bond as familiarity with the mate will lead to a reduction in both sexual and aggressive tendencies as other activities maintaining proximity (e.g., contact behaviour) come into play.

(3) Courtship is probably important in selection of an appropriate mate. Two factors are involved according to Lack (1940), sex recognition (the male and female must recognise one another as such) and individual recognition (the mate must be distinguished from other conspecifics). In species in which males isolate themselves in a territory individual recognition is probably at less of a precedent than in the social Zebra Finch. Here, both visual and auditory recognition must be rapidly established as pair formation

occurs within the confines of the social group. Sex recognition is facilitated by sexual dimiorphism in the Zebra Finch yet males do on occasions court other males. Caryl (1975, 1976) reported similar tendencies and it is unlikely that this behaviour results from mistaken identity. It seems more likely that it is linked with the maintenance of males in monosexual flocks in captivity. One would expect that given time, and deprivation, courtship of another male could become reinforcing. In any case Butterfield (1969) found that homosexual bonds between males as a result of deprivation were always broken when females were subsequently presented.

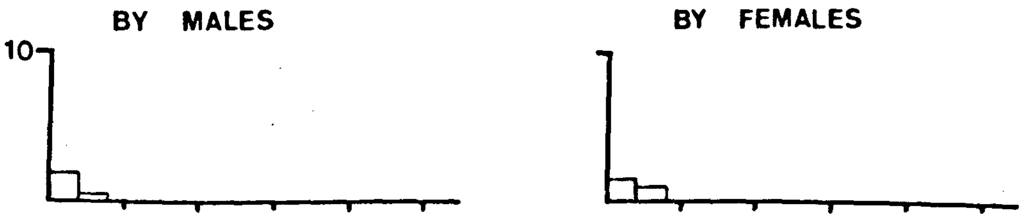
Agonism

(i) Beak-fencing encounters (Fig. 2)

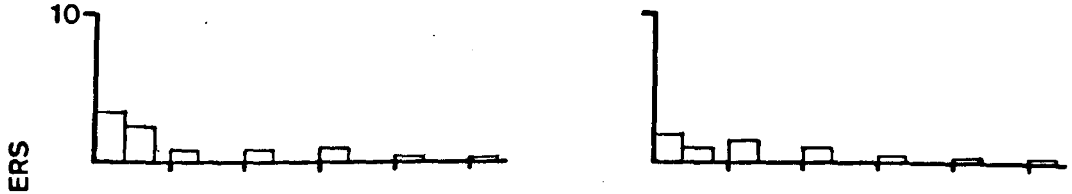
Isolated pairs (Fig. 2(a)). There were only a few signs of aggression between mates in the isolated pairs and no beak-fencing was seen after Day 1b. This decrease in the incidence of beak-fencing is significant ($p < 0.005$, WMP).

Group pairs (Fig. 2(b)). Of the total number of beak-fencing bouts seen in the group situation, 21.5% occurred between mates. Highest amounts were recorded on Days 1 and 1b with a fairly rapid, and significant, decrease to the levels of subsequent days (Day 1 > Day 10, $p < 0.005$, WMP). This decrease was evident in both male and female beak-fencings yet, overall, there were still significantly more encounters than between isolated pairs ($p < 0.01$, MWU).

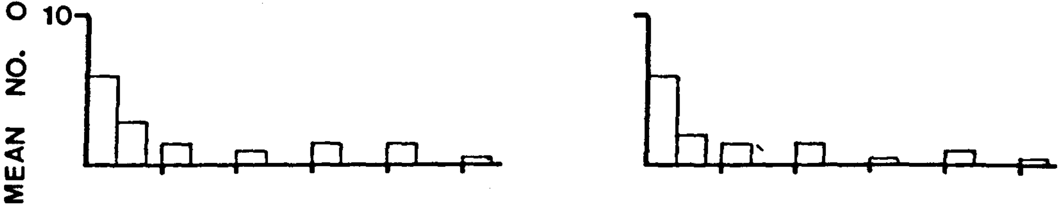
Heterosexual non-pairs (Fig. 2(c)). There was more beak-fencing between the heterosexual non-pairs than between mates ($p < 0.01$, MWU). However, there was a similar rapid decline in the number of male and female encounters after Day 1 (Day 1 > Day 10, $p < 0.05$, WMP) with beak-fencing virtually absent by Day 10.



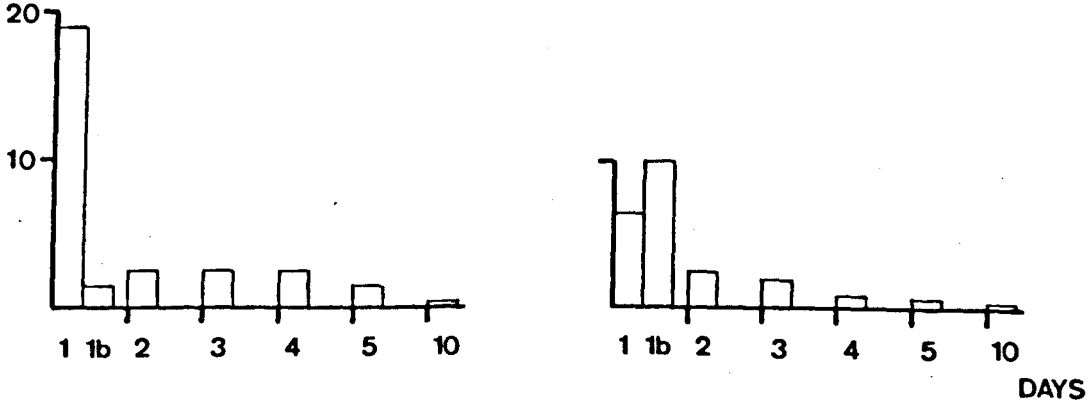
(a) Isolated pairs



(b) Group pairs



(c) Heterosexual non-pairs



(d) Homosexual non-pairs

Fig. 2. The mean number of beak fencing encounters launched by males and females on different days.

Homosexual non-pairs (Fig. 2(d)). The highest scores for beak-fencing were recorded in male-male and female-female encounters on Days 1 and 1b. Summing the data for all watches, however, reveals that the amounts between heterosexual and homosexual non-pairs do not differ significantly and the same rapid decline after Day 1b is in evidence (Day 1 > Day 10, $p < 0.05$, WMP for both sexes).

Thus beak-fencing between non-pairs occurs more frequently than that observed between paired birds but shows a similar tendency to decrease with time.

(ii) Supplanting attacks (Fig. 3)

Isolated pairs (Fig. 3(a)). Supplanting attacks were seen in only 2 of the 11 pairs in the first two watches, Days 1 and 1b. Thus agonism (including beak-fencing) was completely absent after Day 1b.

Group pairs (Fig. 3(b)). As with beak-fencing, supplanting attacks between paired birds were rare. Male aggression towards the mate showed a significant decrease with time (Day 1 > Day 10, $p < 0.005$, WMP); aggression by a single female towards her male on Days 4, 5 and 10 prevented a similar decrease in the females.

Heterosexual non-pairs (Fig. 3(c)). Individual male and female scores vary a great deal, in some watches as many as 200 attacks were recorded for a single bird. Nevertheless trends are evident in the scores. Male aggression towards the non-mate female remained high in all watches and there was no significant fall off comparing Day 1 and Day 10. In a similar fashion, female aggression remained high and showed a peak on Day 2, though there was no significant difference. Overall, a comparison shows that there was more aggression between heterosexual non-pairs than between paired birds

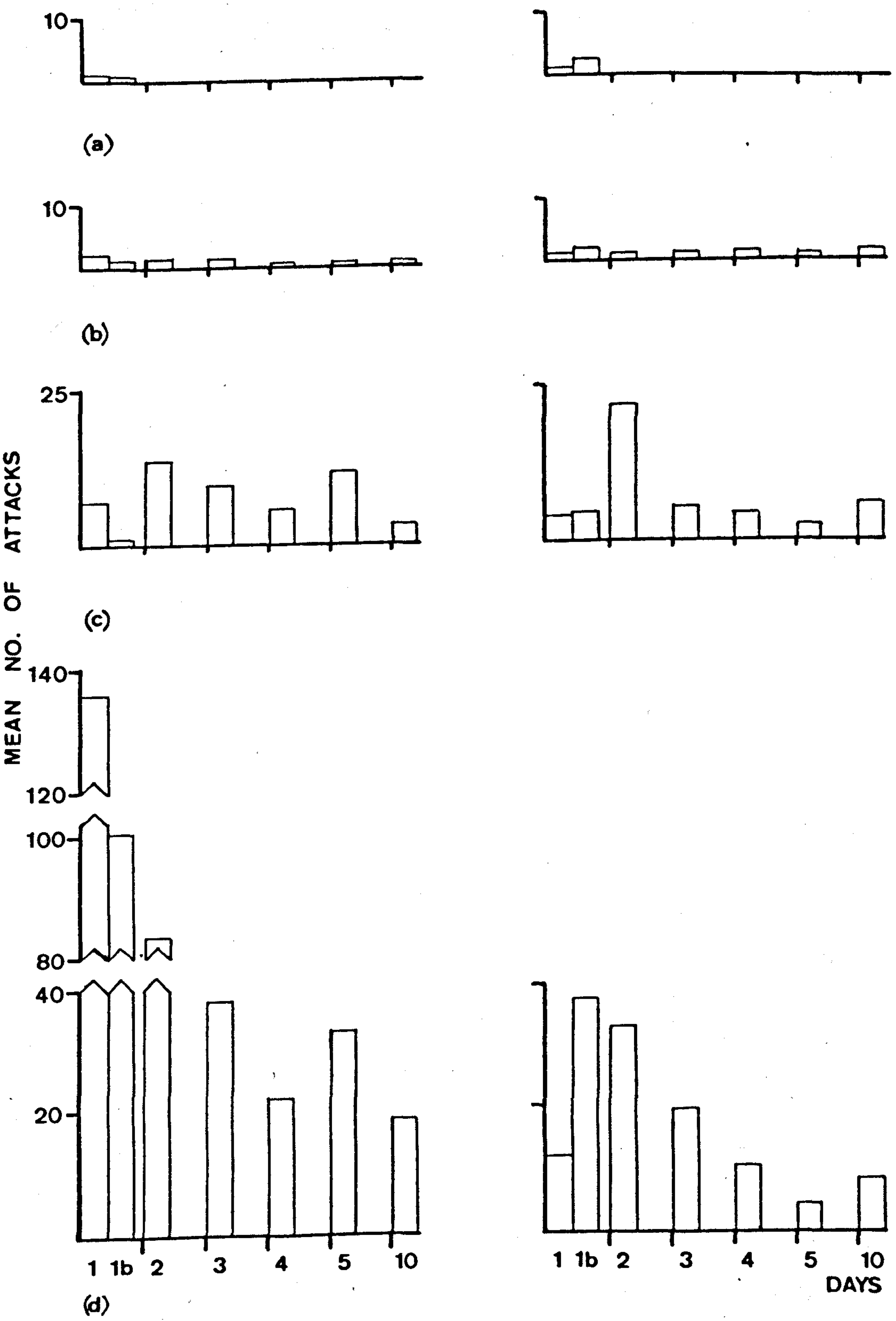


Fig. 3. The mean number of supplanting attacks given by males and females on different days. (a) Those between isolated pairs. (b) Those between group pairs. (c) Those between heterosexual non-pairs. (d) Those between homosexual non-pairs.

($p < 0.001$, MWU).

<u>Homosexual non-pairs</u> (Fig. 3(d)). The greatest number of supplanting attacks took place between birds of the same sex and scores in excess of 300 attacks per watch were recorded in male-male interactions. There were significantly more attacks than between pairs ($p < 0.001$, MWU) and also, between heterosexual non-pairs ($p < 0.05$, MWU) for both males and females.

Male-male aggression was at its highest on Day 1 when courtship was also commonest. The subsequent decrease does not reach significant levels and the situation was complicated in that frequently dominance of one male over another changed between watches (this will be discussed further later). The females, unlike the males, showed few supplanting attacks in the first watch, Day 1, and highest scores were recorded on Day 1b and Day 2. The increase shown is not significant but this can again be explained, at least in part, in terms of reversals of dominance relationships. What is particularly interesting is that male-male aggression on Day 1 is much higher than that between females. Later female-female aggression increases and overall the total number of attacks launched by both sexes is the same.

(iii) Supplanting chases (Table 3)

Many of the supplanting attacks occurred as a series of repeated encounters in which the subordinate bird was vigorously pursued about the cage by the more dominant individual. This was not a prominent feature of supplanting attacks between paired birds indicating an aggressive rather than a sexual basis to this behaviour. In some species (e.g. the Great Tit, Hinde 1952) sexual chases occur during pair formation which take the form of repeated supplanting attacks

TABLE 3 Total numbers of supplanting attacks with those involved in supplanting chases

		No. of supplanting attacks	No. involved in chases	% as chases
Isolated pairs		0	0	0
Group pairs	Males	64	21	32.8
	Females	103	33	32.0
Heterosexual non-pairs	Males	708	315	44.5
	Females	622	344	55.3
Homosexual non-pairs	Males	3026	2464	81.4
	Females	890	534	60.0

of the female by the male. Here chases were most evident between homosexual non-pairs and were probably due to the inability of the subordinate bird to completely flee the vicinity of the attacker. Due to the confines of the cage, the stimulus for attack was repeatedly presented.

Discussion of agonism

Beak-fencing tends to decline in all situations until by Day 10 it is virtually absent whereas supplanting attacks, though reduced in overall number, are still present. Caryl (1975) noted similar fluctuations over a smaller time period and considered that, in the Zebra Finch, the two activities are interrelated such that increases in one lead to a decrease in the other. Beak-fencing is more common in cases where priorities (dominance) have not been decided and attempted supplanting attacks are rebuffed. Later, the subordinate bird retreats and offers no resistance. Hence high incidences of beak-fencing should indicate that relationships are in a state of flux, either because two individuals are strangers or because their present order of dominance is under revue.

(a) Aggression between mates

There was more evidence of aggression between mates in the group situation than in isolation although, in both cases, it was relatively infrequent when compared with aggression between non-mates. The aggression that was seen was largely on the part of females and could indicate that they were unwilling to accept the male's courtship advances. However, the amount of courtship in the two situations did not differ appreciably and therefore this seems an unlikely explanation. Butterfield (1969) found that male aggression was initially high towards the mate and that this gradually waned until the female assumed dominance prior to copulation. This resembles the sequence of reversal of dominance seen between mates in the Chaffinch and carduelines (Hinde, 1955, 1956; Newton, 1972). Though Butterfield's findings refer to the Zebra Finch there was no evidence of a similar sequence in the present results, in fact the data suggests the opposite as it was the females who appeared most aggressive in the early exchanges.

Hinde (1955) noted that in the Goldfinch reversal of dominance did not take the form of overt aggression but was reflected in avoidance behaviour and thus it is possible that it may have been missed in this study. However, copulation was seen much earlier in the pair formation period of the Zebra Finch suggesting that reversal, if it is important at all, must take place very rapidly. Much of the present aggression appeared to be initiated by allopreening attempts and, in the males, may have been linked with courtship as beak-fencing has been observed during courtship song. Caryl (1970) has suggested a possible link between aggression and courtship song.

Sexual chases involving repeated supplanting of the female by the male are common in many passerines and it has been suggested that they may be important in driving the female from the vicinity of the flock so that courtship can proceed without interference (Hinde, 1952). Hinde (1956) went on to propose that this aggression might have a stimulatory effect on the female but, if this is the case, there is no evidence of it occurring in Zebra Finch pair formation, at least in captivity. It is interesting that Hinde (1956) notes that aggression between mates in the Canary is less severe during pair formation occurring later in the breeding season when levels of gonadial hormones will be presumably higher. The Zebra Finch is thought to maintain high levels of such hormones throughout the year and this could account for the very low levels of aggression between potential and established mates.

The highest levels of aggression were recorded in the groups and the remainder of this discussion is devoted to fighting in this situation. For convenience it is separated into male and female aggression; the differences outlined support this dichotomy.

(b) Male aggression

There was a great deal of aggression launched by males. Highest levels occurred on Day 1 and accompanied the highest level of male courtship. This was largely due to male-male supplanting attacks which often reached extremely high rates with persistent chasing of one male by the other. This aggression was probably enhanced by the enforced proximity of the opponent and presumably in the wild would have lead to the subordinate male being driven off. Nevertheless it represents a real phenomenon as high levels of male-male aggression, though falling slightly, are retained throughout the observations. This was also the case in aggression directed at the female other than the mate except that there was no comparable peak on Day 1.

Newton (l.c.) has described pairing in flocks of carduelines and he states that the first sign of impending pair formation is the onset of aggression between males within the flock. In birds setting up a territory before pair formation, the situation is obviously similar. Caryl (1975) reports that male-male aggression in Zebra Finches is usually at a low level but when a female is placed in sight of the two males, fighting increase markedly and then falls off again once the female is removed. It would appear that it is some feature of the encounter with a female that 'sparks off' high levels of male-male aggression in the Zebra Finch.

There have been at least two attempts to explain this male aggression at the onset of pair formation; (i) Bastock et al (1955) suggested that aggressive tendencies which would normally be directed at the potential mate were redirected at other conspecifics, (ii) mates may be competed for by the males (Butterfield 1970). The merits of these two proposals, in the light of Zebra Finch behaviour, will be briefly discussed below with some additional suggestions.

(i) Redirection of aggression.

Experiments with cichlid fish led Rasa (1969) to suggest the importance of redirection of aggression in the mating behaviour of this species. She found that the incidence of intrapair aggression was higher in isolated pairs than between pairs in groups. This is clearly not the case in the Zebra Finch where the isolated pairs did not differ from the group ones. In addition, Caryl (1975) has criticised her results in that the males in the group situation may be preoccupied with interpair aggression.

If aggression is being redirected, then the amount observed will be dependent on the aggression arousing properties of the female. Presumably, after pair formation the female is less likely to elicit aggression from the male and conversely one would expect a strange female to elicit more. Caryl (l.c.) carried out the pertinent experiment and found that in fact the female mate stimulated more male-male aggression than did a female non-mate. This suggests that the aggression is not due to aggressive tendencies towards the female but rather to some other feature which is enhanced during pair formation. Caryl suggests that it is the degree of sexual tendency expressed by the male towards a particular female that determines the amount of aggression she will provoke. Thus during pair formation the female must become more sexually attractive to the male and this affects his aggressive responses. This assumes that aggression is similarly motivated in the male before and after pair formation.

Duncan and Wood-Gush (1972) have recently revived interest in the hypothesis that frustration provokes aggression in their studies of the domestic fowl. This was a theory very popular in the 1950's and they found that in their studies aggression could be induced towards a subordinate when birds were prevented from obtaining visible food. Although Crook et al (1968, etc.) have demonstrated that in _Quelea_ aggression over food is differently motivated, this raises the possibility that sexual frustration brought about by unsuccessful copulation attempts leads to male aggression. Caryl's experimental set-up with a female visible to the males, but unattainable, is reminiscent of Duncan and Wood-Gush's thwarting situation. The sexual tendency induced in the male would still presumably govern the level of frustration.

(ii) Competition for mates

At the beginning of pair formation, it would seem likely that the greatest threat to a courting male would be the proximity of a rival male. Hence, one could argue that aggression between males is due to sexual competition for a limited number of females. This is certainly an important priority for the male and probably explains why he directs the majority of his aggressive acts towards males rather than just any conspecific. However, the aggression recorded did not appear to involve actual rivalry for a particular female, although the results for the incompatible pairs suggest this could be a possibility, and males were still highly aggressive even when they were courting different females. Clearly, sexual competition will be an important feature of the pair formation process but it does not appear to explain completely the high incidences of male-male aggression.

A second possible factor involved in competition is that male aggression may be influenced by selection on the part of females. It is possible that a successfully aggressive male may prove better at breeding and raising young than a subordinate male. There is some research evidence to support such a proposition; Spurr (1974) studied aggressive responses in Adelie Penguins and found that males nesting in the centre of the colony were more aggressive than those nesting at the periphery. The centre nesting birds had better breeding success and though the higher aggression could be related to age or other factors, it is possible that this behaviour is an advantage in this species. Mourning Doves were found to establish 'peck-orders' before mating by Goforth and Basket (1971) and interestingly, high ranking males and females paired off before the lower ranking birds. Too much aggression could be ultimately a disadvantage in a social species but where there is competition for nest sites and food, as there is in the Zebra Finch, a high level of male aggression may be beneficial to the pair.

Thus, it is likely that male aggression at the start of pair formation is beneficial to both the male and the female. Aggression by the male does not end after pair formation and this later aggression may serve a different, though related, function. Caryl (l.c.) showed that the pair bond enhanced the female in that she provoked more male aggression and this would be valuable in prolonging the pair bond. The presence of his mate will induce the male to attack other conspecifics over distances he would normally tolerate, i.e. she would increase his individual distance, and a territory would be built up with the mate at the centre. Caryl suggested the distance involved was about two and a half times the male's normal "social space", and he went on to demonstrate that the further the female was from the male the less she affected his fighting behaviour. Marler and Mundinger (1975) described a similar 'mate territory' in the European Twite and noted that it tended to be smaller away from the nest. Zebra Finches defend their nest site and, clearly, this may have an important influence on both male and female aggression. The mate territory would seem important as a means of separating the pair from their social group for mutual displays, copulation and nesting to occur without interference.

(c) Female aggression

The major difference between male and female aggression was in the timing of its onset. The females showed very little aggression on Day 1 and hence there does not seem to be the same relationship with sexual tendencies that was suggested for the males. High scores appeared on Day 1b and day 2; Butterfield's (1969) findings were similar in that she found male Zebra Finch aggression fell off with time whereas, female aggression did not.

In the Chaffinch and carduelines Newton (1972) reports that female aggression only becomes apparent after initial pair formation has been completed. Zann (1972) found that in the *Poephila* spp. females were only aggressive when their preferred male was close. Thus it would appear that the female needs to have established some sort of bonding relationship before she begins to show aggression towards conspecifics. Caryl (1970) was able to induce some female-female aggression by the sight of the male but, perhaps significantly, the male was not a mate of either of the females concerned. This proposed link between pair establishment and female aggression is further supported by the evidence for the incompatible pairs which will be discussed later.

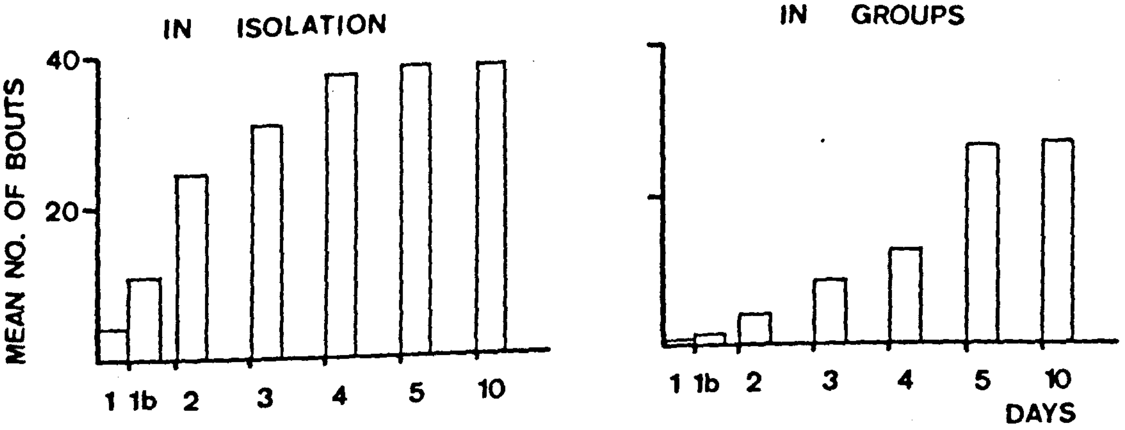
Summary

Aggression has proved an interesting behavioural parameter in this study. Aggression between mates is never very marked and would not be a useful indicator of the completion of pair formation. However, high initial male aggression would appear to indicate a willingness to pair whereas subsequent aggression by both the male and female mate show that a pair is becoming established. In individual cases the changes can be very marked from day to day and averaging the results tends to mask the effects of reversals of dominance. It is interesting that the control of aggression in male and female Zebra Finches could be different; male aggression is probably linked with his sexual tendency and may be evoked, to some extent at least, by any female, unlike female aggression which is apparently linked more closely with a specific male. The effect of the combined aggression is to set up a mobile territory around the pair which will tend to prolong the length of the pair bond. It seems likely that the size of this mate territory will fluctuate quite considerably in different contexts.

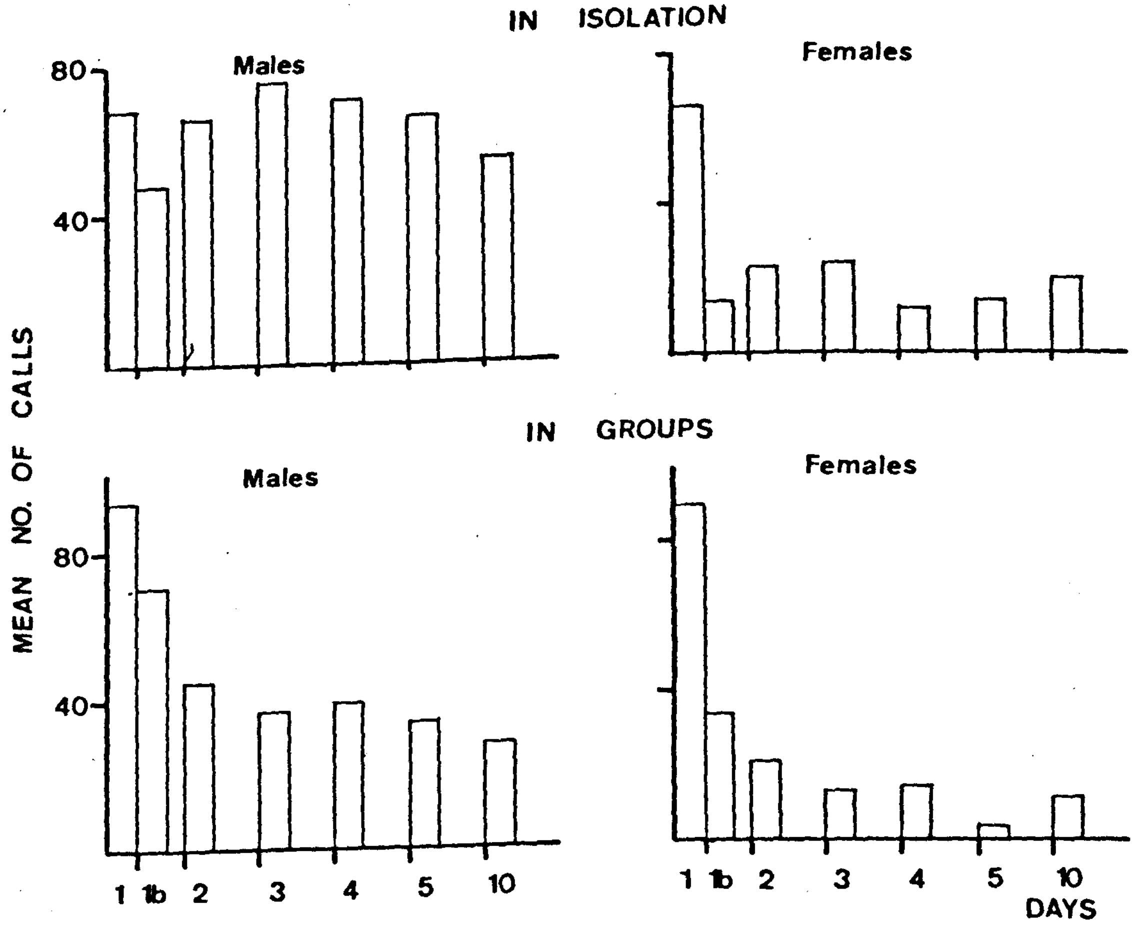
Vocalizations

(i) Undirected Song (Fig. 4(a))

In isolation Undirected song shows an opposite trend to that of courtship song with the lowest amounts occurring on Day 1. The increase to that of Day 2 is significant ($p < 0.005$, WMP) and on the remaining days it is maintained at a high level. The song was



(a) Undirected bouts of song



(b) Loud calls

Fig. 4. Vocalizations other than courtship song.

given in the majority of cases when both the male and female were perched (60.1% of the total bouts recorded), the remainder occurring when the male was perched and the female feeding alone.

In groups The males in this situation introduced undirected song more gradually; the increase over the level on Day 1 is not significant until Day 3 ($p < 0.005$, WMP), and the increase continued until by Day 5 singing reached comparable levels to that heard in isolation. The scores for Day 2 are much lower than in isolation ($p < 0.02$, MWU) but again singing occurred predominantly when both birds were perched (89% of all bouts).

(ii) Loud calls (Fig. 4(b))

In isolation Loud calling was highest on Day 1 and whereas in the males it remained at a high level throughout, there was a marked decrease in calling by the females by the second watch (Day 1b). This decrease in loud calling by the females is significant comparing Days 1 and 10 ($p < 0.002$, WMP), which resulted in significantly fewer female loud calls when compared with calling by males ($p < 0.001$, MWU).

In groups Comparable high numbers of loud calls were counted on Day 1 but in this situation both male and female calling decreased with time (Day 1 > Day 10; $p < 0.01$, WMP, in each case). However, males still gave more calls than did females overall ($p < 0.01$ MWU).

Discussion of Vocalizations

(i) Undirected singing

Undirected singing, that is singing not involved in courtship bouts, was inhibited after introduction in both the isolated and group pairs. There was then a gradual increase in its frequency of occurrence but it was noticeable that the inhibition was more prolonged in the group situation. Morris (1954) suggested it was the presence of another unfamiliar male that led to the suppression and in the group situation this may have been the case here. However, the results for isolated pairs and those of Caryl (1976), who looked at one male with two females, indicate that females may have the same effect.

Zann (1972) noted that singing by unmated males in Poephila spp. was inhibited by the presence of a female and that the onset of undirected song was indicative of a readiness to breed. Certainly in the carduelines undirected song, or something very like it, starts before the onset of pair formation, but here it is linked with an aggressive response by the males (Newton, 1972). In the Zebra Finch, and other estrildids, it is difficult to see what is stimulating undirected song as an aggressive motivation is not apparent. Moynihan and Hall (1954) concluded that in the Spice Finch there was no common denominator although familiarity with the surroundings, as well as other conspecifics, has an effect upon it. Hall (1962) proposed that monomorphic species may use this song as a means of identifying the males but this does not apply in the dimorphic Zebra Finch nor does it seem likely as the courtship song or other differences in behaviour that have a sexual basis could easily fulfil this function.

The mate's activity did not appear to influence male singing. In fact the majority occurred when both birds were on the perch and relatively inactive. The related Bengalese Finch was examined by Birke (1974) and was found to show a tendency for undirected song during the transition between active and inactive phases which suggests it may possibly aid synchrony between the pair. Indeed Birke found that with male-male pairs song tended to be given by a perched male when his counterpart was feeding. This tendency was not apparent in the groups and in isolation it was clear that the female did not return to the perch immediately on hearing the male's undirected song. However, it was equally clear that when she did return the male's song bout was terminated abruptly. Separation of mates could well be important, both Zann and Hall (l.c.) have noted an increase in undirected singing when a male has been isolated from his mate or his flock.

It remains difficult to suggest a function for undirected song though group cohesion is a viable possibility. In the Budgerigar, Brockway (1967) reported that devocalization of males led to testicular regression and this suggests that undirected song may have a self-stimulatory function in the Zebra Finch. In addition, Brockway (1965) showed that male vocalizations were important stimulants to the female and thus undirected song could be involved in developing breeding synchrony between mates. Males certainly spend a good deal of time engaged in singing and it would be surprising if no positive function could be found for this activity.

(ii) Loud calls

The loud calling of both males and females was highest on Day 1 which could be due to distress brought on by the new surroundings and strange conspecifics. Zann (1972) has suggested that the loud call of estrildids is used in the wild as a lost call when a bird becomes separated from the flock and Butterfield's (1969) results support his findings. Thus the calling on Day 1 may have been caused by the disruption of stock cage flocks. In the groups the rate of both male and female calling declines after Day 1 though the males still give more calls in each watch. The isolated pairs are somewhat different, the males continue calling at a high rate and there is no decline with time. This could be due to auditory contact with other males, in separate experimental cages, without the accompanying visual contact. After all the Zebra Finch is considered a social species and it is possible that a single pair is in a similar situation to isolated individuals and the male continues loud calling in an attempt to regain the flock. Whatever the motivation, it certainly seems likely that the sexes differ in their reactions to it and the males appear to have a lower threshold for loud calling than the females.

Allopreening

Allopreening bouts (Table 4)

Isolated pairs Allopreening began early in the experimental period. No significant increase was observed from Day 1 to Day 10 and neither sex emerged as the dominant allopreener as in all but two pairs both male and female were recorded allopreening often within the same watch. Males allopreened more frequently in 5 pairs, in 5 females and in one, two birds allopreened.

Group pairs Allopreening differed in the group pairs in that little was recorded on Days 1 and 1b and the increase by Day 2 is significant ($p < 0.005$, WMP). In addition, there is a further increase from Day 2 to Day 10 ($p < 0.005$, WMP) with the highest scores being noted in the last watch.

As in the isolated pairs, allopreening was shared equally by the sexes but in this case there was an overall greater number of

TABLE 4 Allopreening bouts expressed in terms of mean number recorded per bird per day

		Days							
		1	1b	2	3	4	5	10	Total
Isolated pairs	Males	0.6	3.3	1.1	2.1	2.1	1.5	1.5	12.2
	Females	1.5	4.8	1.8	0.8	1.3	2.6	3.1	15.9
	Total	2.1	8.1	2.9	2.9	3.4	4.1	4.6	28.1
Group pairs	Males	0.1	0.3	1.7	2.7	2.7	3.7	5.2	16.4
	Females	0.4	2.2	2.6	3.6	4.6	3.2	4.7	21.3
	Total	0.5	2.5	4.3	6.3	7.3	6.9	9.9	37.7
Heterosexual non-pairs	Males	0.1	0.2	0.2	0.6	0.1	0	0	1.2
	Females	0.2	0.1	0.3	0.9	0.5	0.2	0.4	2.6
	Total	0.3	0.3	0.5	1.5	0.6	0.2	0.4	3.8
Homosexual non-pairs	Males	0.2	0	0.2	0.3	0.6	0.3	0	1.4
	Females	0	0.2	1.2	0.2	0.2	1.6	1.3	44.4
	Total	0.2	0.2	1.4	0.5	0.8	1.9	1.3	5.8

bouts (group>isolated pairs, $p < 0.01$, MWU) and the amount recorded for Day 10 is higher than that seen on any of the days in isolation.

Heterosexual non-pairs Allopreening between non-mates was rare and showed no tendency to increase with time. The bouts recorded consisted mainly of allopreening attempts which were usually rebuffed by the reactor. Interestingly, 61% were initiated by females suggesting that they might be more prone to such extra-pair activities than are males.

Homosexual non-pairs Here again scores were very low and the relatively high levels of female-female bouts are due to the activities of two females only. As in the heterosexual non-pairs the majority of these bouts were allopreening attempts which met with aggressive rebuffs.

Discussion of allopreening

In the isolated pairs allopreening attempts began almost immediately unlike the group pairs in which it only really became apparent on Day 2. Butterfield (1969) found that allopreening was a good indicator of the end of pair formation as it was the last of the behavioural traits to appear during the process, but this does not appear to hold in this case. The smaller amounts seen in the groups could have been due to a preoccupation with interpair aggression although more clumping was seen in this situation. It might also reflect a greater reticence to approach the mate in the groups or that, as Harrison (1965) has proposed, there are less aggressive tendencies towards the mate in groups where these may be directed against other conspecifics. If the latter is true then this suggests that allopreening allows the release of aggressive tendencies and thus it will prolong the length of the pair bond.

It was clear from the results that allopreening is largely confined to the mate, or future mate, in this species. The rare exceptions that occurred involved females in the majority of cases and it often seemed as if they were unable to 'resist' attempting to preen a nearby unsuspecting or inactive non-mate.

The length of the allopreening bouts also increased with time as they became more frequent but there was no evidence of one individual monopolising the behaviour as Butterfield (1969) had reported in her study. Similarly Harrison (1965) and Wood-Gush and Rowland (1973) who considered other species found no evidence of a 'dominant' allopreener, the activity was shared by the members of a pair.

Clumping and settled distance

(i) Clumping (Figs. 5 & 6)

Isolated pairs (Fig. 5, column (a)). Clumping was observed in all watches and there was no apparent increase from Day 1 to Day 10.

Group pairs (Fig. 5, column (b)). There was more evidence of clumping amongst group pairs and there was an increase by Day 3 both in the number of pairs seen clumping ($p < 0.001$, Sign Test) and in the actual amount of contact behaviour ($p < 0.001$, WMP). The overall amount of clumping recorded between group pairs was clearly greater than that seen in isolation ($p < 0.001$, MWU), and this difference was evident from Day 2 onwards.

Heterosexual non-pairs (Fig. 5, column (c)). Clumping with non-mates was extremely rare; the amount recorded was minimal and

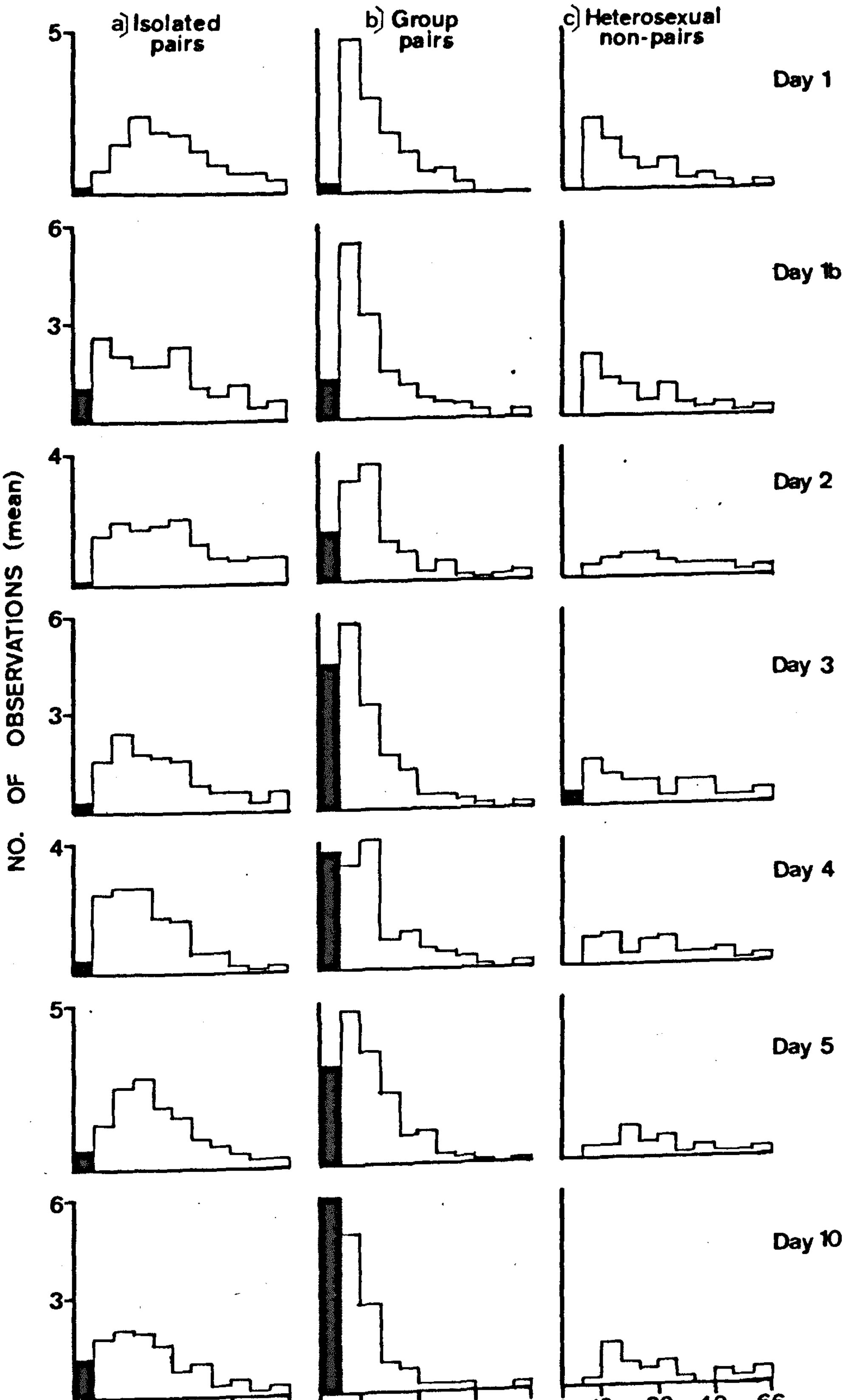


Fig. 5. The settled distance between individuals of different pairs with the amount of clumping on each day shown in black.

concerned three non-pairs only on Day 3. This result is to be expected as clumping with the mate was taken as the criterion for pair formation (see Methods) and the extreme infrequency of extra-pair contact behaviour supports its original choice.

Homosexual non-pairs (Fig. 6, columns (d) & (e)). No male-male clumps were seen on any occasion, but in one group two females clumped briefly on Days 2, 5 and 10. Such transitory contact was associated with allopreening attempts by these individuals.

(ii) Settled distance (Figs. 5 & 6, Table 5)

Isolated pairs (Fig. 5, column (a)). The settled distance, maintained between pairs, decreased with time in spite of the fact that clumping behaviour did not substantially increase. The settled distance measured on Day 10 was smaller than that for Day 1 when compared using the Kolmogorov-Smirnov Two Sample Test ($p < 0.001$) and this difference still showed significance when the clumping data was excluded from the calculation ($p < 0.05$).

Group pairs (Fig. 5, column (b)). The settled distance decreased from Day 1 to Day 10 ($p < 0.001$, K-STX, excluding clumping, $p < 0.05$), and the distances involved, summed for each watch, were clearly smaller than in isolation ($p < 0.001$, K-ST, both with and excluding clumping). The small settled distance between group pairs developed rapidly and was in evidence by Day 1 when compared with the isolated pairs ($p < 0.01$, K-ST). The number of times the mates were adjacent on the same perch (Table 5) did not show the same tendencies suggesting that it was the actual proximity of the two individuals that altered and not their readiness to share the same perch.

Heterosexual non-pairs (Fig. 5, column (c)). Unlike the paired

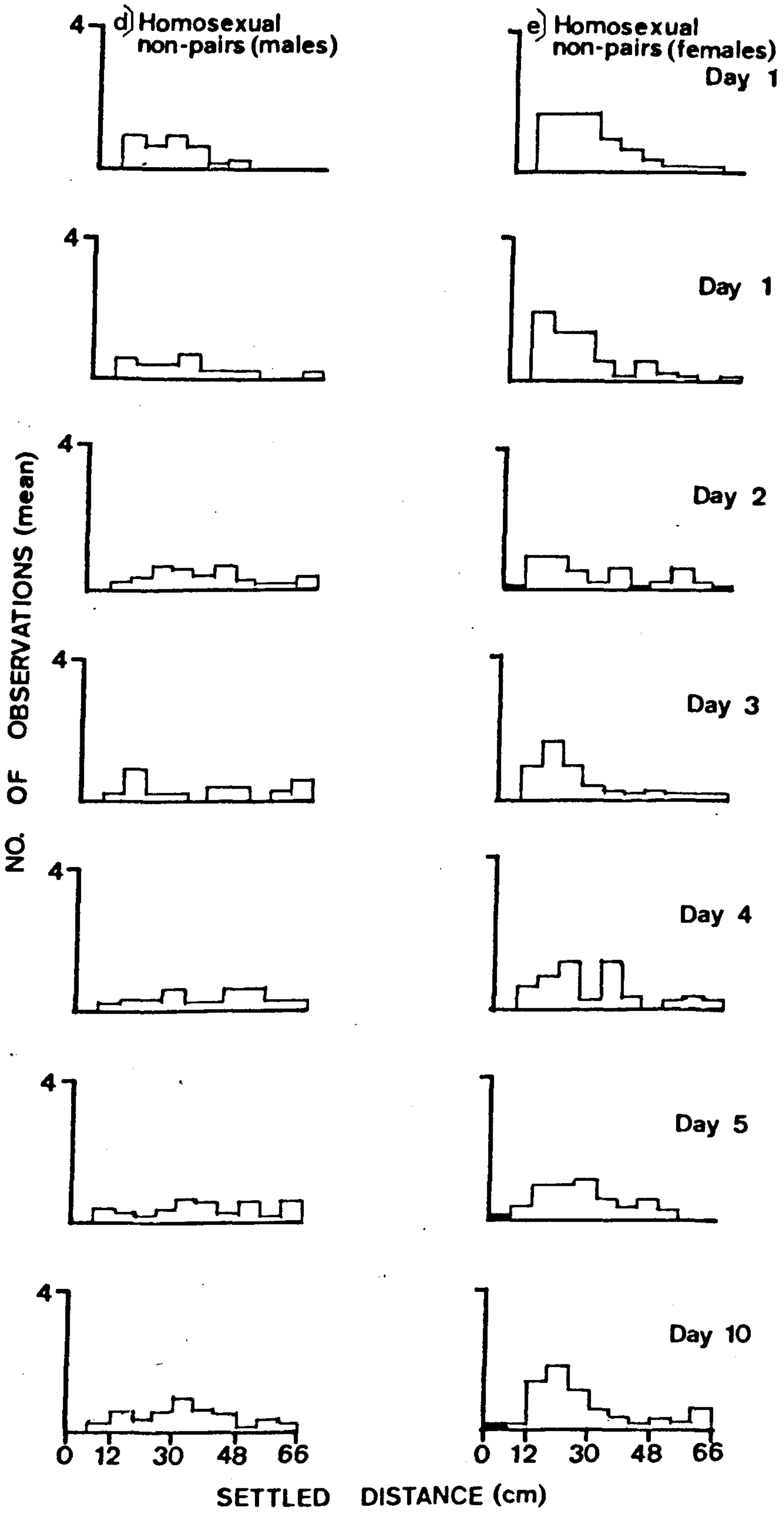


Fig. 6. The settled distance between individuals of different pairs with the amount of clumping on each day shown in black.

TABLE 5 Number of times individuals were adjacent on the same perch (mean no. per pair per day)

	Days							
	1	1b	2	3	4	5	10	Total
Isolated pairs	13.3	15.5	14.3	13.3	14.5	15.4	13.7	156.8
Group pairs	12.4	14.0	12.1	17.6	15.3	15.9	17.2	104.6
Heterosexual non-pairs	7.1	6.7	5.1	7.4	5.3	4.8	5.5	84.8
Homosexual non-pairs ♂-♂	5.1	4.1	4.8	4.6	4.3	4.6	5.9	33.0
♀-♀	8.3	7.0	5.9	5.7	5.1	6.3	7.0	45.3

TABLE 6 Activity expressed as mean scores per pair per day

	Activity		1	1b	2	3	4	5	10	Total
Isolated pairs	Sitting alert	M	16.3	21.2	22.4	21.3	21.1	19.0	19.0	140.3
		F	20.4	20.0	22.7	20.3	19.6	19.2	16.9	139.1
	Sitting drowsily	M	8.5	5.3	4.7	4.7	5.3	6.6	7.8	42.9
		F	6.5	7.1	4.0	4.2	5.2	5.6	6.6	39.2
	Feeding	M	5.3	2.4	2.9	4.0	3.8	4.1	4.3	26.8
		F	3.2	2.9	3.0	5.3	5.3	5.4	6.6	31.7
Group pairs	Sitting alert	M	24.4	18.3	19.8	15.4	16.5	18.2	15.1	127.7
		F	27.0	19.4	18.5	15.8	16.7	16.4	12.4	126.2
	Sitting drowsily	M	1.4	7.9	5.5	10.9	8.7	7.8	10.8	53.0
		F	2.1	8.3	7.1	11.6	9.0	8.5	12.7	59.3
	Feeding	M	4.4	4.0	4.8	3.1	4.8	4.1	4.1	29.3
		F	0.9	2.2	4.4	2.5	4.7	5.1	4.8	24.6

birds, the distance maintained between non-pairs tended to increase with time (Day 1 $<$ Day 10, $p < 0.01$, K-ST). The overall settled distance was much greater than that between group pairs ($p < 0.001$, K-ST) and this became apparent from Day 1b onwards.

The number of times heterosexual non-pairs were adjacent on the same perch (Table 5) were much fewer than for the group pairs ($p < 0.001$, MWU) and, in this case, the difference was even significant on Day 1 ($p < 0.01$, MWU). Thus non-pairs showed signs of avoidance as early as the first watch.

Homosexual non-pairs (Fig. 6, columns (d) & (e)). The settled distance between both males and females increased with time such that the distance recorded for Day 10 is much greater than that for Day 1 ($p < 0.001$, K-ST). The settled distance totalled for all watches was much higher than in the group pairs ($p < 0.001$, K-ST, for both sexes) and they were adjacent on the perches (Table 5) on far fewer occasions ($p < 0.01$, MWU). Signs of avoidance were again evident on Day 1 in that the number of times birds were adjacent in this watch was fewer than for group pairs, male-male, $p < 0.01$; female-female, $p < 0.05$, MWU).

Discussion of clumping and settled distance

(i) Clumping

Clumping is a variable activity that seems to be dependent on low activity levels and a lack of external stimuli which is commonly found during resting periods. Clumping was exclusively between mates, with one or two very rare exceptions, and it was during this body contact that the majority of the prolonged allo-preening bouts took place. It is interesting that more clumping was seen between group pairs when the levels of activity and external stimulation might be expected to be greater than in isolation. Evans (1970) found that in the Avadavat clumping was enhanced when groups of birds were transferred to new cages as in this situation fear, brought about by the strange surroundings, inhibited activity and promoted sitting drowsily and the accompanying bouts of clumping. It would appear from these results that this 'fear' response does not occur readily in the Zebra Finch at least in the group situation, two males and two females, that was considered. The clumping that did appear in the groups was actively sought by individuals and requires a different explanation. Kunkel (1974) surveyed tropical bird species and concluded that those with prolonged pair bonds engaged in clumping and allopreening as a means of maintaining the bond. Certainly, in the group situation one would expect the bond to be under a greater threat of disruption than in isolation and this could explain the observed increase in contact behaviour.

(ii) Settled distance

As well as more clumping between group pairs, their settled distance showed a similar reduction compared to that of the isolated pairs which suggests that close proximity is involved in maintenance of the pair bond. One possible criticism which must be remembered, however, is that there was a higher density of birds in the group situation as the cage size was kept constant. Yet even in the isolated pairs there was a reduction in settled distance and Zann (1972) found that proximity between pair members was important throughout the year in the Poephila group. In his birds mates were seldom seen more than 1 to 2 metres apart.

Fear tends to reduce individual distances, it was noticeable that disturbances outside the cages led to mates drawing closer together, and perhaps in the groups the presence of a potentially aggressive non-mate resulted in the differences observed. The distance maintained between non-mates, both heterosexual and homosexual, was much greater than that between group pairs which supports the suggestion made earlier that aggression leads to the establishment of a defended 'mate territory' around the pair.

Methods of assessing the identity of pairs within a group of Barbets were compared by Fernald (1973) and he came to the conclusion that the average distance between birds was not an accurate measure. He found that the number of times two individuals were adjacent was much better but, in the present study, this measure merely supported the findings for settled distance.

Thus the individual distance of a particular Zebra Finch (i.e., that distance within which other conspecifics are attacked or avoided; Hediger, 1950), is not a constant entity. Dunbar and Crook (1975) have demonstrated how, in Quelea, this distance may vary with the activity engaged in and it seems from this study that the identity of an encroaching bird will affect the individual's response. The distance over which an attack may be launched, or fleeing result, can be affected by the sex of, or familiarity with, an approaching individual and, most clearly, by the existence of a pair bond with that particular bird.

Activity and synchrony of behaviour

(i) Activity (Table 6)

Isolated pairs The pairs were active for the majority of each watch and showed no tendency to increase the amounts of sitting drowsily and/or feeding as the experiment proceeded. The amount of activity shown by each sex is similar.

Group pairs In general the activity of birds in the group situation was similar to that in isolation but the amount of sitting drowsily showed a significant increase by Day 10 (Day 1< Day 10, $p < 0.005$, WMP). In addition, the total amount of sitting drowsily by pairs in the groups was greater than by pairs in isolation ($p < 0.005$, MWU). This is associated with the increase in the amount of contact (clumping) behaviour seen in the group pairs which was noted earlier.

(ii) Synchrony (Table 7)

Isolated pairs The greatest synchrony was evident during active periods; when a bird was sitting drowsily or feeding synchrony scores were frequently low. There was no tendency for members of a pair to become more synchronous with time.

Group pairs The highest synchrony scores for all activities were recorded for group pairs. Synchronous sitting alert was most evident on day 1 and showed a significant decline by Day 10 ($p < 0.05$, WMP). Sitting drowsily and feeding, on the other hand, showed an increase such that scores in excess of those for isolated pairs were obtained by Day 2. A comparison of the amounts of synchrony on Day 10 reveals that group pairs were significantly higher in all activities than the isolated pairs (sitting alert, $p < 0.025$, sitting drowsily, $p < 0.01$, feeding, $p < 0.025$; MWU).

The greatest difference was over synchrony of feeding bouts in which relatively high scores were obtained for group pairs from Day 3 on. It was noticeable that pairs tended to feed on their own and members of the other pair were vigorously driven off if they attempted to approach a feeding pair.

Heterosexual non-pairs Synchrony of all three activities was less than for group pairs ($p < 0.05$, MWU, in each case) and, apart

TABLE 7 Mean numbers of occasions when two individuals were engaged in the same activity

Synchrony

Isolated pairs	Sitting alert		14.5	17.0	17.5	16.0	17.0	16.5	15.5
	Sitting drowsily		11.0	15.0	7.5	5.0	8.0	9.0	10.5
	Feeding		5.5	0.5	4.5	5.0	4.0	6.5	6.5
Group pairs	Sitting alert		20.0	17.0	17.5	20.0	19.0	18.0	15.5
	Sitting drowsily		2.5	13.0	17.0	15.0	16.0	16.5	16.5
	Feeding		3.5	4.5	9.5	16.5	16.0	12.5	12.0
Hetero-sexual pairs	Sitting alert		19.0	14.0	12.0	15.0	11.0	11.5	9.0
	Sitting drowsily		1.5	9.0	5.5	12.0	7.5	7.5	9.0
	Feeding		5.0	3.5	1.5	2.0	6.5	5.0	8.0
Homo-sexual pairs	Sitting alert	M	16.5	11.5	13.5	15.0	13.5	13.0	12.0
		F	21.5	17.0	11.5	16.0	11.0	9.0	8.5
	Sitting drowsily	M	10.0	10.0	7.5	13.0	6.5	7.0	7.0
		F	3.0	10.5	3.0	15.0	7.5	8.0	9.5
	Feeding	M	4.0	2.5	2.0	2.0	4.0	3.5	4.5
		F	3.0	5.5	1.5	2.0	5.0	4.5	7.0

from high scores for sitting alert on Day 1 (when all 4 birds were especially active), scores were low in all watches. Synchrony of feeding bouts remained at a low level throughout.

Homosexual non-pairs These are based on a sample size of 7 only in each case and show similar trends to the scores for heterosexual non-pairs. Interestingly, feeding attained its lowest scores of any category.

Discussion of activity and synchrony

(i) Activity

The activity scores tell us little of relevance to the pair formation process. The birds in both situation were active for the majority of each watch and this was to be expected from behaviour of males in morning sessions (see Ollason and Slater, 1972). The major difference between groups and isolation comes in the amount of sitting drowsily. There was more in the groups and this is largely due to the greater amounts of clumping between group pairs which suggests that the clumping may have been actively sought rather than merely a consequence of rest periods occurring in the morning.

(ii) Synchrony

The isolated pairs showed most synchrony whilst active although not when engaged in feeding bouts. In fact it often appeared that mates were taking turns in going down to feed, the non-feeding bird remained on the perch and flew down to the bowl only when the mate returned. The group pairs were synchronous in all three measures and, in marked contrast to the isolated pairs, this included feeding bouts after Day 2. Each pair took a turn in visiting the feeding bowl and it was only on Day 10 that cases of all four birds feeding simultaneously were observed. In large stock cages flocks of birds tend to feed as one group and this could indicate that the separation of the pairs during the early stages of pair formation was beginning to break down by the end. This could result from greater familiarity with the non-mates and the waning of aggressive tendencies, in other words they are beginning to establish social bonds that are common in established flocks of Zebra Finches.

Synchronised behaviour is thought to be largely due to two responses (Crook, 1961), the following response and social facilitation. The latter refers to the immediate copying of a behavioural act by another conspecific. Birke (1974) demonstrated that familiarity with an individual enhanced the effect of that individual in eliciting synchronous responses. It seems likely that pair formation further enhances this tendency, the mate becoming the most effective model for both the following response and social facilitation. This means that the mates, after pair formation, maintain a close proximity and engage in bouts of activity or rest at similar times. It seems important to the maintenance of the bond that they should be in close contact at all times, with the possible exception of periods of incubation when the mates are forced to separate.

Changes in dominance

It is difficult to satisfactorily represent dominance in tabular form and this will not be attempted here. A measure could be taken from the results in terms of numbers of wins and losses during supplanting attacks. This was carried out and the results are presented below as short case histories for each group studied. Dominance was ascribed to a bird, in any watch, which built up a clear excess of wins over losses (+60% of all attacks). In cases in which the subordinate bird managed no wins, dominance was only designated if more than 5 attacks had been recorded in that watch. For the sake of the discussion, males are labelled A and B, their respective mates, C and D.

Group 1

In this group male A and female C emerged as the dominant pair on Day 2. Male B was dominant over both A and C on Day 1 but on Day 2 a clear reversal took place and B became subordinate to both individuals. Female C was particularly aggressive towards B and this may have facilitated A's improvement. Day 2 also saw changes in aggression directed at female D; A renewed his early aggression and C reversed D's previous dominance.

Allopreening first developed between AC on days 1b and 2 suggesting that the reversal occurred at or around the time the pair were becoming established.

Group 2

This group provided a clear example of the interaction between members of a pair affecting their dominance over conspecifics. On Day 2 AC emerged as the dominant pair. B was initially exceedingly aggressive towards A and recorded over 600 successful supplanting attacks on Days 1 and 1b. However, on Day 2 the reversal occurred and this was coupled with extreme aggression towards B by female C (over 200 attacks). A also became aggressive towards D for the first time and, though B was dominant on some of the later days, he never again assumed the same sort of preeminence seen on the first day.

Clumping between AC was first noted on Day 2 and became increasingly more evident.

Group 3

No dominant pair emerged in this group but it is interesting to chart the progress of male A. On Days 1 and 2 A was heavily defeated by B in over 900 encounters and then, on Day 3 he began to show aggression for the first time and by Day 10, as B's aggression appeared to wane, he assumed dominance in the exchanges. A's aggression towards female D also appeared on Day 3.

Allopreening by AC appeared for the first time on Day 3 whereas BD were allopreening as early as Day 1b.

Group 4

On Day 3 BD became the dominant pair. There were no excessive scores but A's initial dominance disappeared in this watch and B also became aggressive towards his non-mate C. At the same time female D began supplanting C in quantity.

Clumping and allopreening developed in both pairs on Day 1b.

Group 5

AC were the dominant pair. A dominated over male B throughout the watches and female D in all but the last watch where D won most of the exchanges. Female C, on the other hand, was initially subordinate to D but assumed, and retained, dominance from Day 1b and became aggressive towards B on Day 3.

D's aggression towards male A on Day 10 is difficult to explain in the light of pair establishment.

Group 6

A was the most dominant bird on most occasions, successfully defeating both B and D. Female D became aggressive towards A on day 4 but this was accompanied by renewed aggression towards her own mate, male B, and thus is difficult to explain.

Group 7

The dominant pair were AC and this was clearly evident by Day 2. A's aggression towards both B and D emerged and C reasserted herself over female D. A's aggression remained high in subsequent watches but that between the females died out rapidly.

An overall comparison of the results reveals certain trends or tendencies. Where clear reversals of initial dominance occurred this was invariably during the first few watches, Days 1b, 2, and 3. Clumping between pair members first became evident at this stage and it seems likely that these changes in aggression are related to the establishment of the pair identity, i.e. the formation of the pair.

Discussion of changes in dominance

This section was included because measures of overall aggressive success, presented earlier, tended to mask individual fluctuations of dominance observed in encounters between hetero- and homosexual non-mates during different watches. In addition, these changes in success tended to cancel one another out giving the impression that aggression between individuals did not decline at all during the course of the experiment.

Short-term fluctuations in Zebra Finch dominance were reported by Caryl (1975) in male-male aggression resulting from the sight of an inaccessible female. Changes were often abrupt and Caryl suggested they were due to variations in the tolerance of a rival from moment to moment and because of this individual variation Caryl was unable to make any conclusions about group dominance hierarchies. Such fluctuations in aggression are found in many passerines (Hinde, 1966) and work on several species has shown that dominance is characteristically fluid and is dependent on previous experience, hormonal states, individual differences and many other independent variables (e.g. Tsuneki, 1966, Kirkawa, 1968, and Williams et al, 1972). Tsuneki concluded that dominance relations in the Java Sparrow indicated, at the most, the state of affairs on a particular day. An additional variable that has emerged from Dunbar and Crook's (1975) study of *Quelea* flocks is that the activity engaged in may affect aggression. They found that dominance in a feeding situation was not necessarily similar to dominance over nest sites or nesting materials.

There has been little to suggest how such short-term variations may be controlled in birds. Perhaps Delius (1973) has provided a possible explanation in his work on electrical stimulation of the brains of juvenile gulls. He found many loci which elicited an aggressive response but he also located places where stimulation caused changes in mood lasting as much as 15 minutes. He postulated that these might be controlled by "liquor hormones".

Whatever the controlling mechanism it is clear that sudden changes in dominance occurred during the experiment, both in male and female aggression. These marked changes tended to occur on or around Day 2 when other behaviour, such as clumping and allopreening, tended to indicate that preferences had been established. It thus seems likely that they are due to the formation of pairs and evidence from the 'incompatible' pairs (see below) supports this. Individuals which in the previous watch were totally subordinate or uninvolved in encounters were quite suddenly repulsing challenges and in many cases actually reversing the direction of dominance altogether.

The "Incompatible" pairs

This section reviews the behaviour of those birds which did not satisfy the criterion for pair formation (i.e., they did not show exclusive clumping with their partner). They include one pair form the isolated situation in which no clumping was recorded and aggression persisted, and three groups in which bonds failed to crystallize clearly.

The isolated situation (Table 8)

No clumping was observed in any watch and the female behaved aggressively towards the male on Days 3 and 4 which differed markedly from the other isolated pairs. Undirected singing by the male developed normally, but courtship was unusually high on Days 4 and 5. Allopreening was rare, although the settled distance was not unduly increased.

Thus the main difference from the 'true' isolated pairs lies in the high female aggression and the lack of contact behaviour. Such apparent rejection of a male had also been observed in some preliminary studies and the particular stimulus for female supplanting attacks, in all cases, appears to be male undirected song. It was particularly noticeable that on Days 3 and 4 the female would launch an attack as soon as the male gave the introductory notes even before the full song was heard. After Day 4, behaviour appeared more typical though there was still an absence of contact behaviour.

The group situation (Table 9)

The scores for the three 'aberrant' groups are presented with the behaviour between all possible pairs shown. The average scores for the more typical group pairs are shown in parenthesis.

A complex situation arose in all three groups largely due to both males, here designated A and B, showing a preference for the same female, C. This is clearly evident in the courtship behaviour where bouts were directed towards female C by both males (note that the amount of total courtship by each male is comparable to that for the typical pairs).

TABLE 8 The 'incompatible' pair(isolated pairs average scores shown in parenthesis)

	1	1b	2	3	4	5	10
CLUMPING							
	0(0.2)	0(1.1)	0(0.1)	0(0.3)	0(0.3)	0(0.7)	0(1.2)
COURTSHIP							
	4(12.4)	2(1.7)	3(0.8)	1(1.3)	7(2.1)	6(1.5)	3(0.9)
UNDIRECTED SONG							
	0(2.4)	0(3.0)	3(11.1)	15(13.9)	55(33.8)	33(13.9)	33(15.8)
BEAK FENCING							
Male	0(1.0)	0(0.1)	0	0	0	0	0
Female	2(0.8)	0(0.2)	0	2	2	0	0
SUPPLANTING ATTACKS							
Male	0(0.5)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Female	0(0.6)	0(2.3)	0(0)	28(0)	21(0)	0(0)	0(0)
ALLOPREENING							
Male	0(0.6)	1(3.6)	0(1.2)	0(2.3)	0(2.3)	0(1.6)	0(1.6)
Female	0(1.6	1(5.1)	3(1.6)	1(0.8)	0(1.3)	0(2.8)	0(3.4)
SETTLED DISTANCE (Average)							
	22.0 (32.5)	41.1 (27.0)	25.5 (30.9)	35.3 (28.4)	22.4 (25.3)	28.0 (26.3)	27.3 (22.7)

TABLE 9 The 'incompatible' groups

CLUMPING	AC	AD	BC	BD	AB	CD
8	0	0	15	0	0	0
9	16	0	39	3	0	0
10	26	1	11	6	0	0
$\bar{X}$	14 (21.4)	0.3 (0.2)	21.7	3.0	0(0)	0(0)
COURTSHIP						
8	12	1	11	1	28	0
9	4	0	40	0	0	0
10	17	0	8	0	0	0
$\bar{X}$	11 (23.9)	0.3 (2.3)	19.7	0.3	9.3(0.2)	0(0)
SUPPLANTING ATTACKS - females scores in brackets						
8	4(2)	85(0)	38(35)	75(0)	75(59)	78(13)
9	61(32)	117(14)	27(3)	19(11)	538(478)	298(221)
10	6(0)	141(1)	6(4)	45(1)	373(40)	59(2)
$\bar{X}$	23.7 (11.9)	114.3 (95.1)	23.7	46.3	328.7 (432)	145 (127.2)
ALLOPREENING						
8	0	0	24	0	0	0
9	6	0	55	32	0	6
10	84	5	22	3	1	9
$\bar{X}$	30 (37.7)	1.7 (3.7)	33.7	11.7	0.3 (1.4)	5.0 (4.4)
SETTLED DISTANCE (Average)						
8	22.4	32.1	16.3	32.1	20.5	32.5
9	13.8	45.1	9.2	21.4	26.9	20.5

/Continued

Table 9 (continued)

10	7.2	31.9	12.8	22.3	12.9	13.1
$\bar{X}$	14.5 (14.3)	36.4 (30.7)	12.8	25.3	20.1 (32.2)	22.0 (24.1)

In groups 9 and 10 both males clumped with C, often simultaneously, and it was amusing to note beak-fencing encounters taking place above the intervening female's back. In group 8, C showed a distinct preference for B and rejected any of male A's allopreening attempts. In fact it was female C who made the first advances to male B on Day 2 by approaching and allopreening him.

Both males showed aggression towards the non-preferred female and were clearly dominant over her in all cases. Aggression with the preferred female was also quite high in groups 8 and 9 in which the female, C, was dominant in encounters with both males A and B. This high aggression was not reflected in the amount of clumping with either of the males. Male-male aggression was high and in each group one male was usually clearly dominant in the early watches. The dominance by one male did not apparently affect his success with female C although he courted her on more occasions in groups 9 and 10. The amount of female-female aggression was not particularly high with the possible exception of group 9.

Allopreening showed a similar trend to aggression but in group 9 a considerable amount was noted between B and D. This culminated on Day 10 in clumping and it appeared that at this, the eleventh hour, they had formed some kind of pair for in this watch female D suddenly, and quite dramatically, assumed complete dominance over female C supplanting her on 220 occasions! A similar reversal in dominance occurred accompanied by clumping in group 8. Here, male A was dominant on Day 1b and attacked B so successfully that the latter was forced to spend the complete watch on the floor of the cage. However, on Day 2, C made advances towards male B and allopreened him whilst he was on the floor. Within the same watch, B became aggressive towards male A and was able to retain a position on the perches for the first time. Thereafter clumping occurred between B and C and B remained dominant over A for the remaining watches.

The settled distances are similar to those for group pairs but it was interesting to note that the non-preferred female was driven off by both males. Male-male distances are somewhat reduced but this was probably due to the fact that they were both attracted to the same site in the cage (i.e., female C).

In general, therefore, the scores are similar to those for the typical group pairs but the situation is complicated by one female capturing the attention of both of the males with the resulting exclusion of the non-preferred female.

Discussion of the incompatible pairs

(i) The isolated pair

The one incompatible pair from the isolated situation continued aggressive encounters and were never seen to clump successfully. The female was the aggressor and her attacks seemed to be triggered by the undirected singing of the male which increased normally during the experiment. The past history of individual birds was not known and it is possible that this female had formed a bond prior to the experiment and was rejecting the male in favour of the former mate. Alternatively, her rejection could have been due to selection and her 'dislike' of this particular male. One thing that is suggested by the results is that the increase in male undirected song as the experiment proceed was not dependent on the formation of a normal pair bond.

(ii) The groups

In these cases two males seemed to favour the same female, both courted and clumped with her whenever possible. The female invariably showed aggression towards one of the males but this did not appear to deter him. The non-preferred female, on the other hand, was treated aggressively by both males and there was no tendency for the subordinate male to pair with her. For the first time clumping in excess of two individuals was seen, both males clumped with the one female at the same time. There was thus evidence of both males and females executing a preference for a particular individual. Previously, Immelmann (1962) had suggested that only the female was responsible for mate selection yet in this study female aggression did not appear to influence male choice though admittedly that choice was limited. In addition, the non-preferred female often approached one of the males but she was either ignored or attacked.

Caryl (1970) reported four or five cases of atypical pairing in Zebra Finch triad situations involving one male and two females. The male in these cases behaved bigamously and seemed unable to choose between the two females. Caryl chose to ignore these results and, to my knowledge, this is the first time incompatibility in the Zebra Finch has been described. There are other instances of atypical behaviour in the literature. For example, Goodwin (1960) cited the case of a female estrildid rejecting the advances of a male and demonstrating a preference for a second male who in turn rejected her. Zann (1972) found that female _Poephila_ spp. showed preferences for particular males even when they ignored their attentions.

Research has suggested that the female is involved in mate selection as selection pressures against her are thought by some authors to be greater if she were to make a wrong choice (Orians, 1969) as she then must incubate and rear the young alone. In birds with prolonged bonds, however, Hinde (1970) has suggested that the pressures are probably more equal and hence males would be involved in mate selection as well. The results suggest this is likely but it is important to remember that the females used in the experiments described were different colour mutants. Both Immelmann (1972) and Walters (1973) have shown that males imprint on the colour of their parents whereas females do not. Thus the males may have rejected the non-preferred female on the basis of her plumage colour alone.

(iii) Dominance

Dominance relationships within the incompatible groups were interesting. Male-male aggression was high and one male was usually clearly dominant over the other. This did not apparently affect his success with the female as far as time spent clumping was concerned but he was able to court her more frequently. It is possible that the female was uninterested in both males and, as a last resort, allowed both to clump with her.

The cases of reversal of dominance were described at length in the results and these clearly support the suggestion that the establishment of some sort of bond with an individual can markedly affect aggressive levels shown by both males and females at any one time.

In conclusion, there is some evidence to suggest that both male and female selection may occur during the pair formation of Zebra Finches. Even in cases where the female rejected a male repeatedly he still showed a distinct preference for her. It is possible, however, that this male preference could have been due to plumage colour differences between the females.

GENERAL DISCUSSION

The aim of these first two experiments was to discover what changes in behaviour were associated with pair formation and the temporal sequence involved in the establishment of a pair bond. The results indicate that the situation is not as simple and clear cut as might have been imagined.

There is an initial burst of activity on introduction which, in the group situation, revolves around selection of mates and during which preferences for individuals are shown. This is a relatively short period and is heralded by high levels of male-male rivalry. Once this mate selection period is concluded behaviour that is important in the maintenance of the pair relationship appears including courtship and copulation, clumping and allopreening, proximity maintenance and aggressive defence of the mate. Activities promoting proximity occur only between pair members and will presumably continue for the duration of the particular pair bond. In reference to prolonged pair bonds Kunkel (1974) termed such activities 'pair maintenance behaviour'. Thus there is a short period of mate selection followed by active maintenance of the pairs that emerge.

The term pair formation as such can only be accurately used to describe the first period of mate selection as, to all intents and purposes, once this is concluded the pair identity is formed and the pair maintenance period ensues. However, one could ask if this is all that occurs. Is the bond complete after what amounts to in many cases a mere 30 minutes, or does familiarity with the mate increase during the long maintenance period and the bond become more secure and resistent to dissolution? Newton (1972) writes that in the carduelines it takes a matter of days, or weeks for the pair relationship to develop; Frickson (1973) postulated that it might take as long as two or more breeding cycles in the Ring Dove before the bond became resistent to separation; in the budgerigar Brockway (1964) correlated the length of time the members of a pair were together with the ease with which they would re-pair on separation. Thus there could be two features of the pairing process in the Zebra Finch - mate selection (= pair formation) followed by pair maintenance leading, at some vague, unspecified time in the future, to a relationship that is highly resistent to separation and disruption.

Lack (1940) wrote that though pair formation might differ, even between members of the same family, it was possible that bond formation did not in that its salient features consisted of familiarization, individual recognition and changes in responses to mates and non-mates. In other words pair formation (mate selection) will vary, for example where it takes place, a nest, territory or flock may be involved, but the remaining processes could be similar. Crook (1962) has clearly demonstrated the variations in pair formation types of the Ploceidae. Thus the pair maintenance activities involved in the pair bonds of different species may be similar although one could expect that in birds with prolonged pair bonds such activities will be accentuated.

When is pair formation complete? Immelmann (1962) suggested it was, in Zebra Finches, when the pair were first seen to clump. Butterfield (1969) thought allopreening was most important and Caryl (1976) picked out maintenance of close proximity and male-male aggression. Such behavioural parameters are quite useful, in individual cases, but is it in fact necessary to select out a particular behavioural trait? Mate selection is complete once two birds show a preference for one another and during this period the birds have quickly learned each others identity. This may take anything from 30 minutes to several days, the incompatible groups show that, if choice is limited, it may take considerably longer and may not occur at all. From then on this tentative relationship is continuously maintained and it remains to be seen how resistent to separation the 'bond' then becomes. What reinforcement is necessary to prevent mates re-pairing once they have been separated? Such questions are considered in later sections of this thesis.

The differences noted between pair formation in the individual and group situations can now be considered in the light of the arguments outlined above. The main differences involved an increase in the amount of pair maintenance behaviour in the group pairs; there were greater amounts of contact behaviour, closer proximity and defence of the mate was intense. It is possible therefore that pairs formed in the individual situation were weaker than those formed in the groups and would have been less resistent to disruption had a choice of mate been subsequently presented. Craig et al (1965) examined domestic hens and compared the learning of dominance relationships in isolated pairs with that in groups. They found that though dominance relationships learned in groups could be transferred intact to the individual pairs situation the converse was not possible. Thus the individual pairs might have proved weaker in the present study in that no competition was provided and there was less time spent in maintenance of the pair bond.

This first examination of the pair formation of the Zebra Finch tells us little as to the processes underlying the establishment of bonds. There must be a rapid period of learning during which the mates come to recognise one another and to adjust their behaviour appropriately. Subsequently mutual displays will stimulate the two individuals and these presumably act as reinforcers. In isolated pairs, where less reinforcement is necessary, it is possible that bonds may be weaker. Butterfield (1970) reported that the sight of the mate was reinforcing, though she was not able to establish this in females. Longer term hormonal changes are also probably involved. Chains of behavioural events culminating in nest building and ovulation have been shown in a number of species to be controlled by varying levels of different hormones (e.g. Lehrman et al, 1961, Lehrman, 1964, 1965). It is probable that similar changes occur in the Zebra Finch. However, such changes cannot explain the rapid individual recognition of the potential mate which is common to most pair formation situations. It is this feature of the process which may well prove to be the 'bond' itself. What is it that makes one individual attractive in the face of numerous others? Stettner et al (1971) have shown that, at least in the Bob-white Quail, the bond is not dependent on the males territory or nest site so one can assume that the fidelity observed is to the individual rather than the environment in which he or she is situated, though, of course the latter may affect mate selection.

Thus the terms 'pair formation' and 'pair bond' emerge rather shakily. Pair formation can be equated with the mate selection period although further changes in the strength of the bond may still occur. It is thus of an indefinite length but would appear to be at its simplest interpretation usually rapid and quickly concluded. The bond itself requires continual expenditure of energy to maintain it and relies on a number of different activities the amount of which will depend on the particular situation of the pair concerned. It remains to be seen whether the bond becomes more resistent to disruption as it is established or whether it dissolves once the pair maintenance activities can no longer be performed.

SECTION 5. CHANGES IN COURTSHIP AS A RESULT OF PAIR FORMATION

Introduction

The experimental work described in the last section raised many questions concerning the behaviour of Zebra Finches during the pair formation period. One of the most interesting, and the one which has received the most attention in the literature, is that concerning changes in courtship behaviour between mates. Morris (1954) noted variations in courting Zebra Finches. For example, he found that components of the displays might be omitted or given at different intensities and frequencies. A similar situation was reported by Hinde (1953) in the Chaffinch. Morris proposed that the difference between courtship responses of individuals were due to differences in underlying motivational states, possibly arising from the pairing process. Therefore, it should prove interesting to compare courtship behaviour between paired Zebra Finches with that occurring between unpaired birds.

In addition to changes in responses between members of a pair, there may also be changes in reactions of mated birds to the appearance of unmated conspecifics (i.e., potential mates). These elicit a curious reaction in many estrildids. There are numerous examples of apparent promiscuous behaviour by males on the introduction of "novel" females (e.g., in the waxbills, Kunkel, 1967; the Spice Finch, Moynihan and Hall, 1954; the Poephila spp., Zann, 1972). Such extra-pair sexual activity often involved attempted, and sometimes successful, "rapes" by the males and similar behaviour has been reported in the Zebra Finch by both Morris (l.c.) and Caryl (1976).

The experimental work described in this section revolves around two potential changes in behaviour as a consequence of pair formation, (a) changes in the courtship directed at the mate, and (b) changes in courtship towards a non-mate.

Methods

Procedure

During the experiments a male and a female were separated in a two compartment cage for a period lasting 30 minutes. The wooden partition between them, which kept them in visual isolation, was then removed. The birds were still in auditory contact during the separation time. Birds were transported from the stock cages to the experimental room as in the previous experiments (see Section 4).

Experiment 5.1 Changes in courtship associated with the formation of pair bonds

In this experiment the initial courtship reaction of a male and female was tested and then compared with that between the same birds after they had been together for 7 days. 12 pairs were used and care was taken to ensure that the males and females concerned in the respective pairings had never met before. After the separation period (30 minutes) they were introduced for the first time and their behaviour analysed for 20 minutes. This first introduction is referred to as Day 0 (zero) in the discussion. Each pair was then housed in individual stock cages for seven days during which time they could establish pair bonds. They were then reintroduced and exactly the same procedure was followed as on Day 0. This second introduction was termed Day 7.

Experiment 5.2 A comparison of responses of birds to their mates and to 'strangers'

10 pairs of birds were used which had been paired for periods

in excess of one month in individual stock cages. They were considered to be 'established' pairs. The same apparatus was used as in Experiment 5.1 and the established pairs were tested first. They were then rehoused together for a period of one week after which the male of each pair was introduced to a strange non-mate female. After rehousing with the mate for a further seven days the female was tested with a non-mate male.

Behavioural measures

Recordings were taken live and also from videotape recordings. The VTR equipment used was described in Section 4.

Measures taken were,

(a) Courtship - The number of song bouts and the number of song phrases in each bout were noted live. The duration of singing and the latency of the male's response to the female were taken from the recordings. The latency was the time from the removal of the partition to the onset of the first bout of courtship song.

(b) The Courtship dance - The distance from the female that the male began his courtship song was measured and also the number of pivots involved in his dance. The proximity during courtship was assessed in terms of the minimum distance between the male and female during the actual bout.

(c) Beak wiping - The number of beak wipes was counted, both those occurring during courtship bouts and those outside of the courtship situation. In each case it was possible to distinguish between three types of action. Full wipes (F) in which the beak was lowered below the level of the perch in a functional movement, a touch (T), in which the bill was lowered but only touched against the top of the perch, and no contact (NC) which, as its name applies, involves a bowing movement without the bill making contact with the perch.

(d) Copulation and copulation attempts - It was possible to make a distinction between full copulation, involving apparent cloacal contact and mounting of the female, in which the male was able to "climb" on to the female's back but proceeded no further, and attempts to mount, in which the male "leapt" for the female but made no, or only very brief, physical contact.

(e) Aggression - The frequency of any aggressive acts and the identity of the initiator was recorded in all watches.

(f) Contact behaviour - An estimate of the amount of clumping was made by recording behaviour as either clumping or not clumping at 60 second intervals. Allopreening bouts were also noted.

Results and Discussions

(a) Courtship song

Experiment 5.1 (Fig. 7 and Table 10)

Levels of courtship in birds which were introduced to one another for the first time (Day 0) were high, and comparable to those seen in the pair formation experiments. The amount of singing by the males declined rapidly as is shown in Fig. 7. There was also a high level of courtship on reintroduction of these birds on Day 7 (after pair formation) but there were significantly fewer courtship bouts, fewer song phrases and shorter durations of displays than on the first introduction ($p < 0.01$, WMP, in all cases).

The speed or latency of the male's response on introduction is shown in Table 10 and this was significantly shorter after pairing than before it ($p < 0.01$, WMP). Thus though the males sang less on Day 7 they began their singing more quickly once the partition was removed. In three pairs no courtship at all was recorded on

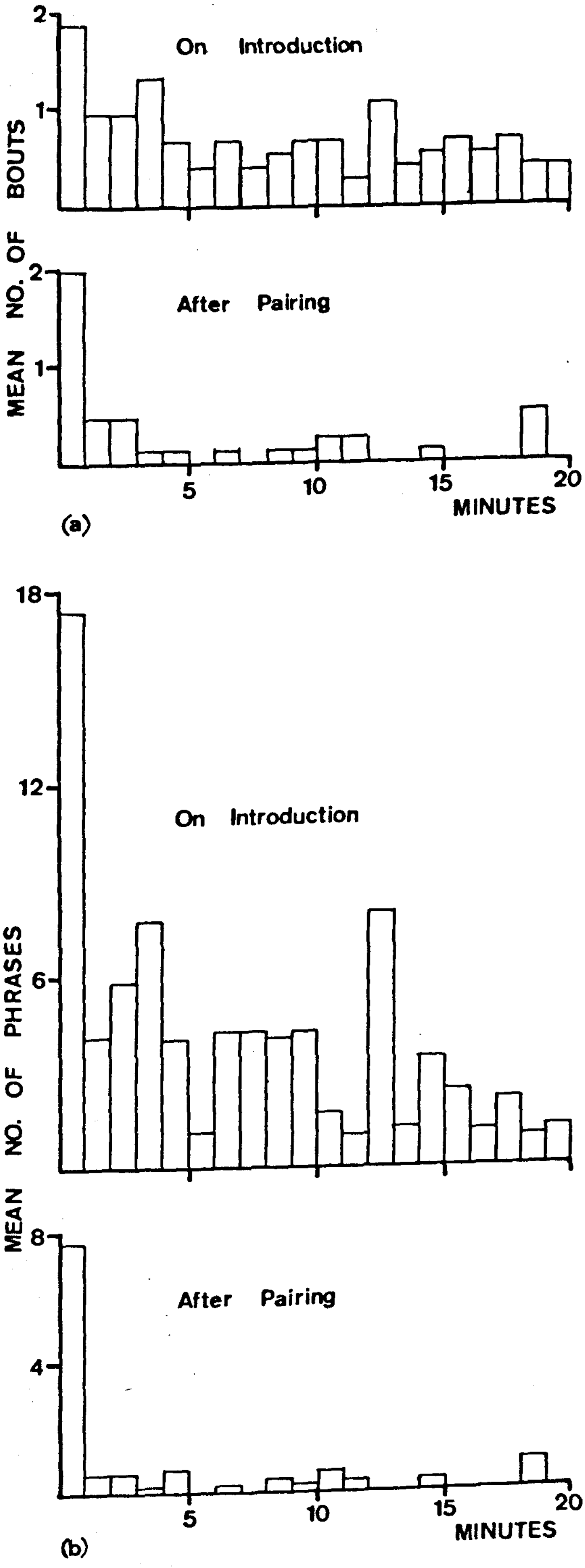


Fig. 7. The use of courtship song by males on introduction to a female and then on reintroduction after pairing with that female. (a) No. of song bouts. (b) No. of song phrases.

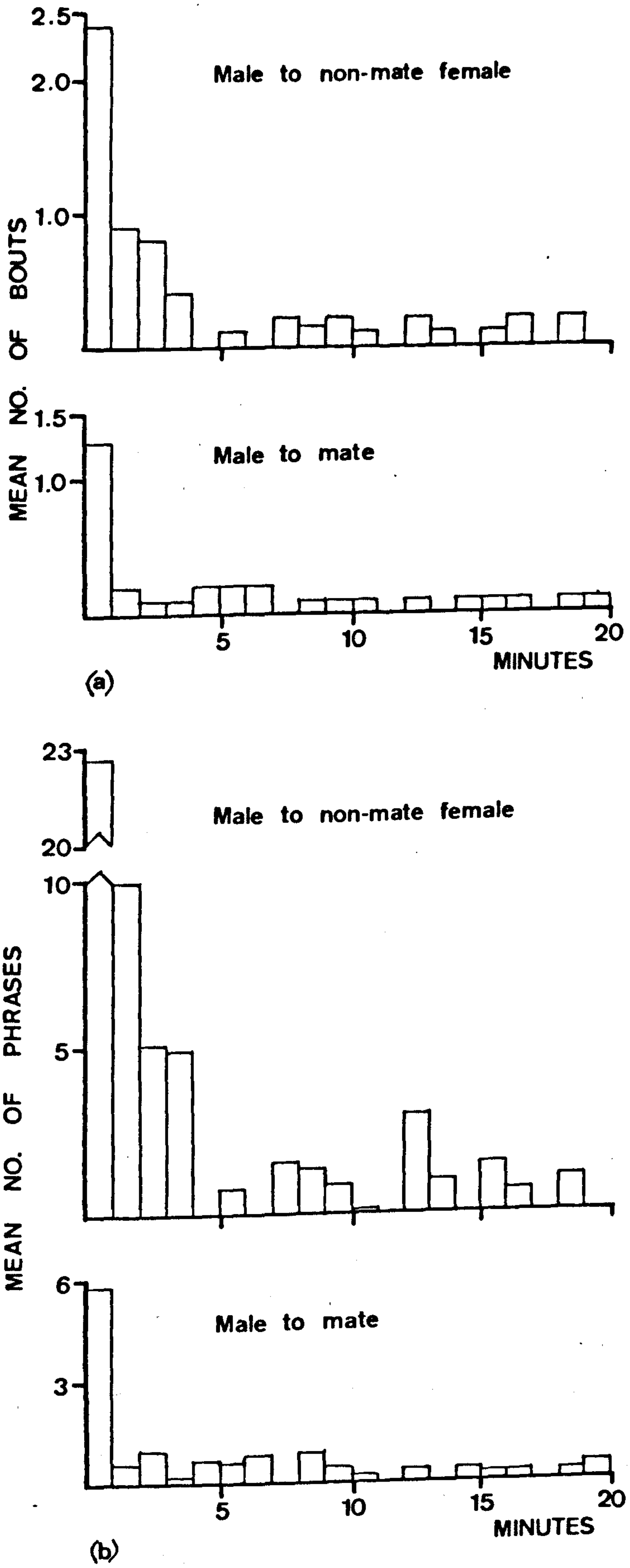


Fig. 8. The use of courtship song by males on reunion with their mate and on introduction to a strange non-mate female. (a) No. of song bouts. (b) No. of song phrases.

TABLE 10 Features of courtship song and the courtship dance

(i) Experiment I

		Day 1	Day 7
Duration of courtship bout (average)		11.3 secs.	6.9 secs.
Latency, time to first courtship song (average)		7.9 secs.	2.9 secs.
Distance from female song began (average)		11.7 cm	10.4 cm
No. of pivots during courtship bout (average)		2.2	0.7
No. of pivots per second during bout		0.21	0.12
Proximity, minimum distance during bout		9.8 cm	9.2 cm
Initiator of the courtship bout	M	13.3	0.6
	F	3.4	0.1

(ii) Experiment II

		Between mates	♂ with non-mate	♀ with non-mate
Duration of courtship bout (average)		7.6 s.	15.1 s.	13.3 s.
Latency of male's response		109.3 s.	7.1 s.	14.3 s.
Distance from female song began		13.4 cm	15.8 cm	16.5 cm.
No. of pivots during courtship bout		1.0	2.8	1.4
No. of pivots per second during bout		0.13	0.13	0.11
Proximity, minimum distance during bout		8.9 cm	10.1 cm	13.7 cm
Initiator of the courtship bout	M	2.6	5.3	6.6
	F	0.4	0.4	1.3

the first introduction and it was interesting to note that the same response was obtained from these pairs on Day 7 presumably after pair formation.

Experiment 5.2 (Fig. 8 and Table 10). The mated males showed a marked increase in the amount of singing on introduction to a strange female compared with that shown on reunion with their mates. The number of song bouts differed, though not significantly, whereas the number of song phrases and the duration of the bouts (table 10) showed a large increase ($p < 0.01$, WMP). The latency of the male's response was reduced towards the non-mate (Table 10, $p < 0.01$, WMP) and in both this measure and the amount of singing it resembled the unmated male's behaviour towards the mated female.

(b) The Courtship dance

Experiment 5.1 (Table 10). The mean distance from the female at which the male began his courtship song did not differ significantly in the birds on introduction and after pairing but the number of pivots involved in his dance were fewer on Day 7 ($p < 0.01$, WMP). Proximity during courtship, i.e. the minimum distance between individuals during the bout, was smaller after pair formation ($p < 0.01$, WMP) suggesting that the females did not move off as much during the courtship bout. The males initiated most of the courtship bouts on Day 1 ($p < 0.01$, WMP).

Experiment 5.2 (Table 10). Again, the mean distance of the male and female at the start of courtship was not significantly different between mated birds and strangers. Birds stayed furthest apart in the mated female / male non-mate situation and the distance involved was significantly higher than that between the mates during courtship ($p < 0.01$, WMP). This was due in part to the female's avoidance of the male and also to her aggression towards the non-mate (which is discussed later). In all the possible pairings, the male initiated the majority of the courtship bouts.

Discussion of courtship and the courtship dance

Male courtship song ceases after pair formation in the majority of passerines, although it reappears briefly at, or around, nest building during the period in the breeding cycle when copulation occurs (Andrew, 1961). The male in most species (unlike the Zebra Finch) does not court strange females once he has paired, which suggests that he has undergone some physiological change. This change could be a hormonal one and may be dependent on the mate's presence for its duration. During and after the incubation period the bond between a pair is thought to weaken since they must now separate on occasions, such as those that occur when one remains at the nest and the other forages for food. In many passerines the male has been found to become sexually active again at this stage, singing and courtship being renewed; Tinbergen (1939) described this in the Snow Bunting. This seems to suggest that it is the continued presence of the partner which inhibits male courtship.

Zebra Finch courtship behaviour does not appear to follow this general pattern. The results of these experiments suggest that courtship song directed at the mate is continued long after pair formation is probably completed, though at a reduced level, and that the male remains sexually active to non-mate females to which he is introduced.

The first aim, quoted in the introduction to this section, concerned changes in individual courtship patterns as a result of pair formation. As was found and reported in Section 4, the overall level of courtship singing decreased after pair formation. There was, however, no evidence to suggest that the individual components of courtship varied in frequency or emphasis. The Zebra Finch is therefore unlike the Ring Dove in which part of the courtship display is reduced as a result of pair formation (Morris and Erickson, 1972). On the basis of this finding they proposed, as Hinde (1959) had earlier suggested, that this part of the display must be important in pair formation but not in the later maintenance of the bond. Using a similar argument, Zebra Finch courtship in its entirety seems important both in pair formation and pair maintenance.

It has been suggested that aggressive tendencies are important in determining the amount of courtship a male exhibits towards a female. Courtship on reunion of mates can be seen as a means of reducing such tendencies and thus preventing the disruption of the bond. Spurr (1974) describes how in the Adelie Penguin, aggression between the pair is reduced by mutual displays. Kunkel (1967) has pointed out that the greeting ceremonies of the waxbills have probably evolved to overcome aggressive tendencies and, in the case of *Poephila* spp., bill mandibulation on reunion of mates or flock members may serve as appeasement behaviour (Zann, 1972). In contrast, Zebra Finch courtship of either the mate or a strange female appears remarkably void of any overt aggression or, for that matter, appeasement behaviour. Caryl (1976) reported an increase in nest soliciting behaviour by mates on reunion but this was not apparent in the present study, though no nest site was available.

The behaviour of mated males towards strange non-mate females, described in Experiment 5.2, raises interesting possibilities. It was shown that the males remain sexually active after pair formation. Caryl noted similar results for mated Zebra Finches whereas Immelmann (1962) and Butterfield (1970) found that mated males were less responsive. "Extra-marital" relationships in monogamous species have been reported recently by Kushlan (1973), the White Ibis, and MacRobert (1973), Lesser Black-backed and Herring Gulls, but in both these cases males were involved in the incubation period of their breeding cycle; their partners were absent. Zann (l.c.) noted promiscuity in the Poephila both during incubation and after some outside stimulus that generated fear in the birds. It is therefore possible that the sudden introduction of a strange female, with the accompanying noise and disturbance, induces courtship whilst other tendencies, e.g. aggressive ones, are suppressed. Certainly, it is quite common for birds which have escaped from their cages to begin courtship suddenly whilst being actively pursued with a net.

It thus seems likely that fear of a female may play some part in eliciting courtship by a male. The fact that males will even court strange males introduced into their cages suggests that it is a very widespread response. In this case it is worth remembering that Immelmann (1959) demonstrated that males would court a Zebra Finch model the only markings on which was a red beak! It could well be that the male possesses enough of the female releasers to elicit courtship by other males. This need not necessarily only be a feature of domesticated birds; Zann noted similar male-male courtship in Poephila although he attempted to explain these sightings as cases of mistaken identity (the Poephila spp. are monomorphic). Other monomorphic species do not appear to have recognition problems (e.g. Snow Bunting, Tinbergen, 1939, Robin, Lack, 1939, and the Black-headed Gull, Moynihan, 1955), and this seems to be an unlikely explanation of the phenomenon.

(c) Beak wiping during courtship

Results (Table II)

Experiment 5.1 Beak wipes given during courtship show that this behaviour is more common in males than it is in females both before and after pair formation ($p < 0.01$, MWU). In other respects males and females were similar. Nearly all beak wipes were directed towards the partner in both sexes, and both beak wiped more on introduction than after pairing ($p < 0.01$, WMP).

The majority of these beak wipes appeared to be all full ones (F) and similar to the functional wipes seen outside of courtship. Touching the bill against the perch (T) was seen in the males and, more rarely in females, whereas incomplete wipes in which no perch contact was made (N), were only given by males and only whilst courting.

Nearly all beak wiping observed outside of courtship appeared fully functional. Again, there were differences in male and female behaviour. The males gave more beak wipes on introduction than they did after pairing ($p < 0.01$, WMP), whereas the amount given by females outside of courtship remained the same. The direction in which the wipes were given also differed in that, on introduction, males gave more on the side nearest to the female than they did to the side away from her ($p < 0.01$, WMP); this was not the case after pairing.

Experiment 5.2 In all three situations males gave more beak wipes than did females during courtship ($p < 0.01$, MWU). The direction of the wipes were significantly more frequent towards the female in only two cases in the male with a non-mate female

TABLE 11 <u>The mean amount and type of beak wiping during and outside of courtship</u>

		Experiment I			Experiment II	
		Day 1	Day 7	Between mates	♂ mate with ♀ non-mate	♀ mate with ♂ non-mate
Total during courtship	M	32.5	4.5	5.2	11.3	20.3
	F	4.5	0.4	0.5	4.9	1.5
Total outside of courtship	M	36.3	14.0	14.7	17.5	20.2
	F	16.6	13.8	8.7	14.5	9.2
Direction during courtship (Male)	+	31.0	4.1	3.8	11.3	20.5
	-	1.4	0.4	1.4	0	0.3
Direction during courtship (Female)	+	3.5	0.4	0.1	3.7	0.5
	-	1.0	0	0.4	1.2	1.0
Direction outside of courtship (Male)	+	26.8	8.5	7.9	8.9	12.4
	-	9.5	5.5	6.8	8.6	7.8
Direction outside of courtship (Female)	+	8.7	7.9	5.1	8.5	5.0
	-	7.1	6.7	4.2	6.0	4.2
Type during courtship (Male)	F	24.5	3.1	4.0	4.7	14.2
	T	7.0	1.2	0.8	4.4	5.0
	N	0	0	0.4	2.2	1.6
Type during courtship (Female)	F	4.2	1.7	0.4	3.8	1.2
	T	0.3	0.1	0.1	1.0	0.3
	N	0	0	0	0.1	0
Type outside of courtship (Male)	F	35.7	13.5	14.4	17.3	19.4
	T	0.5	0.4	0.3	2.0	0.8
	N	0	0	0	0	0
Type outside of courtship (Female)	F	16.1	13.4	8.7	13.7	8.9
	T	0.5	0.4	0.6	0.8	0.3
	N	0	0	0	0	0

<u>KEY</u>

M = Male	F = Functional beak wipe
F = Female	T = Touching the beak on the perch
+ = Towards the individual	N = No contact with the perch
- = Away from the individual	

and the female with a non-mate male ($p < 0.01$, WMP). The mated male's beak wiping increased when courting the non-mate female though not significantly. Non-functional beak wiping (T and N) was again largely restricted to the courting situation of the males.

Outside of courtship there were no apparent differences in the number, direction, or type of beak wipes observed.

Discussion of beak wiping

Beak wiping is worth some discussion as its occurrence is thought to be linked with ambivalent or conflicting tendencies common in the courtship situation. During courtship males tended to give more wipes than did females in all the pairings studied. This may suggest that displacement wiping, if that is what it is, is linked with high levels of sexual motivation rather than aggressive tendencies. This is apparently the case in the females since they frequently showed aggression with the non-mate male (discussed later) but did not show an increase in the incidence of beak wiping.

The decrease in beak wiping by males after pair formation suggested a reduction in sexual tendencies towards the female, probably as a result of pair formation. The high levels during courtship on introduction appeared to carry over into beak wiping outside of courtship for the males suggesting an overall enhancement of this behaviour possibly due to sexual "excitement" on their part.

(d) Copulation and attempts at copulation

Results (Table 12)

Experiment 5.1 Complete copulation (i.e., that including female soliciting) was observed once in birds on first introduction, although four males mounted females during this watch, without any

TABLE 12 <u>The occurrence of copulation, mounts and attempted mounts with or without soliciting</u>

	Experiment I				Experiment II					
	Day 1		Day 7		Between mates		♂ mate with ♀ non-mate		♀ mate with ♂ non-mate	
	No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.
No. of attempted mounts	0	0	0	0	1	0.1	3	0.7	3	2.3
No. of mounts	4	1.4	1	0.1	0	0	6	2.2	1	0.1
No. of copulations	1	0.2	0	0	0	0	4	0.6	0	0
No. of soliciting acts M	0	0	0	0	0	0	0	0	0	0
F	1	0.1	0	0	1	0.1	1	0.1	0	0

signs of soliciting, but did not copulate. Only one male mounted a female in this way after pairing.

Experiment 5.2 The highest numbers of mounts and copulations were seen when mated males were introduced to non-mate females. Attempted mounts (i.e., those in which the male 'leapt' for the female unsuccessfully) were also observed and similar behaviour was noted in the female with non-mate male situation. Female soliciting was seen only once in these encounters. In the courtship of the established pairs there was only one case of a mount and this followed female soliciting.

Discussion of copulation

As in the experiments of Section 4 successful copulation was an unusual feature in these experiments. However, males made frequent attempts to mount non-mate females without the stimulus of soliciting. Other writers reviewing this copulatory behaviour on introduction of birds speak in terms of "rape" (e.g., Moynihan and Hall, 1954, Morris, 1954, Caryl, 1970, and Zann, 1972), and it certainly appears as if the female is an unwilling partner. Attempted mounts are uncommon between mates on reunion after separation.

(e) Aggression

Results (Table 13a)

Experiment 5.1 Very little overt aggression between the birds was seen either before or after pairing. What little there was occurred on Day 0 invariably during male courtship.

Experiment 5.2 For the first time marked aggression was observed between a pair of birds in the isolated situation. Five

TABLE 13a The amount of aggression shown

		Experiment I				Experiment II					
		Day 1		Day 7		Between mates		♂ mate with ♀ non-mate		♀ mate with ♂ non-mate	
		No. of Indls.	Av.	No. of Indls.	Av.	No. of Indls.	Av.	No. of Indls.	Av.	No. of indls.	Av.
Bill pointing lunges	M	0	0	0	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	1	0.2	4	2.8
Beak-fencing	M	1	0.1	0	0	0	0	1	0.1	3	0.6
	F	1	0.1	0	0	0	0	2	0.7	5	2.4
Supplanting attacks	M	0	0	0	0	0	0	0	0	1	0.1
	F	2	0.2	0	0	0	0	1	0.8	0	0

TABLE 13b The amounts of allopreening and clumping recorded

		Day 1		Day 7		Between mates		♂ mate with ♀ non-mate		♀ mate with ♂ non-mate	
		No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.	No. of indls.	Av.
No. of allopreening jabs	M	3	2.8	4	1.5	4	2.8	5	3.9	1	2.1
	F	3	1.0	3	0.3	1	0.9	4	1.6	3	1.1
No. of allopreening bouts	M	0	0	4	0.8	4	0.5	0	0	0	0
	F	1	0.1	3	0.3	2	0.5	0	0	0	0
Amount of clumping		0	0	6	4.0	5	4.8	1	0.3	0	0

mated females responded to non-mate male courtship with bill pointing, supplanting attack attempts and beak fencing. There was no aggression between mates and only a relatively small amount between the males and non-mate females.

Discussion of Aggression

These results indicate that mated females are less inclined towards promiscuity than are the males. This was particularly clear in some cases in which females attempted to rebuff and curtail non-mate courting attempts. This occurred even in the absence of the mate and may suggest, as Immelmann (1959) has intimated, that female Zebra Finches form a stronger pair bond than do males. This behaviour by mated females was very interesting in that it constituted the first occasions in which females had behaved aggressively to courting males (i.e., had indicated a rejection of the presented male).

f) Contact behaviour

Results (Table 13b)

Experiment 5.1 Clumping was only seen after pair formation and significantly more occurred on Day 7 than Day 0 ($p < 0.01$, WMP). Allopreening showed a similar trend.

Experiment 5.2 Only one case of clumping was seen between non-mates and allopreening bouts exclusively occurred between mates. 5 out of the 10 mated pairs clumped by the end of the watch.

Discussion of contact behaviour

Clumping and allopreening behaviour does not really relate to the topic of courtship which is under discussion here. However, they are both believed to be appeasement behaviour important in reducing aggression between pair members and promoting proximity (see Section 3 for discussion), and as such may reflect the motivational states involved in the sexual behaviour observed.

Clumping and allopreening was exclusively (with one exception) between mates, unlike the bill mandibulating display of Poephila (Zann, 1972) which is thought to have a similar appeasement function. In these species all conspecifics are greeted with the display and it is merely enhanced when it is directed at the mate. Clearly, in the Zebra Finch, appeasement behaviour present in their repertoire is not extended towards unfamiliar conspecifics.

A General Discussion

In this section it has been the changes in behaviour due to pair formation that have been examined. It is clear that the male's courtship behaviour on introduction to a female changes as that female becomes his mate. This change does not, however, affect his responses to an unfamiliar conspecific whom he will court readily on introduction. It has been shown that rearousal occurs when a sexually satiated male rat is introduced to a novel female, the so-called Coolidge effect (see Brown, 1974) and the Zebra Finch response may be essentially similar. The decrease in courtship directed at the mate as a result of pair formation may not be confined to the mate alone. In a group the male's initial courtship response falls off to all females present. Caryl (1976) highlighted this point and suggested that it was familiarity with an individual which reduced the courtship response. The pair bond has the effect of making courtship between the mates more likely and familiarization with any individual reduces the tendency to exhibit courtship on reunion after separation.

In some estrildids reunion with conspecifics, mate included, takes the form of a ritualized greeting ceremony involving some or all of the components of courtship behaviour. The curtsey dance of the waxbills (Kunkel, 1967) is accompanied by courtship song if the conspecific greeted is a strange female, and in the Poephila spp. head bobbing, bill mandibulating, and tail quivering are common in both sorts of display (Zann, 1972). There is no evidence to suggest that a greeting ceremony exists in the Zebra Finch; introduction and reunion are marked by complete courtship of variable duration. It may be that in the wild such responses lead to familiarization with other conspecifics which would be important in the establishment of social groups. In addition separation and reunion will occur between mates during incubation at a time when the bond between them is in danger of being weakened. Courtship between mates at these times may help to strengthen and maintain the pair bond. It is possible that the greeting ceremonies of other estrildid species have evolved from complete courtship on introduction which is seen in the less ritualized behaviour of the Zebra Finch.

The results presented here suggest that a male by no means restricts his courtship to his mate. Yet, clumping and allopreening are still restricted to pair members which indicates that such contact behaviour may be very important in pair maintenance. Indeed Arnold (1975) has shown that contact behaviour by Zebra Finches appears to be independent of gonadial hormone levels as it continues in castrated males whereas courtship is reduced. Thus in the non-breeding season it may be more important in prolonging the bond than would be the occasional courtship bouts that continue throughout this period.

The elicitation of courtship on introduction has been linked with aggressive tendencies on the part of the male. Kunkel (1967), for example, noted a relationship between aggressive (territorial) behaviour and the display song given to unfamiliar females in Estrilda spp.. Similarly, Andrew (1961) pointed out that many of the responses given in reproductive fighting by passerine species are not just aggressive but may also include nesting, fear, flight and sexual displays and similar behaviour is commonly directed towards strange females as well. Such observations led Caryl (1976) to suggest that there is a link between the sexual and aggressive motivational systems of the Zebra Finch whereas in the past, these have been considered to be mutually antagonistic. In the Three-spined Stickleback, Wilz (1972) demonstrated that aggression could have an enhancing effect on later sexual behaviour and Brown (1974) showed that sexual arousal in the rat could well be linked with aggressive relationships between the individuals concerned. Thus the responses of male Zebra Finches to an unfamiliar female may be aggressive but, because of the sexual releasers she possesses, these are expressed as courtship behaviour.

SECTION 6. A DESCRIPTION OF ZEBRA FINCH VOCALIZATIONS

Introduction

It seems likely, from the results of Section 4, that pair formation in the Zebra Finch involves a period of time during which mates come to recognise one another as distinct individuals from within the social flock. Visual characteristics are almost certainly involved in their recognition process and it seems likely that auditory signals, in the form of vocalizations, will play a major, if not equal part in the maintenance and establishment of the pair.

Auditory cues could assist pair formation in a number of ways. For example, they might be used to recognise and locate a lost or temporarily hidden mate; they could have a contact function, eliciting an approach response on the part of the receiver of the call or song; they might stimulate gonadial development in the mate thus promoting the performance of mutual displays and enhancing pair maintenance activities. Clearly, if any of these proposed functions were to operate then the vocalizations given by mates would need to be individually distinct and, moreover, the birds capable of accurately detecting such differences.

The recognition of individuals by their vocalizations has been reviewed by Beer (1970c) and it would appear that in many species individual differences are used both in recognition of the mate and of the parents by their young. In the Zebra Finch subjective impressions suggest that there is a good basis for individual recognition (Morris, 1954, Immelmann, 1965) but there has not been a thorough descriptive and experimental approach to the problem.

Beer suggested three possible approaches to the investigation of individual recognition in birds. These were,

(a) field observations,

(b) a descriptive analysis of vocalizations,

(c) an experimental investigation of the reactions of birds to the sounds of their conspecifics.

Unfortunately, field observations were not possible in the present study but work by Immelmann (e.g. 1965) and Zann's (1972) exhaustive descriptions of similar vocalizations in related *Poephila* species, suggests that individual variation does occur in the wild. In this section, and the following Section 7, work will be concentrated on approaches (b) and (c) in an attempt to assess whether Zebra Finch vocalizations provide a basis for individual recognition and, just as importantly, whether birds make use of any differences which are found. The latter, in effect approach (c), will be described in Section 7. It is not enough to demonstrate inter-individual variation in vocalizations it must also be shown that conspecifics are aware of this variation and can make use of it in their social behaviour.

It would be impossible, in a study of this size, to describe the vocalizations of Zebra Finches in the minutest of detail. It is therefore important to bear in mind that interest is centred on the ability by members of a pair of birds to use auditory cues as part of their pair formation and maintenance processes. First then, are there differences between sounds made by individuals which could be used for recognition?

In the discussion which follows calls and song will be treated separately as has been the practise in the majority of previous studies (e.g. Hinde, 1969). This is not only for convenience but can be justified in that definite differences between these vocalizations can be recognised. The song is far more complex consisting of a series of elements and is used commonly in courtship situations. Calls, on the other hand, tend to be mono- or disyllabic and thus of shorter duration. In addition, as Marler (1956) and Messmer and Messmer (1956) point out, calls are apparently entirely genetically determined in the majority of species whereas songs have a variable number of learned components. These are the main differences on which the dichotomy can be based.

6.1 The calls

A. A sonogramic description of selected calls

Introduction

The sonogram provides a two dimensional representation of a sound and has been used extensively in studies of bird vocalizations. It presents graphically the frequency of the call against time; intensity is indicated by the "degree of blackness" of the trace (other representations are also possible). The problem inherent in its use, however, concerns the interpretation and nature of measurements made from sonograms (q.v. Lanyon, 1969). A selection of parameters to be measured must attempt to represent features which birds may in fact be using as informational cues. The problem is, if anything, that they make available too much information rather than too little.

The size of the call repertoire of different bird species varies but Marler and Mundinger (1971) have estimated that it is in the region of 5 to 14 different units in the majority of cases. In the Zebra Finch seven different calls were recognized by Immelmann (1965) and of these four were chosen for close examination in the present study. These were calls described here as "Loud", "Loud/Soft", "Soft" and "Tet". These calls are frequently given by members of both sexes during general movements around their cages. The names of the calls were arbitrarily chosen and, if anything, attempted to indicate their relative aural qualities. This is possibly better than a contextual interpretation, as used by Immelmann (l.c.), with names such as "distress", "contact" and "feeding"calls. The danger is that without the backing up of a quantified experiment such interpretive names can lead to unconcious, or concious, bias in the classification of calls and to avoid this Mulligan and Olsen (1969) used numbers to denote different calls.

Once the calls have been obtained and the sonograms made they must be compared for both intra-individual and inter-individual variations. Marler and Mundinger (l.c.) stress that in view of the "completeness" of the sonogramic record it is necessary to decide which features of the call are most important as auditory cues and then concentrate on these. Methods used in the past to make these comparisons include the superimposing of graphical representations (Bertram, 1963), subjective interpretations of the general shape of the sonogram (Beer, 1970c, Marler and Mundinger, 1971) and quantified measurements of frequency, frequency changes and duration (Falls, 1969, Beer, l.c., Marler and Mundinger, l.c., Emlen, 1972, and Beightol and Samuel, 1973).

The superimposing of graphs of calls is time consuming and it is doubtful whether it gives more information than a subjective impression of the overall shape or 'whole' of the call. The latter, the so-called "gestalt" view, was preferred in this study as it allows descriptions of large and complex individual differences which might be difficult to demonstrate by measurements alone. These differences can then be backed up by a quantified treatment involving measurements of selected frequency and temporal parameters. Both of these measurements are important because, although frequency differences are used for individual song recognition in the White-throated Sparrow (Falls, 1969), and in the Indigo Bunting (Emlen, 1972), temporal patterning appears to be involved in conveying species-specific characteristics in at least the latter species (Emlen, l.c.).

Accuracy in such measurements is also necessary since there is evidence to suggest that the frequency and time discrimination of small birds is good enough to make use of small variations in pitch and duration of calls. Greenwalt (1968) estimated that frequency discrimination was on a par with human standards whereas time measurement was in the region of fifty times finer. Hence the parameters measured in this study are ones which the birds are equipped to make use of and the results will indicate the amount of individual variation of calls shown by each sex. It should be remembered that the aspect of communication that is under consideration is that occurring between mates where individual recognition of one particular male or female from conspecifics of the same sex will, presumably, be of paramount importance in maintaining proximity between the pair.

Methods

Ten "established" pairs of birds were used. These had been housed as isolated pairs in excess of 3 months and had presumably, during this time, completed the pair formation process. Male and female calls were recorded separately using a two compartment cage with a movable wooden partition. By separating members of a pair calls could be elicited quite readily from both sexes. Notes were also made on the classification of calls "by ear alone" during these recording sessions and in previous experiments. They are presented in the form of preliminary observations.

(a) Preparation of the sonograms

Calls were recorded on a Sony TC800B Tape recorder at the highest speed setting (19 cm/sec.) which allowed for maximum frequency resolution and avoided the production of 'spurious harmonics' due to over-emphasis of the lower amplitudes (Greenwalt, 1968). The microphone was a standard distance (approximately 30 cm) away from the calling bird in each case. Calls were usually given from the perch of the cage.

Selected calls were then played back directly onto a Kay Sonograph using a narrow band filter (45 c/s) over an 8 kHz range. Each sonogram has a duration of 2.4 seconds. These settings were chosen as likely to lead to the most accurate representation of the calls without excessive duplication of sonograms. The wide band filter sacrifices frequency representation for an accurate temporal measure whereas the narrow band gives accurate frequencies and can also be used for a measure of duration. Sonograms covering 16 kHz showed that some higher frequencies were present in these calls but the emphasised region, that containing the most sonic energy, fell well within the 8 kHz range.

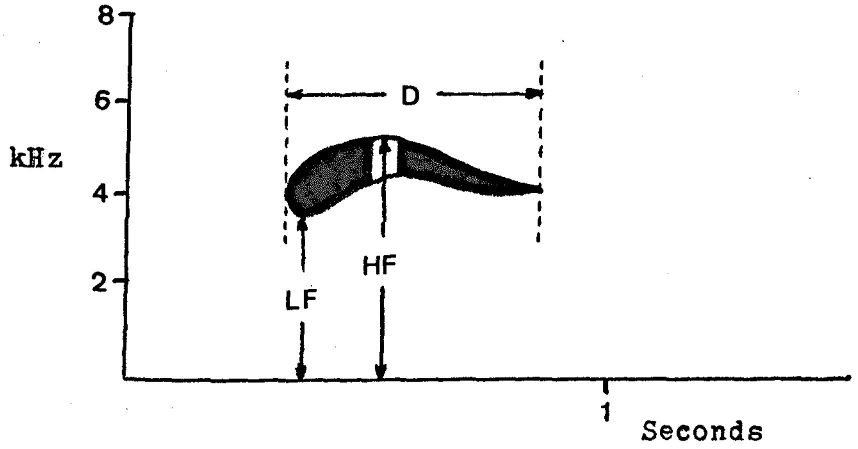
The sample size for each bird was a minimum of 10 calls in each call category making a total of at least 40 sonograms per individual.

(b) Assessment of the sonograms

i) The overall appearance The entire shape of the calls, their "whole" appearance, was compared resulting in a subjective interpretation of the arrangement of the sound energy, its harmonics and attack and decay (the way it started and finished). The harshness of the call could be assessed by the amount of non-harmonic, 'speckled' points on the sonogram which indicate a noisy quality. A pure note, for instance, has no such speckles whereas a harsh call is endowed with a 'nasal' quality. Harshness can be readily discerned by ear but would be difficult to measure quantitatively.

Inter-individual variation (that between individuals) of the whole call can be assessed, where necessary, by visual sorting of calls using impartial human observers. Beightol and Samuel (1973) had some success with this method when analysing the calls of the American Woodcock but it was not used in this study.

ii) <u>The selected measures</u> Measures were taken of the frequency and duration of calls.



LF = Lowest frequency measure.
HF = Highest frequency measure.
D = Duration measure.

Most calls of grassfinches have a harmonic structure and show frequency changes (i.e., are modulated during the course of the call). Previous authors have, to avoid replication of work, chosen a single harmonic and made measures of its highest and lowest frequencies (e.g. Zann, 1972; Beightol and Samuel, l.c.; and

Marler and Mundinger, 1975). Zann chose the fundamental or first harmonic but this falls outside of the emphasised range of the Zebra Finch and is frequently only incompletely represented on the sonogramic trace. In the present study one harmonic (the sixth) was chosen because it falls within this emphasised range. The alternative is to increase the amplitude of the call to ensure clear markings but Greenwalt (1968) warns against this practise as it may lead to the production of false harmonics.

The duration of the sixth harmonic, or its equivalent, was taken as a measure of call length. The 'tail' or smudging which appears on the traces was not included in this measure and only the darker, louder, well-defined part of the call was taken. This tail appears to be a feature of sonograph recording rather than of the harmonic input and was therefore ignored.

iii) Actual measurement Measurements were made to the nearest millimetre giving an inaccuracy level of ± 0.5 mm. This error is equivalent to ± 0.04 kHz and ± 3.9 msec and therefore frequency measures were taken to the first decimal place only and duration to the nearest millisecond. Conversions used were, 1.0 kHz = 1.2 cm and 1 second = 12.9 cm.

iv) The statistical treatment Intra-individual variation (that within individuals) was assessed in terms of the standard deviation (SD), the standard error (SE) and the coefficient of variation (CV) of the measures taken. The latter is computed from the formula, CV = SD/mean, and is expressed as a percentage. It was used by Hutchinson et al (1968) and Thorpe (1968) for the 'fish' calls of Sandwich Terns. They suggested that characteristics showing the greatest variation in proportion to their average values (i.e., the highest CV scores) would be most easily discriminated. Thus in this study, in which each individual is treated separately, a high CV score indicates poor accuracy in successive reproductions of the same call and presumably less likelihood of individual recognition.

The amount of variation within individuals (intra-individual) were compared with variation between individuals (inter-individual) by means of a one way analysis of variance (as in Maxwell, 1970).

Results

(a) The preliminary observations

The four calls of both sexes could be readily distinguished and categorised by ear with little difficulty. Subjective observations and impressions suggested the following points,

Loud (L) calls	These were relatively long calls which tended to be given in alarm situations such as disturbances in the stock room. They were usually given by perched birds, rarely in flight, and many birds might call or "chorus" together producing a particularly strident and effective noise. Loud calls of different birds appeared to show individual qualities that could be detected by ear.
Loud/Soft (L/S) calls	These were heard frequently when birds were in flight and resembled an incompletely delivered loud call or a lengthened soft call, hence their name.
Soft (S) calls	These were calls of shorter duration and variable amplitude though always quieter than the above. Their communicative value, therefore, could only be useful for conveying messages over short distances.
Tet (T) calls	As the name suggests these calls had a harsh nasal quality. On occasions their delivery was rapid and regular such that they resembled the staccato of a machine gun. They, like the soft calls, were short and of low, but variable, amplitude. Individual variations in the soft and tet calls of birds were not pronounced and could not be detected by ear alone.

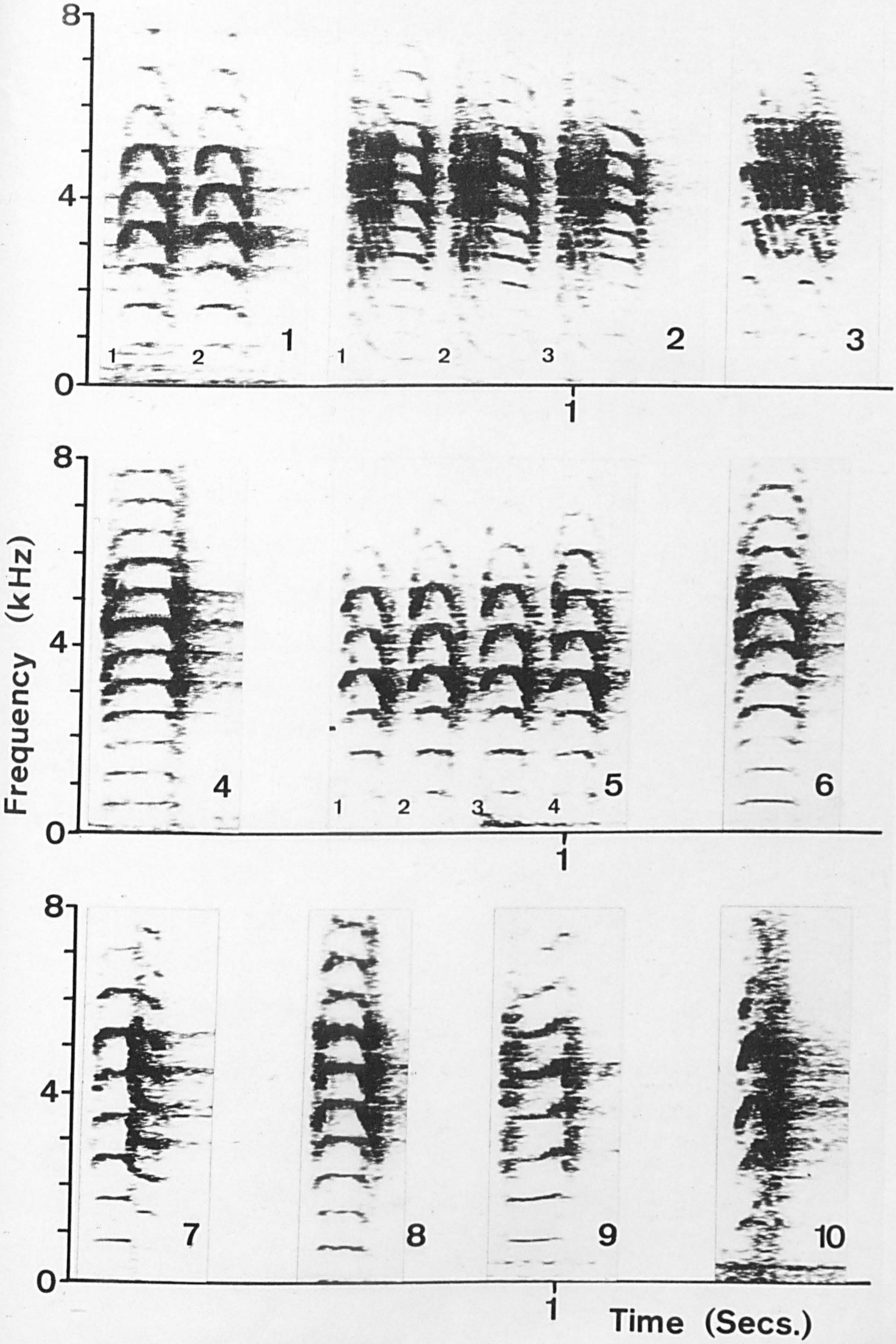
(b) The structure of the calls

Unfortunately the space available restricts the number of sonograms which can be used as illustrative material. 'Typical' calls have been chosen and where possible more than one, of each call type, is included. In some cases the second or third calls demonstrate unusual, but interesting deviations from the more normal type.

The first and possibly most striking result of this survey is immediately evident from an examination of the male loud (L) calls (Pl. 1). The inter-individual range of different call structures is quite remarkable even in such a small sample. The female L calls show similar variations but by no means to the same degree.

The second feature is that all the calls for both the males and the females show a harmonic structure with varying proportions of harsher overlying components. The harmonics extend above the 8 kHz range illustrated but the emphasised region of each call, that through which the majority of the sound energy has been delivered, falls between 2.0 and 6.0 kHz in all calls for all individuals. This emphasised region thus appears to be a characteristic of the species as a whole.

Finally, the shape of the harmonics in each call type show similarities (with the exception of those males with non-harmonic L calls). Generally, they are dome shaped with a steep attack or start of the call showing a rapid increase in frequency followed by a decay during which the frequency falls, often more gradually than it rise. This is well shown by the L and Loud/Soft (L/S) calls of females. In the shorter calls, the soft (S) and tet (T), the rate of decay is more equal to the rate of attack and a more rounded appearance results in many cases.



Pl. 1 Male Loud Calls

There are differences in the structure of each of the four call types and these will thus be dealt with in turn. The relevant sonograms should be referred to in each case.

(i) <u>The loud calls</u>

Males (Plate 1)

The L calls of males 1, 4, 5, 6, 7, 8 and 9 show variations on the domed harmonic theme with the number of harmonics visible varying from 8, in male 9, to 12 in male 4. 1 and 5 have rounded harmonics whereas 4 and 6 incorporate an extended, flattened middle portion to their calls. Males 7 and 9 have interesting alterations to the general domed form; 7 has an overlying harsh component partially obscuring the more typical display whereas, male 9, shows a second increase in frequency part way through the call.

Males 2, 3, and 10 are atypical in that they incorporate more extensive harsh elements which transpose the harmonic appearance.

Male 2 has an initially harsh portion showing rapidly decaying components distinguishable particularly in the lower frequency range. It is difficult to describe the quality of this sound as it resulted in the call but it contained a more grating, less musical tone. The terminal part of this call is more typically harmonic and resembles the decay portion of male 4's L call.

Male 3 has even more extensive harsh elements such that no domed harmonics are in evidence in the call. The harsh, rapidly decaying components seen in male 2's call are here strongly emphasised and the call appears to be disyllable. This double structure could be discerned by the human ear and the male's song, presented later in this section, suggests that he was capable of producing it in a monosyllabic form. The notes preceeding male 3's song, the so-called 'warm-up' notes, are exactly the same as the first half of this L call.

Last, male 10, shows a reduction in the number of harmonics in the measured range and an overlying harsh quality.

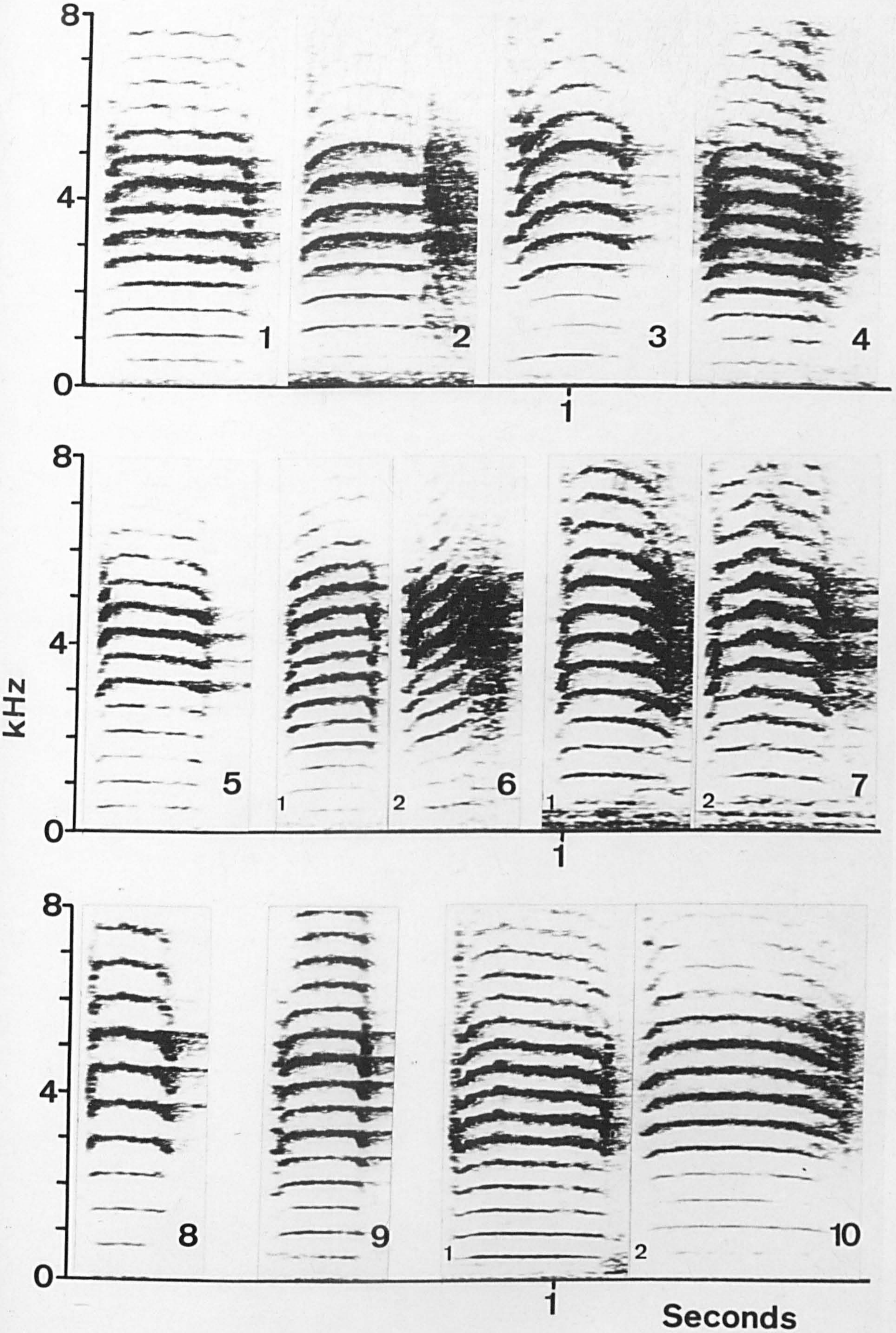
In summary, the L calls of the males show considerable structural variation, so much so that it is surprising that they are all given by the same species of bird.

Females (Pl. 2)

The L calls of the females show less marked individual variations than those described for the males and they all possess curved harmonics, at least in this sample. One immediately apparent difference is their greater length and there is some evidence that the female can alter the duration of different L calls without affecting the frequency parameters. An example is illustrated in the case of female 10, the second call is quite obviously of longer duration than the first. In addition, atypical changes in frequency were observed on different occasions. An example is the second call of female 6 which shows an extended attack with each harmonic rapidly increasing in frequency and becoming harsher. This call had a distinctly "mournful" quality to a human listener and was given after a prolonged silence whilst the female was separated from her mate. Typical female 6 calls accompanied the production of this call.

Female 7 demonstrates another example of intra-individual frequency variation. The call shown has a peculiar 'hiccup' half way through it where the frequency suddenly changes for a short time only. This particular call was given whilst the female was manipulating seeds at the food bowl and possibly this interfered with its production. However, females 1, 4, and 10 (the first call) show traces of a similar sudden small increase in frequency.

The general appearance of the harmonics show some interesting



Pl. 2 Female Loud Calls

structural features. The attack is stepped in many cases (i.e., it is preceded by a short horizontal component). This is particularly pronounced in female 3 but can also be seen in the calls of females 1, 4, 6, 7, 9, and 10 whereas it is apparently absent from the calls of females 2, 5, and 8. The rest of the attack is generally steep although female 3 has a more gradual increase in frequency leading to a rounded appearance. The decay involves a gradual tailing off and decline in frequency. The lengthened call of female 10 suggests that it is the middle portion of the call which is actually increased. The call of female 1 illustrates this admirably in that the three parts of the call, the attack, middle and decay appear to be almost separate components.

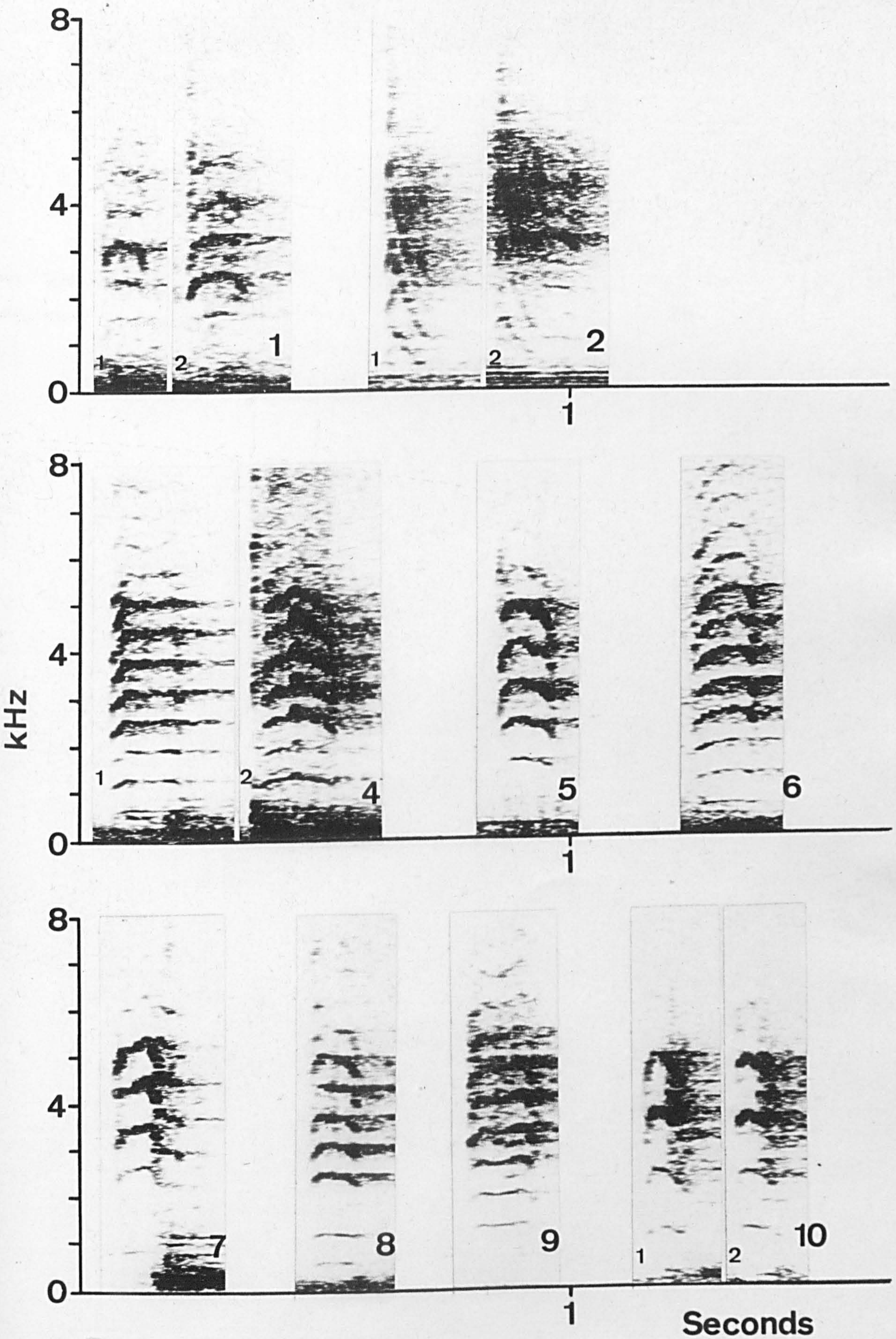
Females 6 and 9 are similar in that, unlike calls of the other females, they are quite short and the frequency of the middle portion of the call continues to rise after the initial attack has been completed.

The structure of female L calls shows a considerable range of individual qualities though these are less marked than in the males. There is some evidence to suggest that the exact form of the calls, both frequency and duration, may be altered in successive deliveries of the same bird which was not a feature of male L calls.

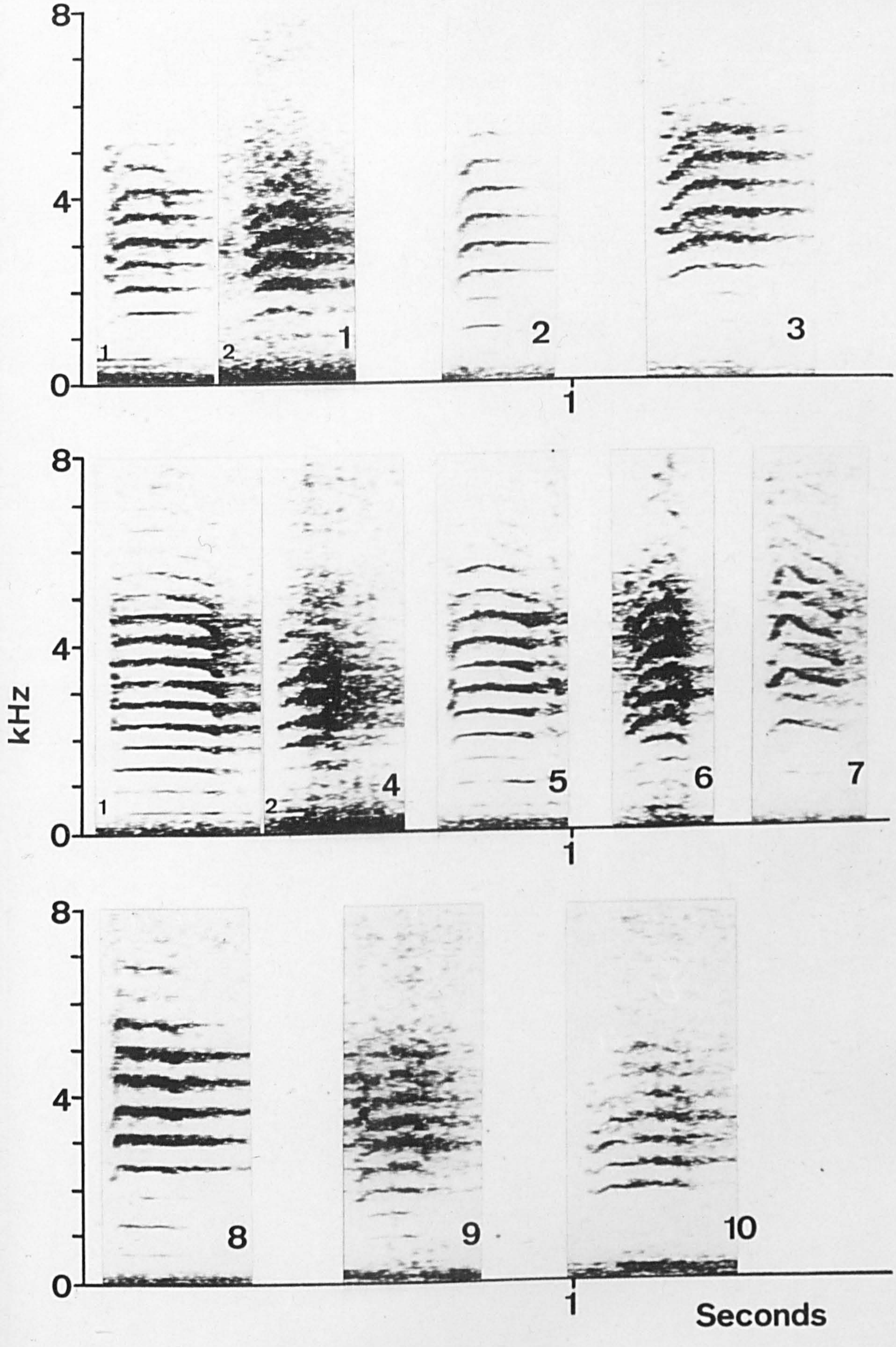
(ii) <u>The loud/soft calls</u>

Males (Pl. 3)

First, an omission, there are no L/S calls presented for male 3. In fact this male was never heard to utter such a call. The structure of the remaining calls confirms the aural impression, quoted earlier, that they consist of incompletely delivered L calls. The calls are softer and the traces that result are less complete yet in all the males, with the exception of male 2, it is possible



Pl. 3 Male Loud/Soft Calls



Pl. 4 Female Loud/Soft Calls

to see the harmonic structure of the L call. One difference is the frequency of the harmonics which is generally lowered and there are fewer recorded resulting in a softer, lower pitched note.

The second call illustrated for male 4 is interesting as it shows a fluctuation in frequency similar to the female L call 'hiccup' (female 7). This call was recorded as the male took off, the shaded appearance of the trace is due to wing noise, and delivery could have been influenced by the sudden exertion.

Male 2 seems to be the 'odd man out' in the sample. His L/S call consists of a definite reduction of the L call. If these two are compared it is clear that the L/S is the first harsh component suggesting that the L call could really be termed disyllabic, a harsh L/S call followed by a harmonic component.

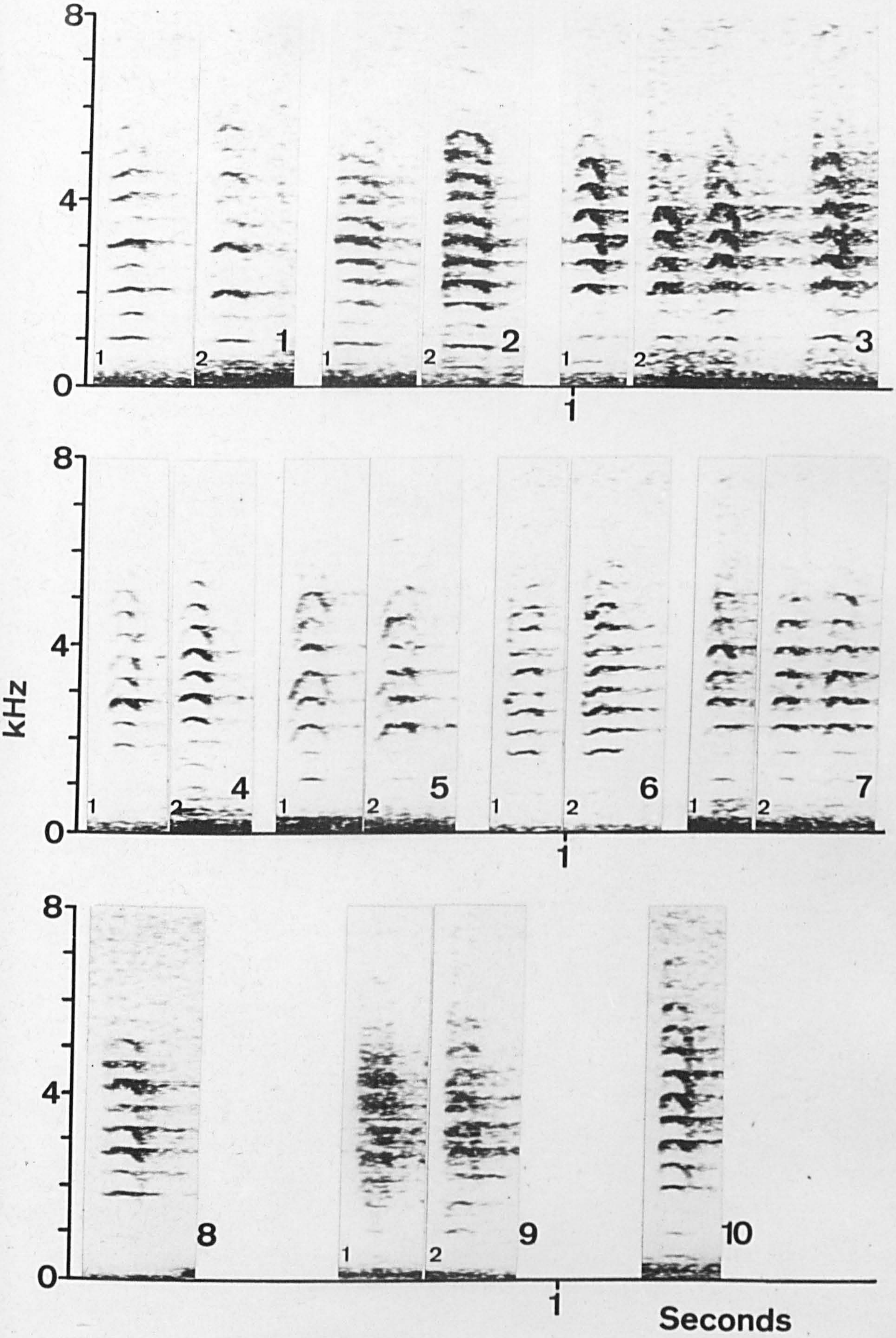
Females (Pl. 4)

As in the males, these resemble the respective female L calls but are generally shorter, softer and show more frequent irregularities in their structure. The attack of the calls appears to be unaltered, those with a step in the L call retain this feature in their L/S calls. Harsher qualities are in evidence which result in a thickening of the harmonics particularly noticeable when the call was given as the female took off (e.g., females 1 and 4, their second calls; 6 and 8). As their name suggests these calls, especially in the females, showed similarities with both loud and soft calls.

(iii) <u>The soft calls</u>

Males (Pl. 5)

The large structural variations found in the male L calls are strikingly absent from their soft calls. All the S calls are harmonic even those of males 2, 3 and 10 whose L calls contained mainly harsh elements. More harmonics are in evidence on the traces (up to 17 as



Pl. 5 Male Soft Calls

in male 2) and their structure is based on two major themes.

Males 1, 2, 6 and 8 incorporate a stepped attack reminiscent of that seen in female L calls. This is especially evident in the calls of males 6 and 8.

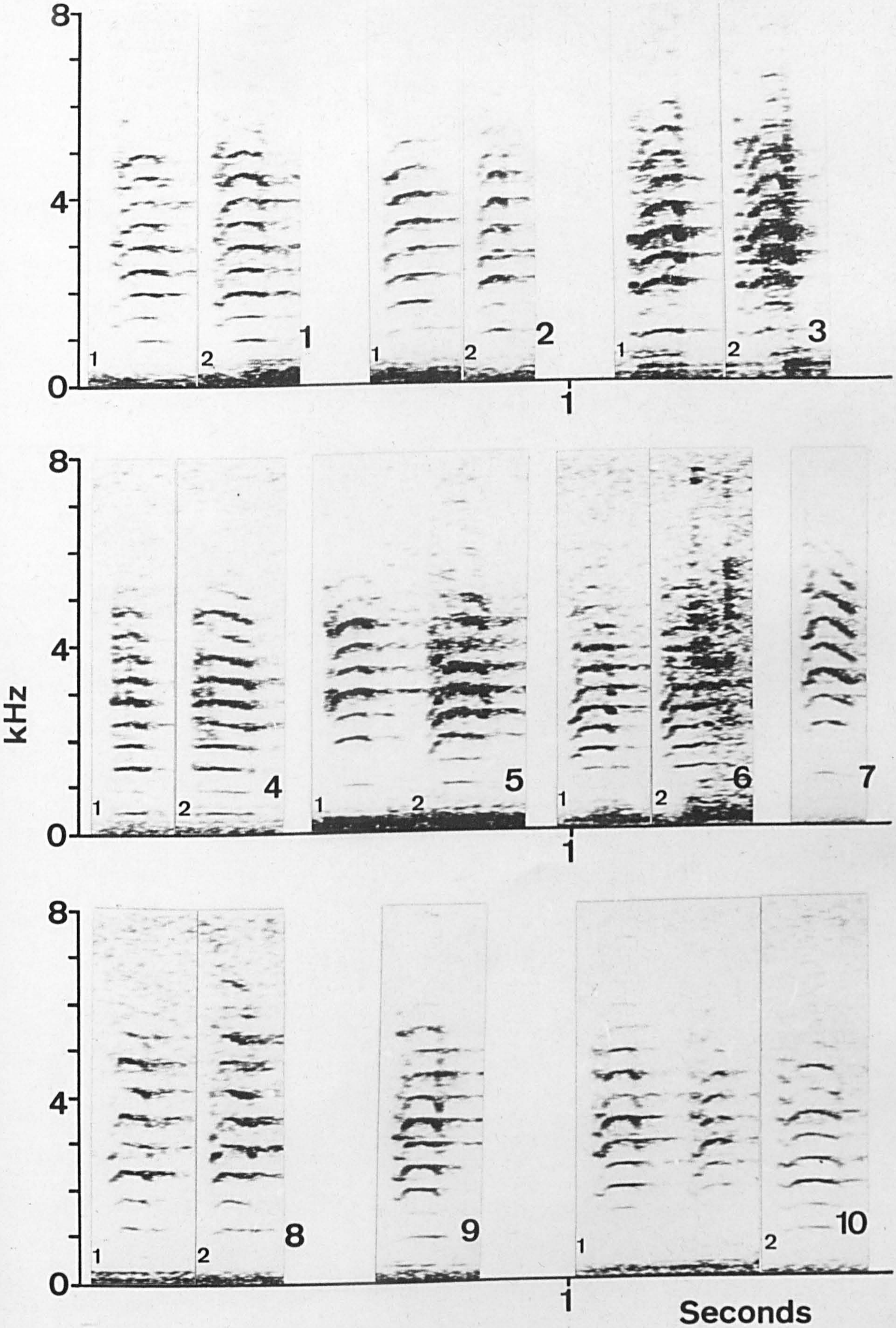
Males 3, 4, 7 and 10 share a domed harmonic with no visible step. However, the second group of three S calls illustrated for male 3, given whilst the male was in flight, show traces of a stepped appearance. As yet, the significance of this step in the attack in terms of the sonic quality resulting in the call is not clear.

The two exceptions are males 5 and 9. Male 5 has a more extended harmonic structure similar to that seen in his L call. The attack and decay is not emphasised as much as the middle portion which, if taken alone, resembles the S calls of the other males. This raises the possibility that the S call may be derived from the middle portion of the L call which is produced at a lower frequency and amplitude, or vice versa. In the case of male 2 his S call resembles the terminal part of his L call.

Male 9 is atypical compared to the other males in that his S call was harsh as illustrated in the first call shown. All his S calls contained this quality.

Females (Pl. 6)

The S calls of females appear to show a further shortening of the L call from that represented by the L/S calls. The shape of the attack of the harmonics remains in evidence but the middle and decay portions are severely reduced. Less variability is in evidence, for example the calls of females 6, 9 and 10 are visually identical. Some intra-individual variation is illustrated in the second calls of females 3, 4, 5 and 6 but it is difficult to decide whether these



Pl. 6 Female Soft Calls

are lengthened S calls or merely shortened L/S calls.

(iv) The tet calls

Males (Pl. 7)

The structure of the male tet calls reveal a marked harsh component provided in all cases by an emphasis on the middle or the decay (tail) parts of the call. All the calls are short and, where they are visible, the harmonics resemble those seen in S calls.

The harsh elements tend to fuse together as is particularly shown in the calls produced by males 4 and 10. Male 5 is again unusual in that no attack is apparent in his call, it is made up of continuously falling frequencies.

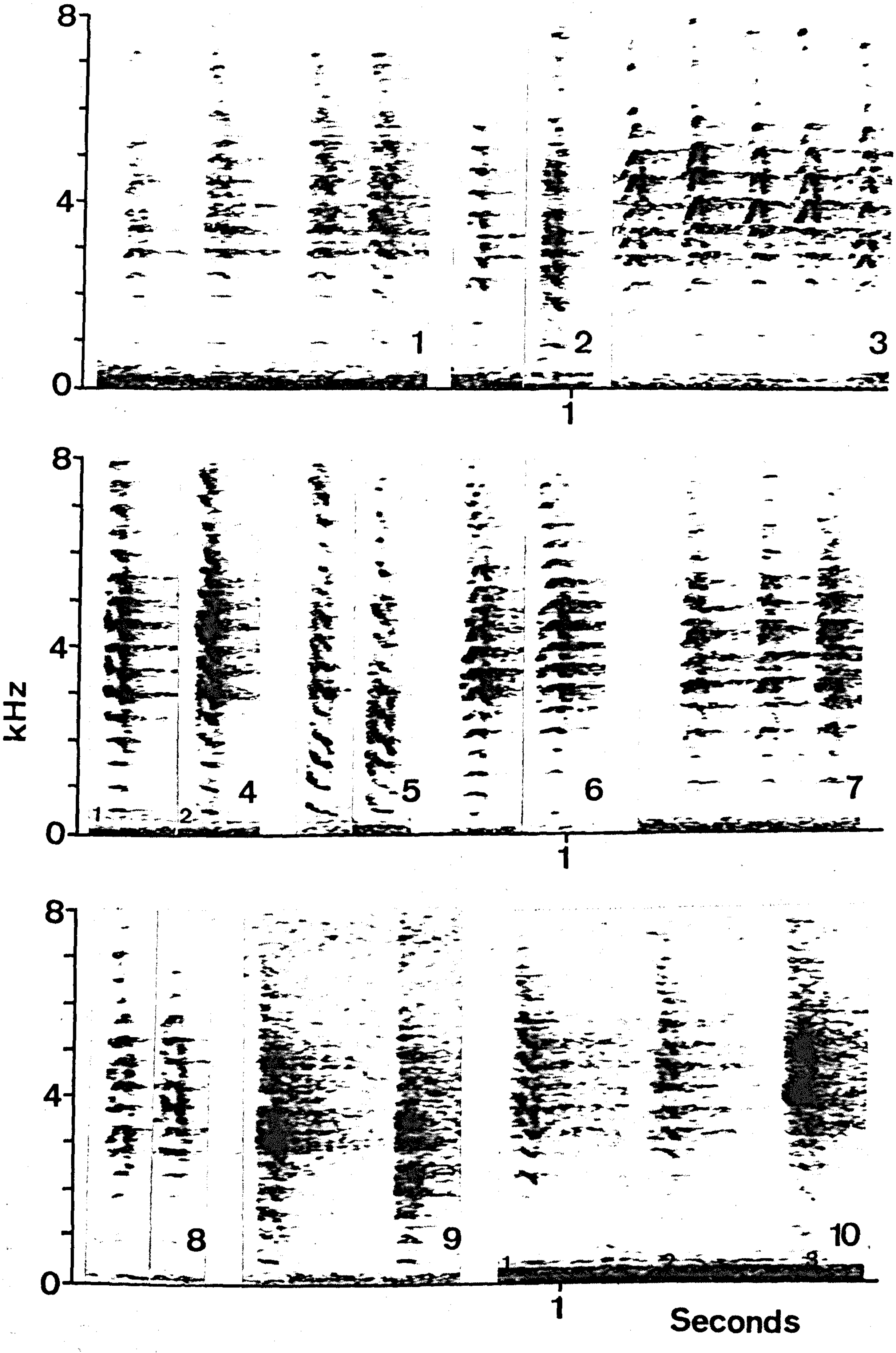
Females (Pl. 8)

Like the S calls, the T calls of females resemble those made by the males. They are short, harmonic and the harsh quality is again provided by emphasis on the middle and tail of the harmonics. The attack of the call is similar to that seen in the S calls and interestingly, though possibly not significant, the call of female 5 is very similar to the T call of her mate, male 5.

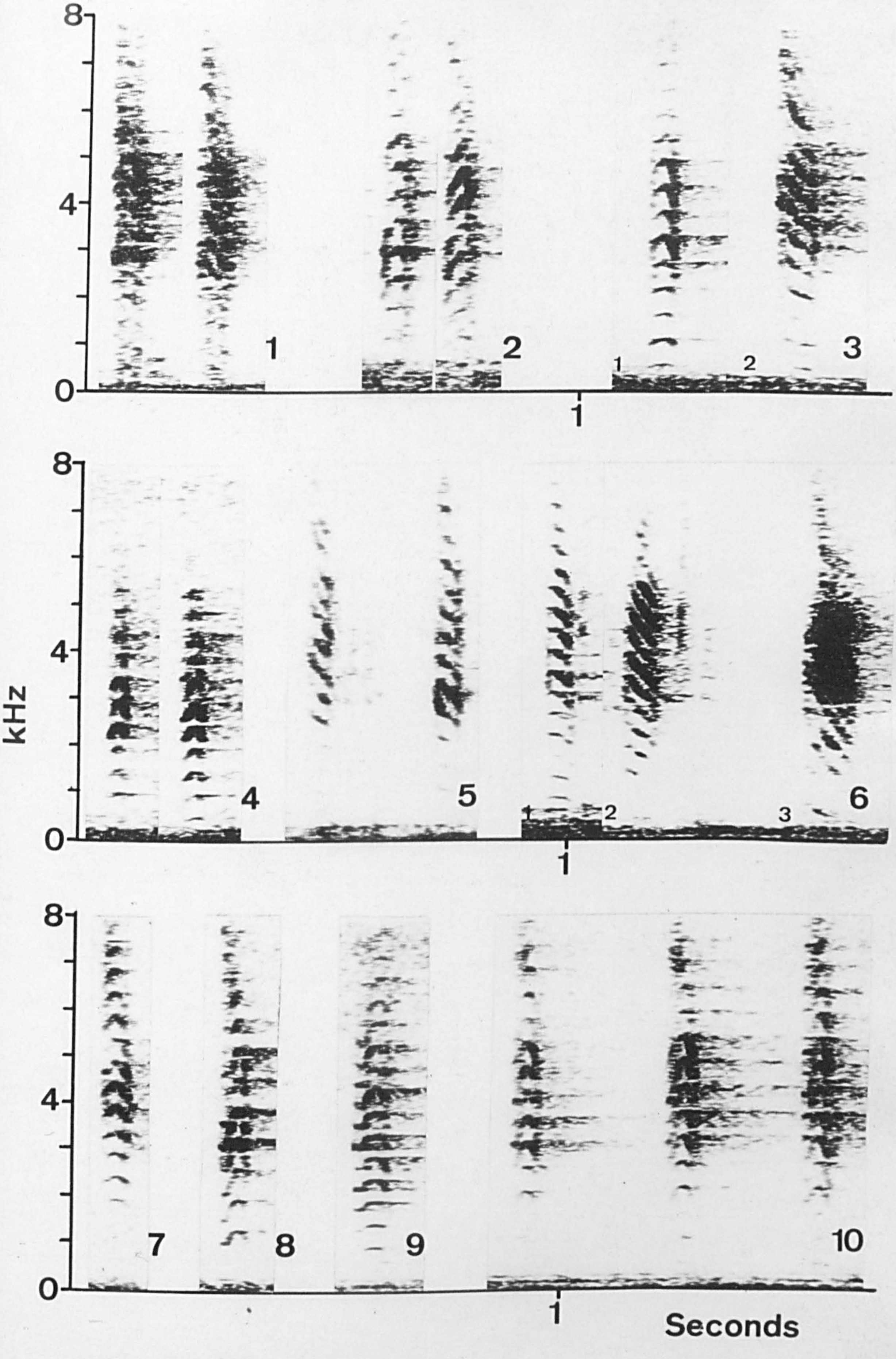
There is some intra-individual structural variations as shown particularly in the calls of females 3 and 6. In the latter, the last call illustrated is much longer, louder (indicated by the darkness of the trace) and consists of components showing a steep fall in frequency. These are similar to the harsh elements in the L calls of males 2 and 3 and are also apparent in the T of female 3. Other females show an extension of the middle part of the call, it rises to a higher frequency in some calls, e.g. females 2 and 10.

(c) Intra-individual variation (Appendix I and Table 14)

The Tables in Appendix I show that the standard errors calculated



Pl. 7 Male Tet Calls



Pl. 8 Female Tet Calls

for the means of all the parameters measured are of low magnitude which indicates a high degree of accuracy in the successive production of calls. In addition, the coefficient of variation scores for each individual rarely rise above the 5% level with the exception of duration measures where higher values were frequently obtained; the maximum is 22.2% for the L/S calls of female 10. This is of obvious importance if the calls are to be used for individual recognition as it must be accurately reproduced if its characteristics are to be learned.

Using a One-way Analysis of Variance it was possible to compare the amount of variation within individuals with that between individuals. Table 14 gives the results in terms of 'F' ratios and their probability of occurrence and in all cases variation between individuals was by far the greatest. Again, duration measures, though still showing significance, had the lowest F ratios.

It would appear from these results that all four calls examined are stereotyped and accurately produced such that any one could include features that might be used in individual recognition. Yet, in some cases, birds did tend to vary their delivery of certain calls and these are worth examining briefly.

(i) Loud calls

Male L calls were very stereotyped, a possible exception was provided by male 9 who tended to alter both low and high frequencies. The duration of all these calls was accurately timed, more so than for any other call type of either sex.

The frequency of female L calls were accurately reproduced but the duration of calls showed variability. Females seemed capable of prolonging certain calls and this raises the interesting possibility that L and L/S calls may be extreme varieties of the same call.

Presumably an extended call could carry additional information over that of the normal type and may show that male and female L calls have different functions.

(ii) Loud/Soft calls

The males did not show an excessive amount of intra-individual variation whereas, the female calls varied considerably for the measure of duration. The frequency scores, on the other hand, were consistent though always lower than those for the L calls.

(iii) Soft calls and tets

Both of these calls were accurately reproduced by the males. The same tendency evident in the female calls was apparent (i.e., duration of the calls showed the highest coefficient of variation scores). Most noticeable variations were the extended loud tet calls given on infrequent occasions. The females similarly showed variability of duration whilst retaining individual frequency characteristics. Extension of some tet calls was, if anything, more prevalent in the females than in the males.

(d) Inter-individual variation (Tables 14 & 15)

As noted above, the analysis of variance revealed that all the calls of both sexes were produced accurately enough to render them individually distinct. In other words, the amounts of intra-individual variation were small. There was certainly no evidence to suggest that the calls of mates were more similar than those of non-mates as Mundinger (1970) found was the case in some carduelines. In fact, in general terms, the L calls of mates differ widely and the S and T calls of all males and females are superficially similar but differ in detail as the majority show individual frequency and duration parameters.

TABLE 14. The results of a one-way analysis of variance (the ratios are shown, their probabilities are all $p < 0.01$)

(a) Males

CALL	N	Low frequency F value	High frequency F value	Duration F value
*Loud	80	95	43.5	81.6
*Loud/soft	79	42.1	55.9	32.3
Soft	143	108.6	216.8	30.1
Tet	125	72.8	82.6	9.6

(b) Females

CALL	N	Low frequency F value	High frequency F value	Duration F value
Loud	100	77.9	31.7	30.1
Loud/soft	89	136.5	67.8	13.2
Soft	138	162.7	18.3	13.1
Tet	127	48.6	24.4	9.2

* The calls of males 2 and 3 were not included in this calculation as they are both non-harmonic in structure.

TABLE 15 <u>The results of t tests comparing calls of particular individuals for inter-individual variation</u> (t values are shown)

	MALES				FEMALES		
(a) Loud calls	Low frequency	High frequency	Duration		Low frequency	High frequency	Duration
1 v 5	1.8	10.5*	3.4*	1 v 10	0	5.2*	5.7*
1 v 8	14.1*	14.0*	7.1*	6 v 8	34.2*	6.8*	2.5
5 v 8	14.6*	21.1*	9.7*	5 v 7	3.9*	6.4*	0.7
(b) Soft calls							
1 v 8	7.4*	9.3*	2.2	9 v 10	4.3*	2.7	5.8*
6 v 8	10.9*	15.3*	2.7	6 v 9	0	0	1.7
3 v 10	9.5*	14.9*	0	6 v 10	4.5*	3.1	2.4
(c) Tet calls							
3 v 6	17.4*	18.0*	0	1 v 4	0	0	4.0*
4 v 6	2.7	6.1*	1.9	5 v 6	9.0*	2.0	4.2*
				8 v 10	10.0*	5.7*	0

t values marked with a * have probability values of p 0.001

A visual inspection of the sonograms suggest that certain birds give very similar calls. These "pairings" were compared using the 't' test and the probability levels associated with the results obtained are shown in Table 15. Few calls share the same values for all three measures. Male L calls with strikingly similar harmonic shapes show large frequency differences, e.g. males 1 and 5 have a similar low frequency score but in male 5 the high frequency peaks a clear 300 Hz above that of male 1. Similarly the call durations appear critical.

Female L calls, with their more variable durations, show greater overlap but again individual frequency scores are in evidence. The L/S calls of both sexes show inter-individual variation much as was recorded for the L calls they resemble. In the S and T calls the greatest degree of overlap was located particularly in duration measures. The S and T calls of males 6 and 8 were identical as far as the measures used could show and this was also true of the S calls of females 6 and 9. It seems safe to argue that the amounts of inter-individual variation in these softer calls is reduced, compared to the L calls, though there still remain significant differences between the calls of most individuals. It is interesting to note that whilst males 6 and 8 share the same, or very similar S and T calls their L calls are significantly different.

Thus it would appear that the softer calls of the Zebra Finch, the S and T, are not particularly reliable as far as individual distinctiveness is concerned, though they can still provide some clues to the identity of a caller. This tendency towards more uniform short-range calls is revealed in Appendix 1which shows the coefficient of variation calculated for the means of all the individuals in each call category. These CV scores become progressively smaller from L calls down to the lowest values for S and T calls in both sexes. A large CV score in this case can be taken as indicative of greater amounts of inter-individual variation.

Discussion

In answer to the question posed in the introduction to this section, it is clear from the results that the Zebra Finches used in this sample produced calls which were individually distinct. All four call types examined showed significant variation in both frequency and duration measures for both sexes. This was nowhere more apparent than in the loud calls of the males. In addition, the amounts of intra-individual variations were small and the accuracy with which the same call was reproduced was remarkably consistent with two possible exceptions, the duration of female loud and loud/soft calls. Thus these calls could provide ample and predictable clues as to the identity of a calling individual.

In view of this large variation it is difficult to pick out any characteristics of the calls which could be considered species-specific (i.e., features which are common to the calls of all individuals). Certainly they are all harmonic and they share a similar emphasised range (that part of the range with the most sonic energy). Zann (1972) found that in related estrildids, the *Poephila* spp., the frequency of the fundamental harmonic of their loud calls was species dependent, at least its maximum frequency appeared to be. However, Zann's sample size, only five individuals, was rather small and, although the fundamental was not measured in the present sample, it seems unlikely that it could be the same in all cases.

Thus, there is a strong basis for individual recognition, particularly of the male loud calls. The calls of lower amplitude, the soft and tet calls, show more signs of convergence whilst retaining some individual features. These calls can be heard only over short distances and presumably could have different underlying motivations and separate functions to the louder calls. The female loud and loud/soft calls showed the greatest levels of intra-individual variation in their duration which suggests that they could be variations of the same call which is modified and thus carries additional information. This will be discussed in more detail later in this section.

The sexes can readily be distinguished by their loud calls which confirms Immelmann's (1965) subjective impression. Marler (1961) has proposed that the degree of difference between male and female signals in finches is dependent on the amount of sexual dimorphism shown. The Zebra Finch seems to conform to his theory in that it is sexually dimorphic and the calls of the sexes differ markedly. Zann (1972) found that sexual differences were less apparent in the sexually monomorphic <u>Poephila</u> spp.. There is no evidence of mates using the same or very similar calls in the Zebra Finch as Mundinger (1970) found in captive cardueline pairs. In addition, the large differences in the sexes suggest that call matching at the time of pair formation (i.e., calls being part of mate selection) seems unlikely in this species though it has been suggested in other species (e.g. Beer, 1970c, Marler and Mundinger, 1975). This raises the important question as to whether these calls are entirely innate or could be influenced by the effects of experience. A wealth of evidence has accumulated suggesting that in the majority of species calls are entirely genetically determined (e.g., Schjelderup-Ebbe, 1923, Marler, 1965, Lade and Thorpe, 1956). However, Mundinger (l.c.) found that carduelines can apparently learn to copy the calls of their mates during pair formation. It is interesting to note that the Bullfinch, a species with a permanent pair bond, has been found by Nicolai (1959) to possess learned calls. It must be noted that not all the calls need be affected by experience, in the Chaffinch only one call, the "rain" call (Newton, 1972) is thought to depart from an exclusively innate basis.

It would thus be interesting to examine the ontogeny of the calls of the Zebra Finch and in particular, the origin of male loud calls which show such remarkable individual distinctiveness. However, the possibility that domestication may have influenced the genetic basis of these calls cannot be overlooked.

In summary, this section suggests that there is a strong basis for individual recognition by calls in the Zebra Finch. Of the calls examined the loud calls of the males seem to be most adapted for conveying the identity of the caller.

6.1 B. The discreteness of different calls

Introduction

This experiment is a continuation of the previous work (Section 6.1A) and was designed to assess one potential source of error inherent in the method used. The danger in sampling the vocalizations of a species comes in the selection of calls for analysis. 'Good', clear calls are invariably chosen and this may result in a misleading representation of the amount of variation as less clear, possibly more variable, calls are ignored.

It has been shown that in some bird species extensive grading of calls does exist (e.g., Konishi, 1963, Smith, 1965), the exact form of the call varying with the context in which it is given. This grading has also been found in studies of primate vocalizations (Rowell and Hinde, 1962, Andrew, 1963, and Nottebohm, 1972) and thus it is important to examine the scores for intra-individual variation in the Zebra Finch in more detail. The discrete nature of the calls which was apparent in the previous experiment might in fact be a false impression brought about by experimenter selection of similar calls rather than accuracy on the part of the calling bird.

In an attempt to avoid this selection continuous tape recordings of vocalizations made by pairs of Zebra Finches were made and from these a sonogram produced for every call heard in the time allowed. Measures were then taken of the parameters of the calls and a possibly more accurate interpretation of the amount of intra-individual variation obtained.

Methods

Three established pairs of birds were "chosen" from the previous experiment. In an attempt to avoid a biased choice of subjects the pairs numbered 1, 2 and 3 were elected irrespective of their actual calls. Each pair was housed in turn in a flight cage (124 x 90 x 39 cm) equipped with two horizontal perches and wire mesh on the front and top surfaces. A microphone was attached to the wire mesh at the height of the perches and midway along them. Amplitude variations due to birds being at different distances away from the microphone could have occurred but, in this situation, they would be minimal and are unlikely to have affected the parameters measured. Increased distance from the microphone would have resulted in attenuation of frequencies higher than those measured in these calls.

Recordings took place in the morning and lasted for a period of 15 minutes. Each pair was allowed 24 hours in the experimental cage to allow it to become accustomed to the new surroundings. Sonograms were produced as in 6.1A and the same parameters were measured. The calls were classified as before (Loud, loud/soft soft and tet) on the basis of both aural and sonogramic comparisons and the sexes were presented separately.

Frequency distributions of the calls could then be constructed and the amount of overlap between the call types assessed using the 't' test. Measures were treated in terms of millimetres as there was little to be gained from converting them to kHz.

Results

The frequency distributions of the different parameters are shown for each individual in Figs. 9-14. Table 16 gives the mean scores for each call with its standard error (SE) and the t values (and their probability) obtained when the different measures were compared are shown in Table 17.

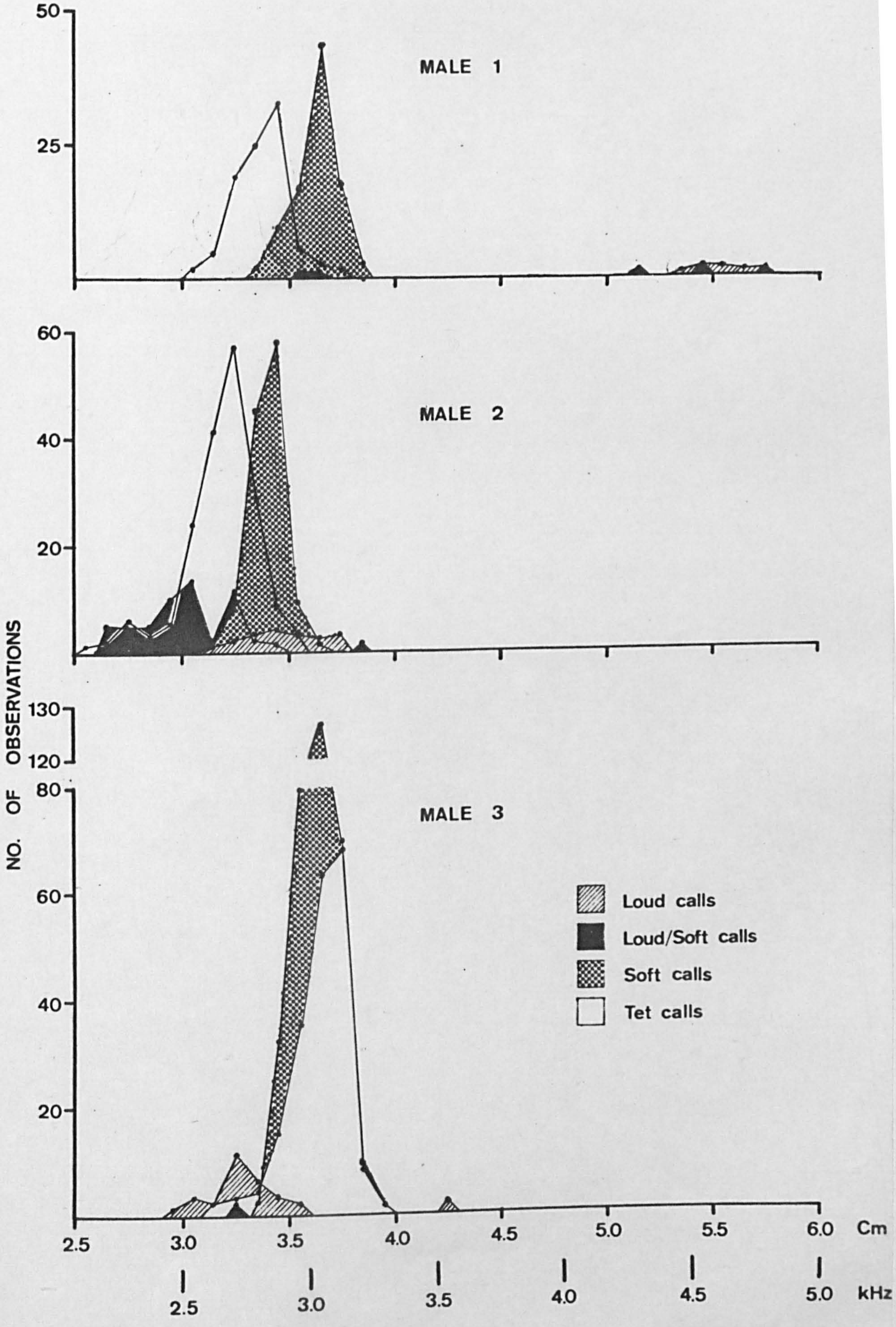


Fig. 9. The frequency distribution of the calls made by three males; a measure of the lowest frequency of each call.

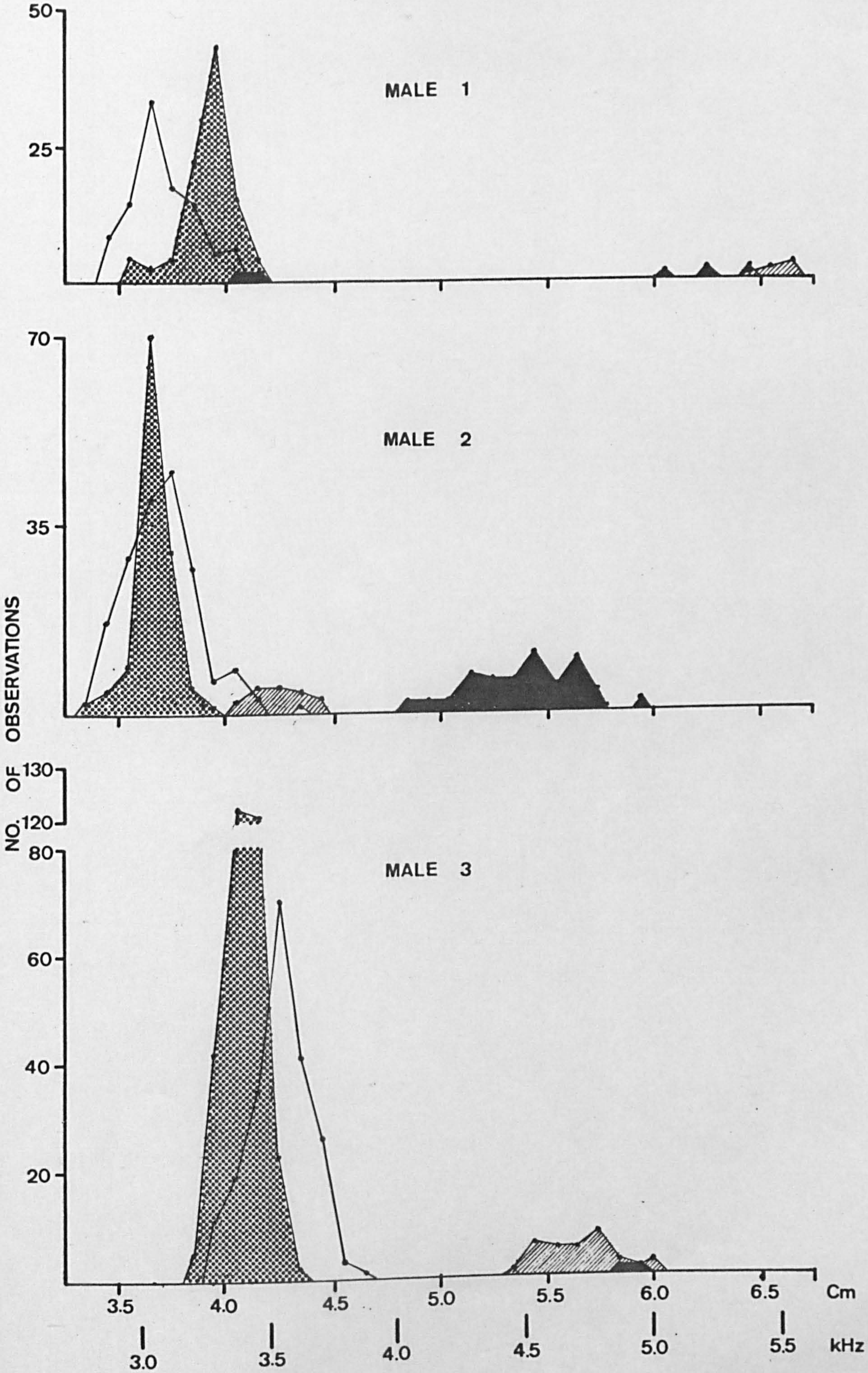


Fig. IO. The frequency distribution of calls made by three males; a measure of the highest frequency of each call.

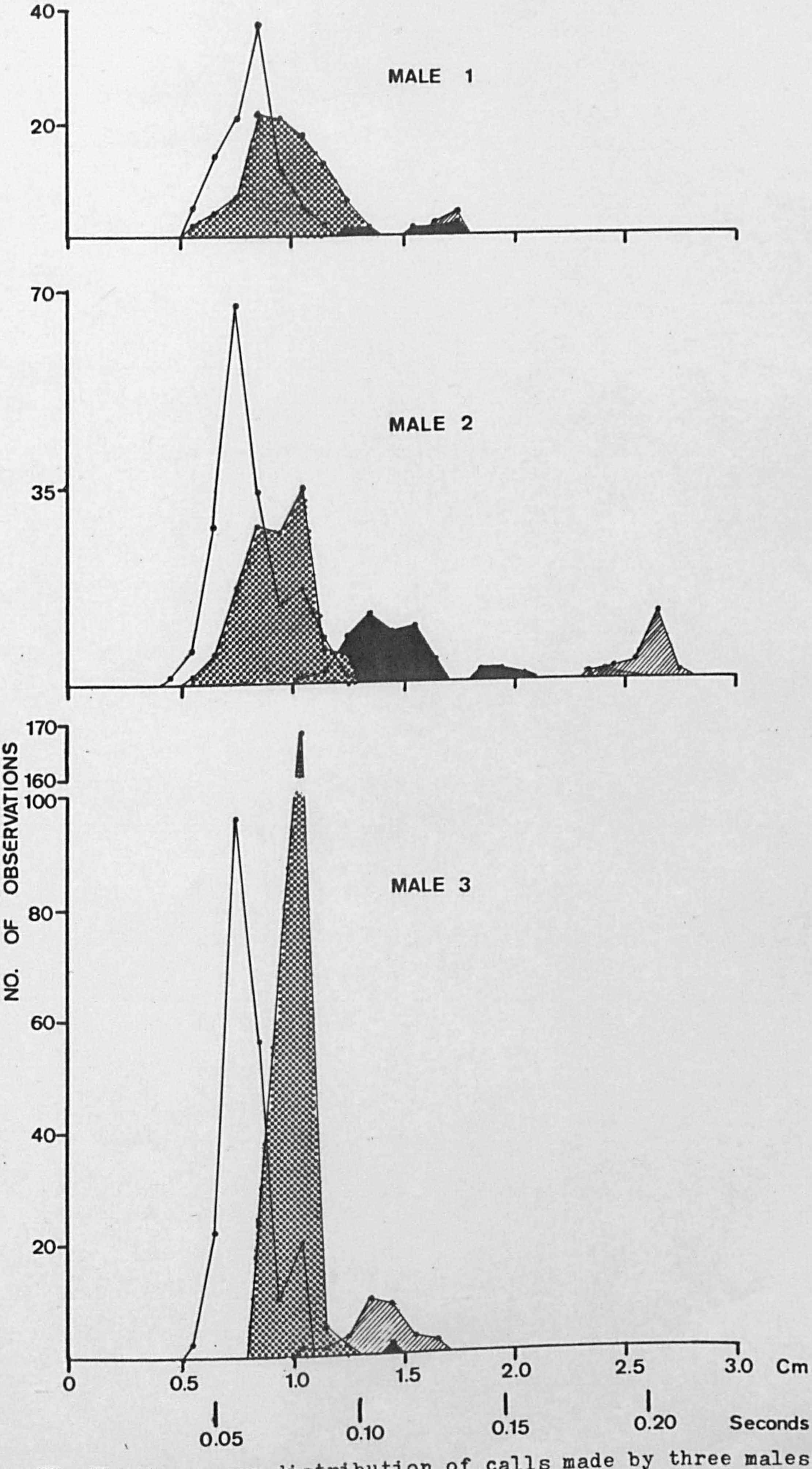


Fig. II. The frequency distribution of calls made by three males; a measure of the duration of each call.

TABLE 16. Measurements of the calls of Pairs 1, 2, and 3. Mean scores are shown together with their standard errors

		MALE				FEMALE			
PAIR 1		No. of calls	Low freq.	High freq.	Dur.	No. of calls	Low freq.	High freq.	Dur.
Loud calls		6				5			
	$\bar{X}$		5.52	6.53	1.67		3.30	3.92	2.28
	SE		0.05	0.03	0.02		0.03	0.02	0.29
Loud/Soft calls		7				44			
	$\bar{X}$		4.86	5.61	1.47		3.30	3.98	1.96
	SE		0.34	0.41	0.08		0.02	0.02	0.05
Soft calls		94				165			
	$\bar{X}$		3.55	3.87	0.94		3.26	3.77	1.45
	SE		0.03	0.01	0.04		0.01	0.01	0.02
Tet calls		97				5			
	$\bar{X}$		3.33	3.66	0.76		3.26	3.48	0.72
	SE		0.01	0.02	0.01		0.08	0.09	0.09
PAIR 2									
Loud calls		19				3			
	$\bar{X}$		3.50	4.21	2.55		4.20	4.90	2.67
	SE		0.05	0.03	0.02		0.10	0.17	0.20
Loud/Soft calls		57				35			
	$\bar{X}$		2.97	5.36	1.40		3.98	4.61	1.68
	SE		0.03	0.03	0.03		0.04	0.03	0.06
Soft calls		122				100			
	$\bar{X}$		3.35	3.62	0.89		3.60	4.19	1.08
	SE		0.01	0.01	0.01		0.02	0.02	0.01
Tet calls		178				62			
	$\bar{X}$		3.12	3.66	0.76		3.50	3.92	0.69
	SE		0.01	0.01	0.01		0.02	0.01	0.02
PAIR 3									
Loud calls		29				21			
	$\bar{X}$		3.26	5.62	1.35		3.62	4.45	2.93
	SE		0.04	0.04	0.03		0.03	0.03	0.06
Loud/Soft calls		0				43			
	$\bar{X}$						3.55	4.20	2.09
	SE						0.02	0.02	0.05

/Continued

TABLE 16 /continued

		MALE				FEMALE			
		No. of calls	Low freq.	High freq.	Dur	No. of calls	Low freq.	High freq.	Dur.
Soft calls		313				165			
	X		3.50	4.04	0.96		3.52	3.98	1.56
	SE		0.06	0.05	0.04		0.08	0.06	0.01
Tet calls		206				35			
	X		3.60	4.20	0.75		3.41	4.23	1.00
	SE		0.01	0.00	0.01		0.02	0.03	0.03

In general terms, the calls of the males show very good evidence of discreteness in all parameters measured. Three distinct peaks are in evidence in the graphs in all cases except for male 3, low frequency (LF). Female calls, on the other hand, indicate more possible overlap between different call types and in the duration measure a continuous overlapping spread of the four calls was obtained. Nevertheless, the results of the t tests indicate that female calls still remain significantly different in many cases. Details of the calls are as follows:

(a) <u>The male calls</u>

Loud and loud/soft calls

These were clearly distinct from the softer calls and little overlap was found except in low frequency scores in some cases. Differences between L and L/S calls were difficult to assess as male 3 gave no L/S calls, male 2 had an atypical harsh L/S call, the frequency of which was difficult to measure, and male 1 gave only a few of the louder calls during the recording period.

In all the males the louder calls were clearly longer than the softer ones.

Soft and tet calls

The ranges for the S and T calls show considerable overlap though their mean values remain distinct in all measures (except the low frequency of male 3's calls). The harsh nature of the Tet meant that, in practice, these two calls could be readily distinguished by a human listener.

(b) <u>The female calls</u>

Loud and loud/soft calls

Unlike the situation reported for the males, the female L and

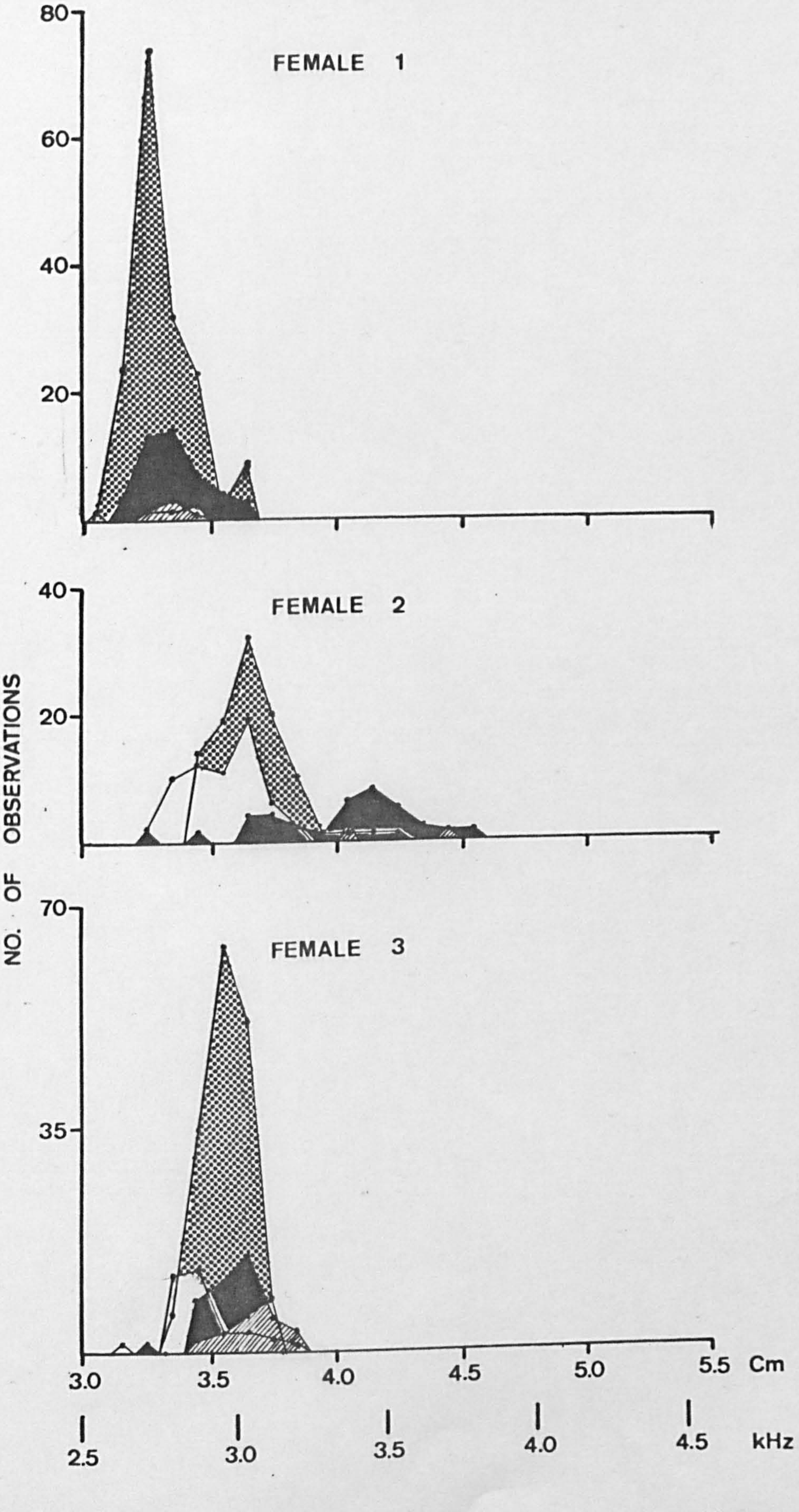


Fig. I2. The frequency distribution of calls made by three females; a measure of the lowest frequency of each call.

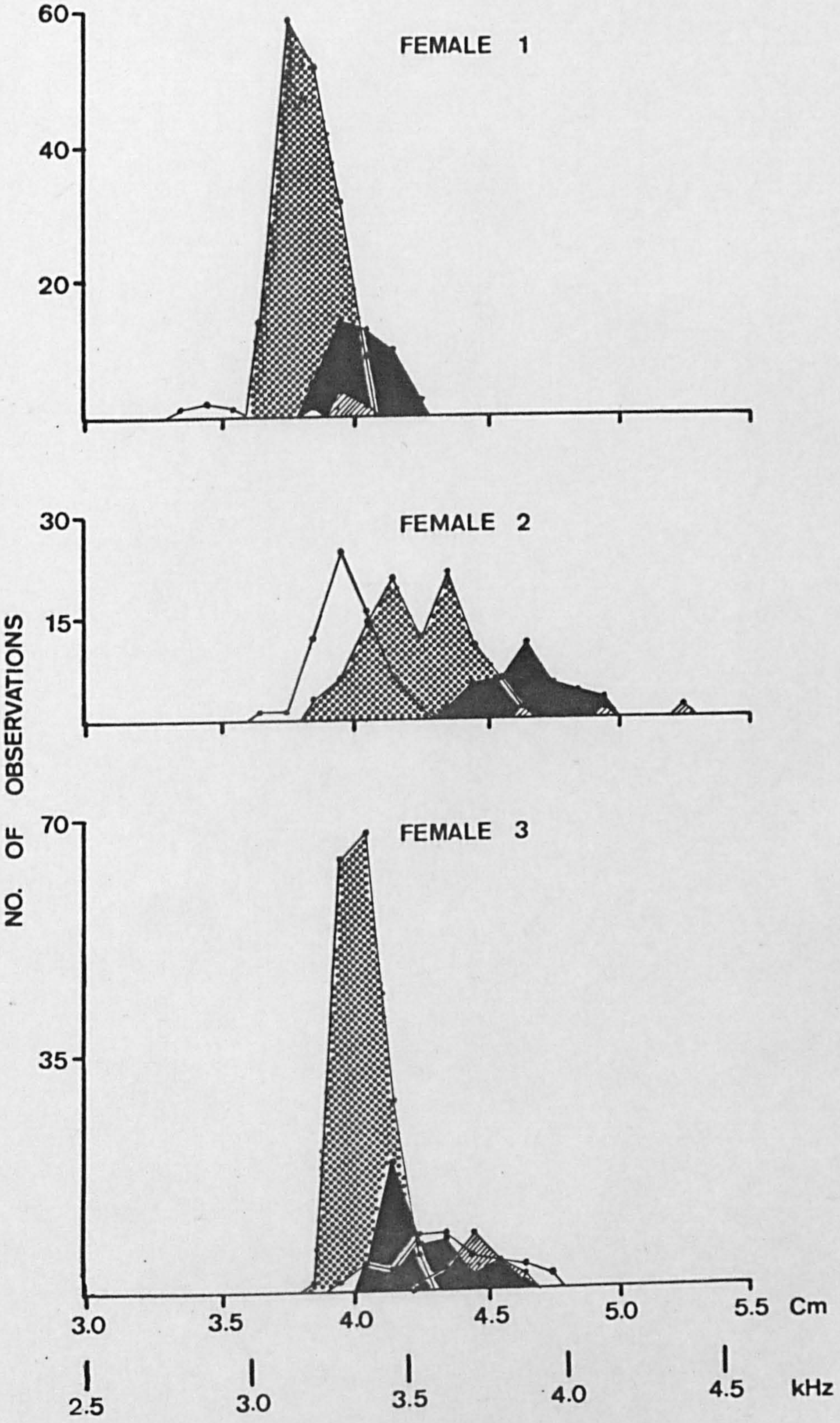


Fig. I3. The frequency distribution of calls made by three females; a measure of the highest frequency of each call.

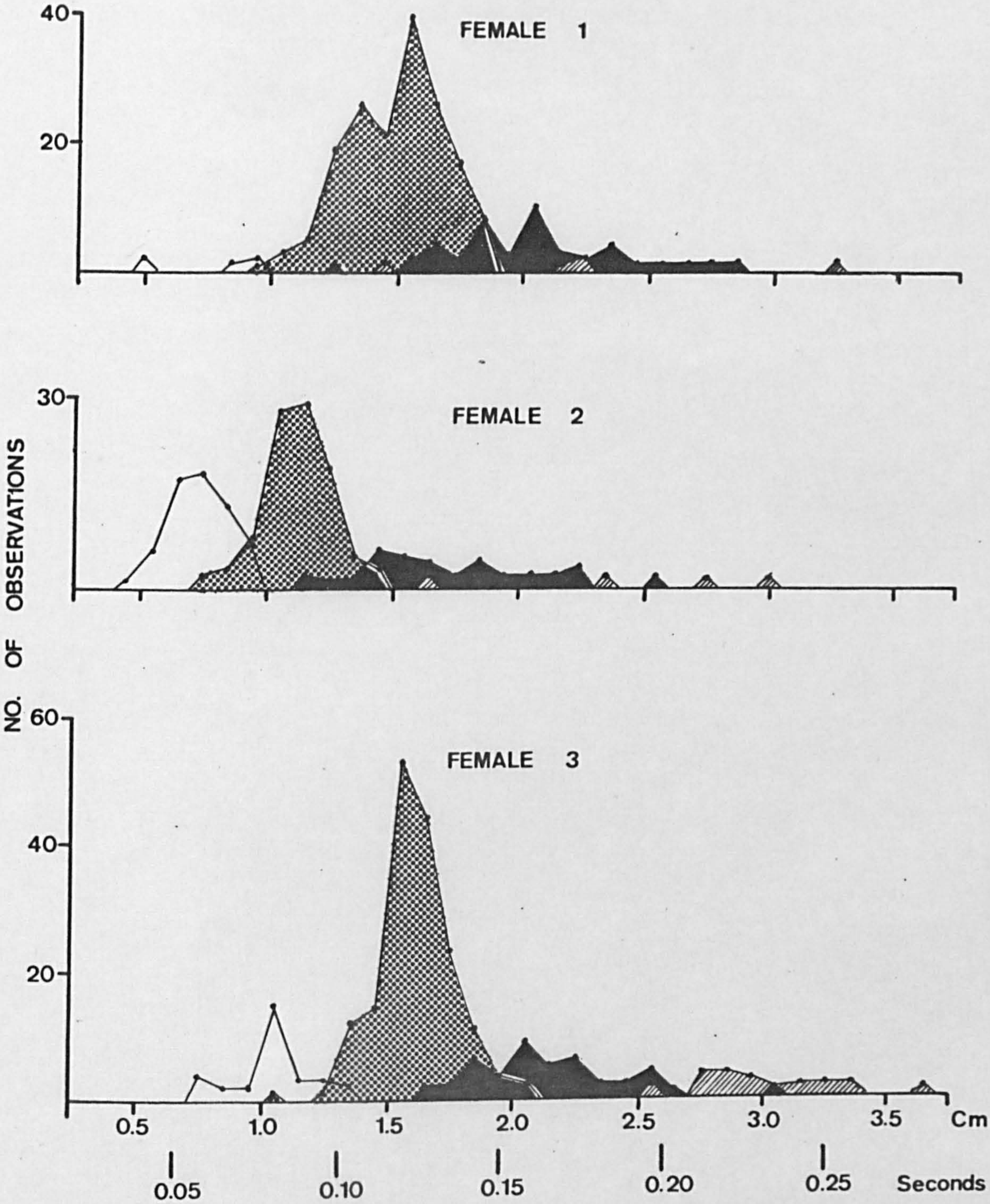


Fig. I4. The frequency distribution of calls made by three females; a measure of the duration of each call.

TABLE 17 A summary of t values obtained when the measures of different calls were compared

	MALE			FEMALE		
Calls compared	Low frequency	High frequency	Duration	Low frequency	High frequency	Duration
PAIR 1						
T v S	6.19***	10.30***	4.57***	0	3.39***	7.70***
S V L/S	3.79***	40.10***	36.04***	1.80	11.30***	9.80***
L/S v L	1.90	17.40***	2.43*	0	2.20*	1.10
S v L	33.30***	44.50***	40.40***	0.20	2.30***	2.90**
PAIR 2						
T v S	15.20***	2.65**	7.37***	4.00***	11.80***	18.80***
S v L/S	11.60***	49.20***	17.10***	8.10***	12.90***	10.10***
L/S v L	9.50***	25.20***	33.40***	2.00	1.70	4.70
S v L	3.22**	19.10***	64.20***	6.00***	4.10***	7.80***
PAIR 3						
T v S	1.90	14.60***	23.20***	4.40***	8.00***	18.60***
S v L/S				1.60	8.70***	11.60***
L/S v L				2.39*	6.70***	11.10***
S v L	7.40***	38.30***	16.40***	3.96***	8.90***	18.40***

T = Tet call
S = Soft call
L/S = Loud/Soft call
L = Loud call

* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

L/S calls were not clearly separated from the softer calls. In fact, the L/S calls tended to form a bridge between the soft and the loud calls. Similarly, the L/S and L calls did not show marked differences; the calls of female 1 were not significantly different by the t test; the L/S was discrete only in the duration measure for female 2; the L/S and L of female 3 shared the same low frequency measure.

Soft and tet calls

Again, as in the males, the low frequency measures showed the greatest overlap. Apparently all the calls of female 1 shared the same low frequency and the S and T calls of all the females tended to share the same range except for duration where they were clearly distinct.

Thus, the four calls studied here in the cases of both the males and the females, appear to be distinct and discrete units in at least one of the three parameters measured. The duration of the S and T calls clearly divides them into two discrete units and of the parameters low frequency apparently shows the greatest degree of overlap in each bird. There was a tendency for female calls to show a greater amount of overlap than male calls, in which the louder vocalizations (L and L/S) are well defined in both frequency and duration from the softer (S and T) calls. It is possible that the S, L/S, and L calls of the female form a continuum in which the high frequency and duration of the call is successively altered.

Discussion

Marler and Mundinger (1971) referred to two types of vocal repertoire in animals; those which are 'discrete' with non-overlapping categories and those which are said to be 'graded' with a variety of subtle variations. The majority of birds studied seem to have the discrete type (see Marler and Mundinger, l.c. for references) and thus, as Marler (1961) pointed out, they appear to obey Morris' (1954) principle of "typical intensity". Morris used this term to describe those displays in which the signal varied little, if at all, with changes in the intensity of motivation of the signalling individual. On the other hand, primate vocalizations have been found to show extensive grading (Rowell and Hinde, 1962, Andrew, 1963, and Nottebohm, 1972).

The evidence, in the case of the Zebra Finch, suggests that the amount of grading of the different call types is limited. However, the separation into four different call types seems no longer justified as the loud/soft calls of both sexes resemble closely the loud calls and cannot be clearly separated from them. They differ only in completeness and intensity with which they are delivered and in the females the suggestion is raised that the loud/soft is possibly an intermediate between the more discrete soft and loud calls. These two, therefore, represent the minima and maxima forms of a continuum. In addition, the tet calls in both sexes can be extended on occasions and intermediates exist between the short tet and this longer, louder, harsher version.

In all the parameters measured the females show more evidence of grading in their calls than do the males. In the latter, the loud calls stand out on their own with the only variation in the call being to produce the incomplete loud/soft type. In the female Zebra Finch, the lowest frequency of the harmonic measured remains roughly constant and it is alterations to the highest frequency reached and the duration of the call which results in the four different call types and their intermediates. In the males this tendency is far less marked and probably holds only for the tet and soft calls. This could be linked with the ontogeny of these different calls as Immelmann (1968) suggests they are all developed as variants of a single juvenile call, the tet being the first differentiated. Zann (1972) agreed with Immelmann in general terms but suggested that, at least in the Poephila spp., there was a separate origin for the loud call in both sexes. The results shown here for the Zebra Finch support Zann and suggest that the sexes may differ in the development of their loud calls; the males appear to have a separate ontogeny for the loud call.

It is interesting to note the possibility of a difference between the sexes in that the female loud call shows signs of grading whereas the male's is very accurately discrete. At first sight, it might appear contradictory to suggest that the female's calls can be both discrete (in terms of loud, soft and tet) and yet, at the same time, graded but a similar situation has been described in the calls of the domestic hen by Konishi (1963) and in the Laughing Gull by Beer (1970c). In both these cases the sexes were similar and Konishi noted that each call type of the domestic hen could be varied in two main ways (in addition to their intensity); (i) discontinuous or digital coding in which the rate of delivery of pulsed or multiple sets of sounds is varied; (ii) continuous or analogous coding of sustained sounds in which the duration of the calls is varied depending upon the intensity of the stimulation.

Both male and female loud calls of the Zebra Finch are relatively short and could show digital coding, but only the females show any evidence of the analogous type of coding, i.e. variation of the duration of the call. The individual frequencies of the female's call does not alter appreciably as the duration is increased and thus only one parameter is apparently involved. Konishi goes on to propose that calls possessing discrete differences function to convey qualitatively different information (i.e., the tet, soft and loud calls), whereas variation within types indicates differences in the intensity of stimulation.

It seems likely therefore that the highly discrete nature of male loud calls is important to convey a particular piece of information, one whose content cannot be jeopardised by grading of the call with the resulting chance of misinterpretation. The information transmitted could well be the identity of the calling bird. If this is the case then the grading of the female's call suggests that less emphasis is placed on conveying predictable information and the call is altered to carry additional information. This raises the possibility of different functions for male and female loud calls which may well have bearing on the way in which they are used in the maintenance of the pair bond.

6.1 C. The context of different calls

Introduction

In sub-sections 6.1 A and B it was shown that the calls of Zebra Finches show considerable inter-individual variation and that they are probably reproduced accurately enough to be used for recognition by mated birds. As yet little has been said about the contexts in which the different call types are used and how they might be of benefit in pair maintenance and hence prolong pair bonds. This is likely to be a lengthy topic and one which would benefit enormously from studies of Zebra Finches in the wild. However, this short report on calling rates, in the laboratory situation only, may be useful in at least indicating the use of different calls in the pair bonding situations considered so far (i.e., flight cages in captivity). It is not meant to be an exhaustive study but will indicate how the distinctive features of the loud, loud/soft, soft and tet calls may be suited to the role they are expected to fill in the day to day life of the pair bond.

The term "context" can be taken to have a number of meanings and thus it is important to define this term clearly at the outset. Smith (1965) discussed the context of vocalizations in some detail and listed two factors that could be of importance to the receiver of a particular call. These were, (a) the immediate context of the call (i.e., the specific environment in which the call was received, where and when), and (b) the historical context of the call as the input will be modified by the receiver in the light of any genetic and/or learned preferences. In the case of the Zebra Finch one must assume, at this stage, that some preference for the mate's calls exists, be it genetic or learned, and in this experiment only the immediate context of calls will be assessed.

Obviously, in the laboratory cages movements of birds will be restricted and conclusions about the functions of the calls difficult to draw. This point was made by Crook (1970) and the observations that follow were undertaken with due regard to the limitations set by studies on captive animals.

Methods

10 "established" pairs of birds were used, the same as in 6.1 A, with the identical flight cage and microphone placing outlined in 6.1 B. Each pair was examined separately for a period of one hour in the morning after spending at least 20 hours in the experimental cage (the preceeding afternoon and night).

The experimenter remained in the room throughout the recording and assessed the activity of the birds. This could be related to the recording by means of the numbered scale on the tape recorder which was zeroed at the start of each session. As the activity of a bird changed the new activity was noted with the accompanying scale reading which indicated its relative position on the tape. On subsequent playback this position could then be recognised and preliminary trials suggested that potential stretching of the tape did not affect this measure appreciably.

The different activities noted were,

(1) both male and female flighting,

(2) male flighting / female sitting alert,

(3) female flighting / male sitting alert,

(4) both birds sitting alert,

(5) both birds sitting drowsily (plus sitting clumped),

(6) both birds feeding,

(7) male feeding / female sitting alert on the perch,

(8) female feeding / male sitting alert.

Clumping was not particularly frequent in these morning sessions and therefore it did not deserve its own category and was included in sitting drowsily. However, the calls given during these few clumping periods are presented separately as well.

On playback of the recordings it was usually possible to distinguish the male's calls from those of his female. The softer calls tended to be the most difficult, as the study of sonograms suggested, but with practise such difficulties were quickly overcome. The length of an activity bout was first measured with a stop watch and then the number of different calls given by the male and female during this period was counted. Where calling was rapid the tape speed could be reduced to make the tabulation easier. In this way it was possible to calculate the rate at which the different calls were given during each activity category for the whole experimental period. From this, computation of the mean calling rate for both sexes was possible.

Different rates of calling were compared, where necessary, using the Wilcoxon matched pairs test (WMP) for related samples, and the Mann-Whitney U test (MWU) for independent scores (Siegel, 1956).

Results

The histograms (Fig. 15) and Table 18 show the rate of calling per minute in each activity. Missing are figures for 'female flighting / male sitting alert'. This is because females were never seen flighting without their mates which is an interesting result in itself. Flighting consisted of short to and fro flights across the cage above the level of the perches and males spent, on average, more than 26 minutes of a 1 hour watch engaged in this activity. The females joined them for more than half of this time (+16 minutes),

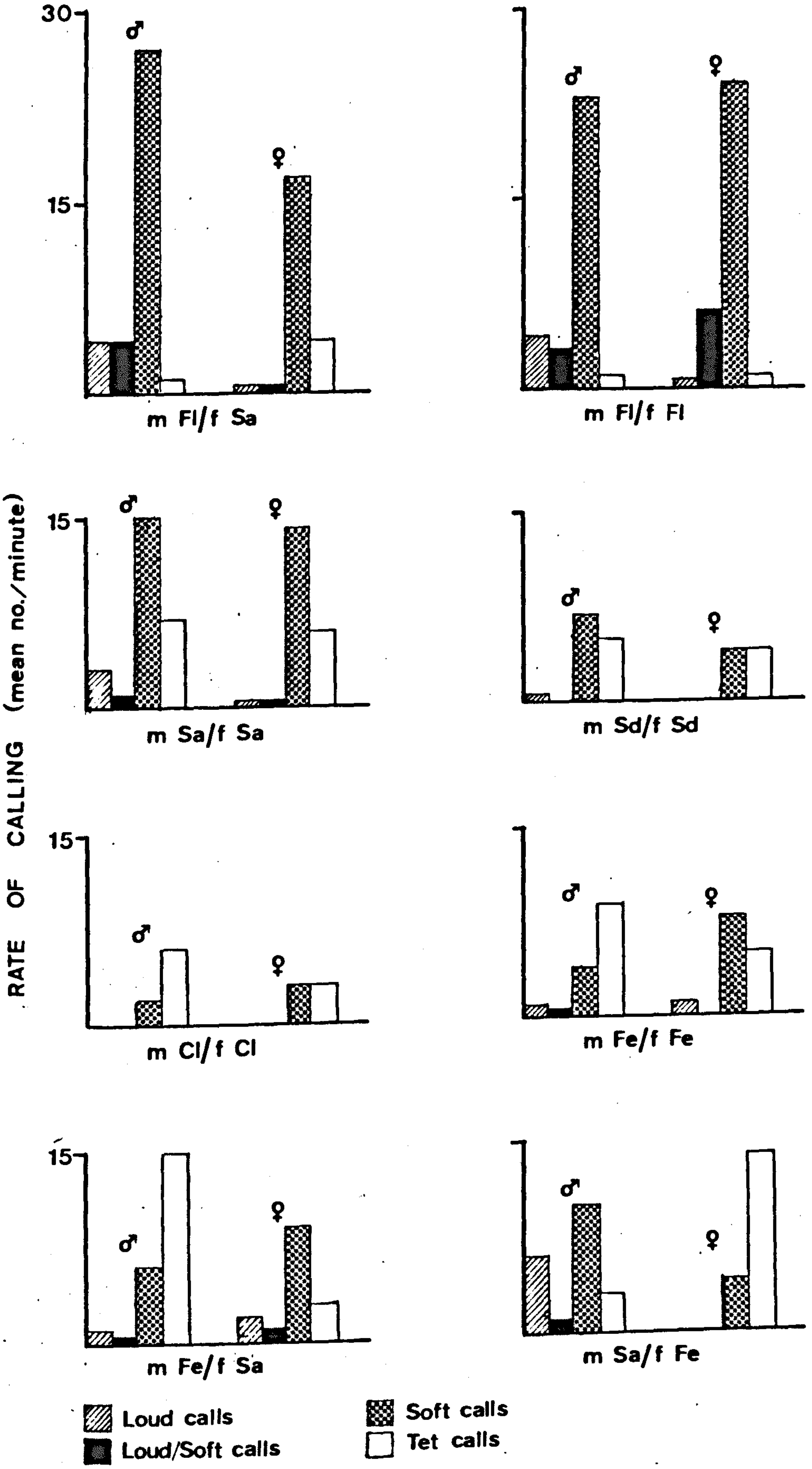


Fig. I5. The rate at which four different calls were given by males and females in eight different contexts. For an explanation of the abbrieviations - see text.

TABLE 18 The rate of calling by males and females engaged in different activities expressed as number of calls per minute

Activity	No. of indls.	Loud calls	Loud/Soft calls	Soft calls	Tet calls	Total calls	Time spent (secs)
Males							
M fl/F sa	10	3.7	3.8	26.6	1.1	35.2	625
M fl/F fl	10	3.9	2.9	22.6	1.5	30.9	994
M sa/F sa	10	2.7	0.6	14.5	7.4	25.2	860
M sd/F sd	7	0.4	0	6.7	5.0	12.1	513
M cl/F cl	3	0.1	0	2.0	5.8	7.9	184
M fe/F sa	9	0.9	0.3	5.6	14.3	21.1	287
M fe/F fe	9	1.2	0.5	4.1	8.8	14.6	105
M sa/F sa	10	5.6	1.3	9.8	3.4	20.1	454
Females							
M fl/F sa	10	0.2	0.5	17.0	4.3	22.0	625
M fl/F fl	10	0.5	6.2	23.8	1.3	31.8	994
M sa/F sa	10	0.5	0.3	14.3	6.2	21.3	860
M sd/F sd	7	0	0	4.4	4.0	8.4	513
M cl/F cl	3	0	0	2.5	2.6	5.1	184
M fe/F sa	9	1.8	1.0	9.1	2.9	14.8	287
M fe/F fe	9	0.6	0.1	8.0	5.0	13.7	105
M sa/F fe	10	0.1	0.1	4.9	14.4	19.5	454

M = Male

F = Female

fl = Flighting

sa = Sitting alert

sd = Sitting drowsily

cl = Sitting clumped

fe = Feeding

they tended to follow the male and each bird alighted on the perch in turn before beginning the next flight across. The birds were thus 'active' for the majority of the watch and only 8 minutes 33 seconds, on average, was spent sitting drowsily. Both birds quickly became active at the end of such a period of rest and hence there were no recorded cases of 'male sitting alert / female sitting drowsily' or vice versa.

From the results it is clear that calling rates varied with the activity birds were engaged in. The highest rates occurred during flighting in both sexes, the lowest were given during periods of rest (sitting drowsily). Overall, with one exception, males called more frequently than females in every category ($p < 0.05$, MWU). The exception was when both individuals were flighting the females in this case gave slightly more calls than the males. A general pattern emerged when comparing the total calling rates of the two sexes. Highest rates were given in flight, then sitting alert, then feeding and lowest rates when sitting drowsily or clumped.

Loud calling

These calls were associated with active periods in both sexes and were given at a higher rate when sitting alert than when sitting drowsily ($p < 0.05$, WMP). The highest rate was recorded for both sexes when the caller was perched and the mate feeding on the floor of the cage though this did not differ significantly from the rate when sitting alert. Calls during flighting periods were mostly given between each flight rather than in flight.

Loud/soft calls

These calls, like the loud calls, were given when birds were active but differed in that far more were given in flight than when sitting alert ($p < 0.05$, WMP for both sexes). The calls were given whilst actually in flight and often immediately after take off and it could therefore be regarded as a "flight" call (see Evans (1972) for the flight calls of Cordon Bleus; Estrildidae).

Soft calls

The soft call was the most frequently heard call and was given, on average, once every three seconds when flighting. Highest rates were associated with active periods and particularly flighting when both sexes gave significantly more than when sitting alert ($p < 0.05$, WMP). Low rates, comparable to those whilst sitting drowsily, were noted during feeding bouts whether these occurred with the mate or alone, the rate during feeding was significantly less than that whilst sitting alert ($p < 0.05$, WMP).

Tet calls

These calls were heard in all situations but, unlike the other call types, lowest rates were given during flighting (flighting < sitting alert; $p < 0.05$, WMP, both sexes). They appeared to be associated with feeding bouts being given from the floor of the cage or the feeding bowl particularly when an individual was feeding alone. In this latter case, the calling rate was increased over that when both birds were feeding simultaneously and this was largely due to an increased number of tet calls (feeding with partner < feeding alone; $p < 0.05$, WMP).

Discussion

The results of this experiment show the consistent use of different calls in different contexts by the Zebra Finch. The sexes tend to be similar though some differences did emerge. For example, in all situations except those in which both birds were flighting, males gave more calls than females. This was noted in the

Budgerigar by Brockway (1968) and she suggested it reflected a lower threshold for calls in the males due to the presence of androgens in their blood stream. This could also be the case in the Zebra Finch.

Taking each call in turn: first the loud call. These were associated with active periods and have been termed 'identity' calls by Immelmann (1965). Zann (1972) points out that they are the loudest signal produced by estrildids. Zann also noted that they were given by members of a pair of Poephila after separation or when an individual was removed from a flock. They could therefore be considered 'lost' calls, he concluded. However, this is not the only context in which this call type is heard as they are also given in alarm situations (e.g., during sudden disturbances) and hence 'lost' call is not an entirely satisfactory term to use.

As shown earlier (see 6.1 A) the loud calls could carry abundant information indicating the individual identity of the caller and the contexts in which they are given suggest an additional message, possibly one of "come to me" as Zann (l.c.) proposed for the Poephila spp.. The calls should therefore be easy to locate and the fact that they cover a wide frequency range, begin and end abruptly and are repeated often suggests that this will be the case (q.v., Marler, 1956). However, Zann queries this basis for location of sounds by birds in that he noted attraction to a pure note, a whistle, which was given in the field and whose auditory qualities were the exact antithesis of those Marler proposed. The fact that these calls may attract the mate, or other conspecifics, does not necessarily exclude their usage in alarm situations. Morgan and Howse (1973) report that in corvids and gulls the initial response to a distress call is one of approach which is only subsequently followed by dispersal of birds. The rate at which the calls are given can be altered and presumably this indicates the degree of alarm registered by the sender. In addition the females, as noted earlier, can increase the duration of the call in exceptional motivational circumstances.

Loud/soft calls are interesting as they appear to be contextually different to the loud calls. The latter were always given from a perched position whereas loud/soft calls were most prevalent during actual flight for both the males and females. Thus, at least in terms of context, this call category seems justified even though Section 6.1 A suggested the loud/soft call was 'only' an incompletely delivered loud call.

The soft call was the most frequently used call by both sexes particularly whilst the bird was active around the cage. It seems to be the same call as Immelmann's (1965) "contact" call and presumably, as he suggested, it serves to keep mates in close contact as it can only be heard over short distances. It may be important in coordinating take off by the mates as its rate of repetition increased just prior to actual flight. The soft call was used in flight accompanying the loud/soft type. Male 3 gave no loud/softs at all, instead he used a rapid repetition of soft calls throughout his flighting activities.

Finally, the tet call appeared to be associated with feeding bouts by the Zebra Finches used in this study. It was given at its fastest rates when a bird was feeding alone, its partner on the perch. Immelmann (1962) noted that tets were used by Zebra Finches to indicate flight and they increased in rapidity of delivery prior to take off. As outlined above, in this study soft calls were used in this context. Zann (1972) reported that tets were never given by Poephila which were feeding in the wild and without similar studies on the Zebra Finch in its natural environment the situation with regard to tet calls must remain unclear. The extended tets given occasionally on the floor of the cage may well have been examples of the alarm or "Cha" call described by Immelmann (1965). If this is the case, evidence from Section 6.1 B suggests that a gradation exists between tet and Cha calls.

6.2 The Song

A sonogramic analysis of courtship and non-courtship song

Introduction

The songs of Zebra Finches have been described by Morris (1954) and Immelmann (1969) and have featured in reviews of estrildid songs (e.g., that of Hall, 1962). They are given only by males and consist of a short individually distinct phrase made up of a series of notes or elements which is repeated several times in any song bout. The sound that results is unmusical, monotonous and has been likened by Morris (l.c.) to a "squeaking wheel". It is not a loud accoustical signal and would presumably therefore only be affective for communication over short distances.

Male song could well have a pair maintenance function similar to that suggested for calls and thus it deserves analysis in this study. Presumably the song may attract the female both during the initial period of pair formation and subsequently during the life of the pair bond. If this is the case, it will be important that the female can recognise and behave preferentially towards her own mate's song. The songs of different males could be expected to show individual characteristics to facilitate this recognition and therefore the songs were examined closely and the amounts of intra- and inter-individual variation assessed.

The same song is given in two situations. One, when accompanying the courtship dance, is most likely sexually motivated and is thus easy to define as courtship song. The second song type, however, is less clear and has been termed undirected song. This is a less useful term as it can only be defined by exclusion of the other song type, that is, it is song given in all situations other than courtship. In addition, it may also be misleading in that this song could well be directed towards some object in the environment on some occasions. One possible situation in which undirected song can be used is on separation of the mates when it may assume a contact-promoting role which clearly is of relevance to this thesis. In view of these considerations, courtship and undirected song of male Zebra Finches will be compared to discover if their structure differs to any extent.

Methods

Song was obtained from the 10 males of the established pairs used in the experiments of Section 6.1. Courtship song was readily obtained by separating the male from his mate and then reintroducing him to her after 30 minutes. The undirected song was obtained from tapes recorded during the course of Experiment 6.1 C.

Sonograms were made of the songs (as in 6.1 A) and at least 10 phrases of each song type was obtained for each of the males. Measures were as for the calls but in many cases harmonics were absent from the song elements. In these cases a recognisable or prominent feature of the element was chosen for measurement. The large differences between songs of different males mean that subjective comparisons were frequently the most useful.

The duration of each song element was measured as for the calls but, in addition, a second possibly more accurate measure was taken. This was suggested by Marler and Isaac (1960) and involves measuring the distance from the start of one element to the start of the next (i.e., it includes the interval between the elements). This, they argue, will exclude possible errors due to incomplete, or variable, representation on the trace of the decay portion of each element.

Results

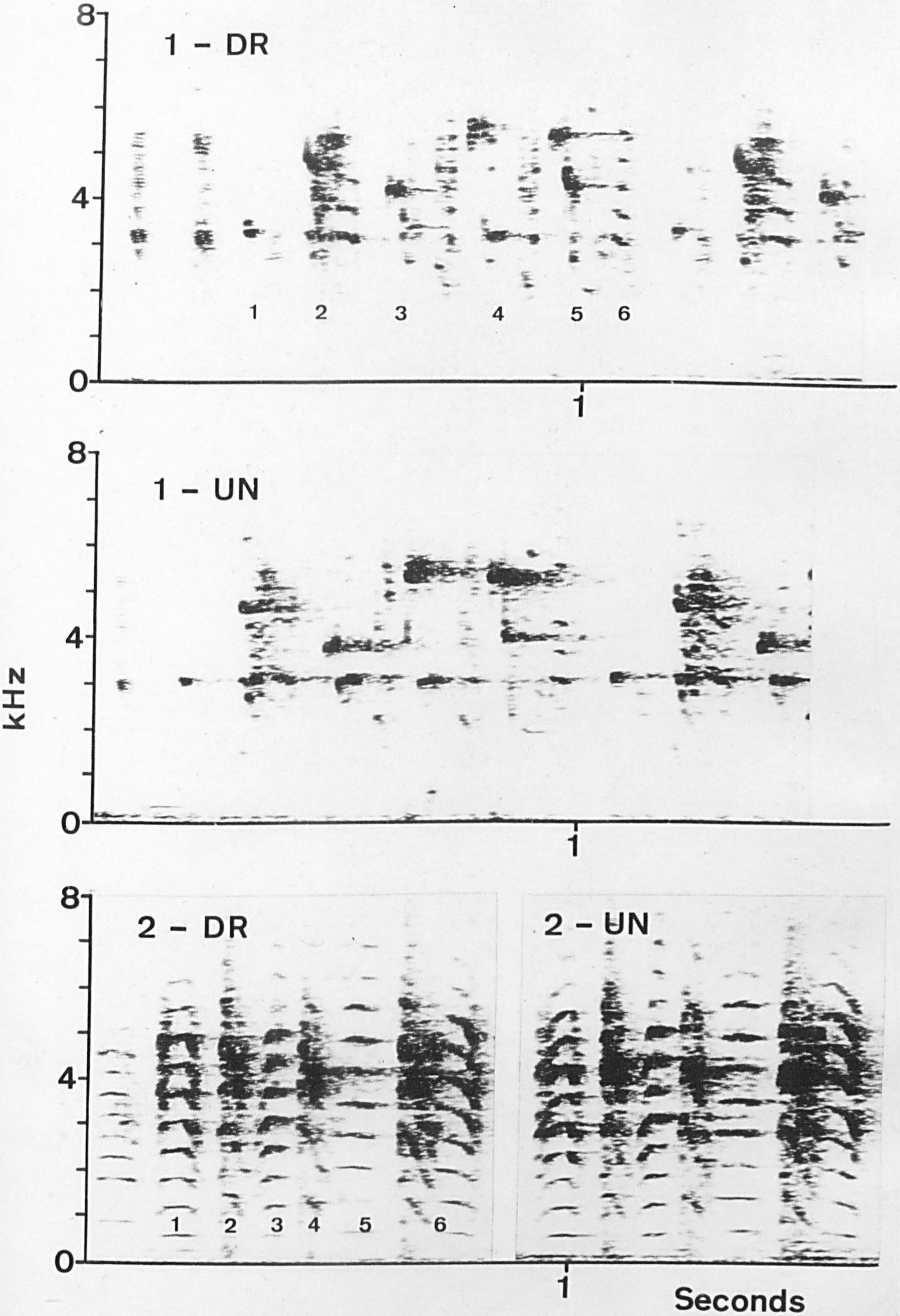
The sonograms are presented (Pl. 9 - 14) and should be referred to with these results. Tables in Appendix II show the quantified measures. To avoid duplication of comments, the courtship songs (labled DR on the plates) will be compared for intra- and inter-individual variation. The numbers on the sonograms indicate the different elements of the song phrase. There then follows a comparison of courtship and undirected (labelled UN) song.

The sample of songs illustrated reveals a tremendous variety both in song phrase construction and the elements of which they are composed. In males 9 and 10 the phrase is of highly variable length and made up of a single element which is repeated in a monotonous fashion; males 1 and 6, on the other hand, possess a short, stereotyped phrase consisting of several complex elements. These songs apparently abound with informational clues which could be used for individual recognition of the different males. The only feature all the males seem to share is the emphasised range of the sound energy comprising the songs. This is from 2.0 to 6.0 kHz, which is much the same as for the calls (see Section 6.1 A).

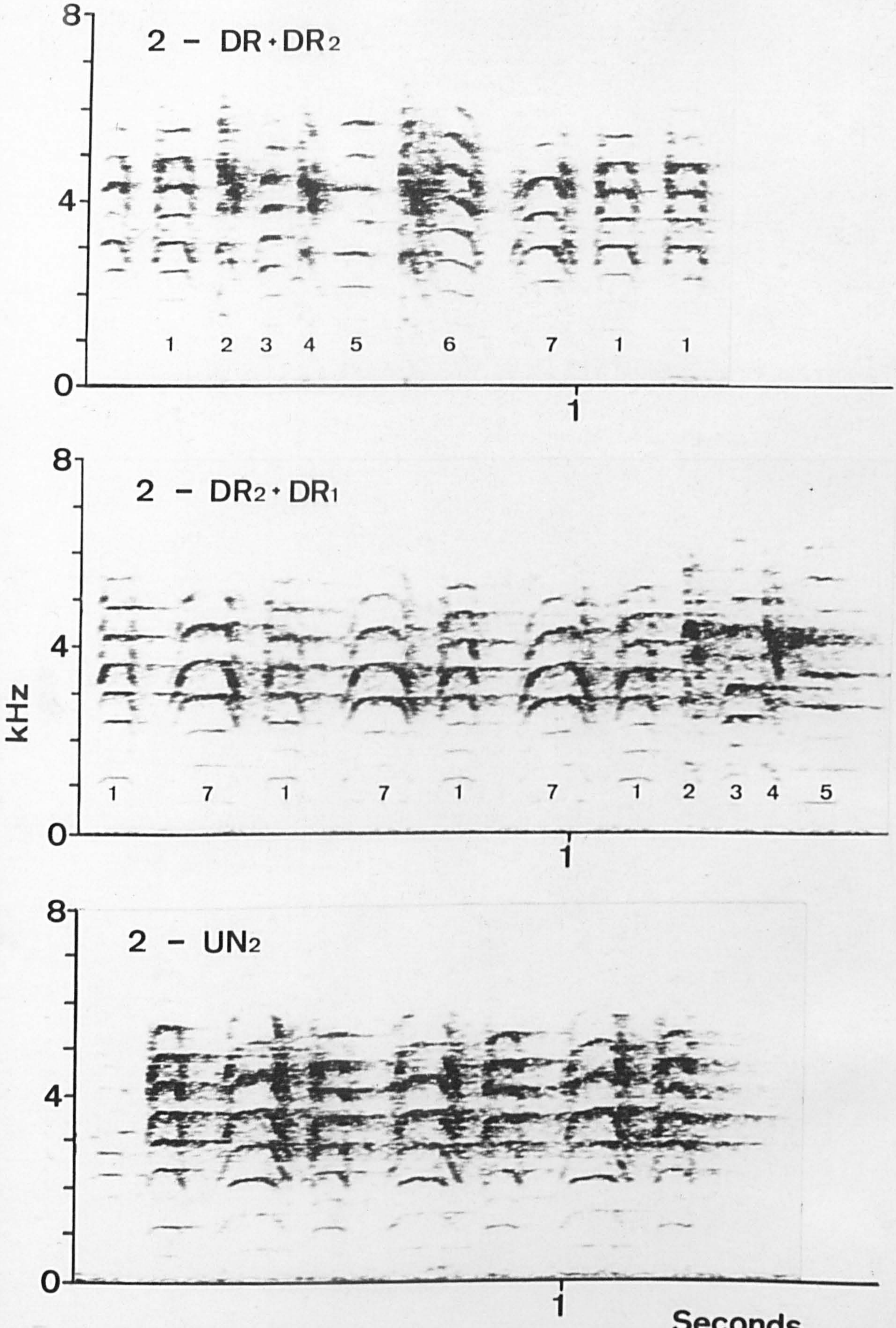
One other general point, the songs, both courtship and undirected, are preceeded by "warm-up" notes. These are given before the actual phrase in variable numbers and are included on most of the sonograms. They often resemble soft calls, but in some cases may represent a new element in the vocal repertoire of the male. They appear to demonstrate considerable variation and a discussion of them is included below.

(a) Intra-individual variation

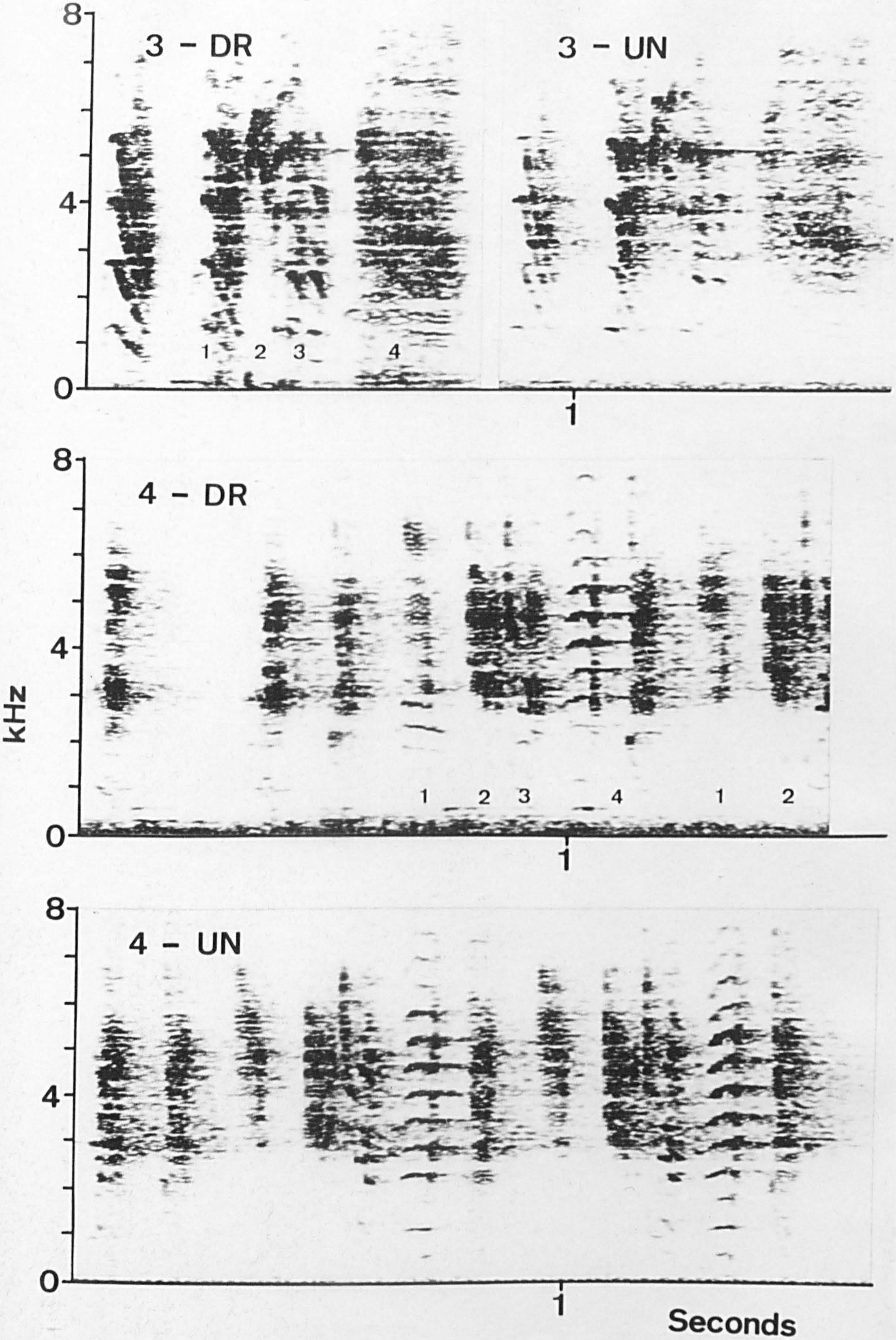
The songs of the individual males are remarkably stereotyped.



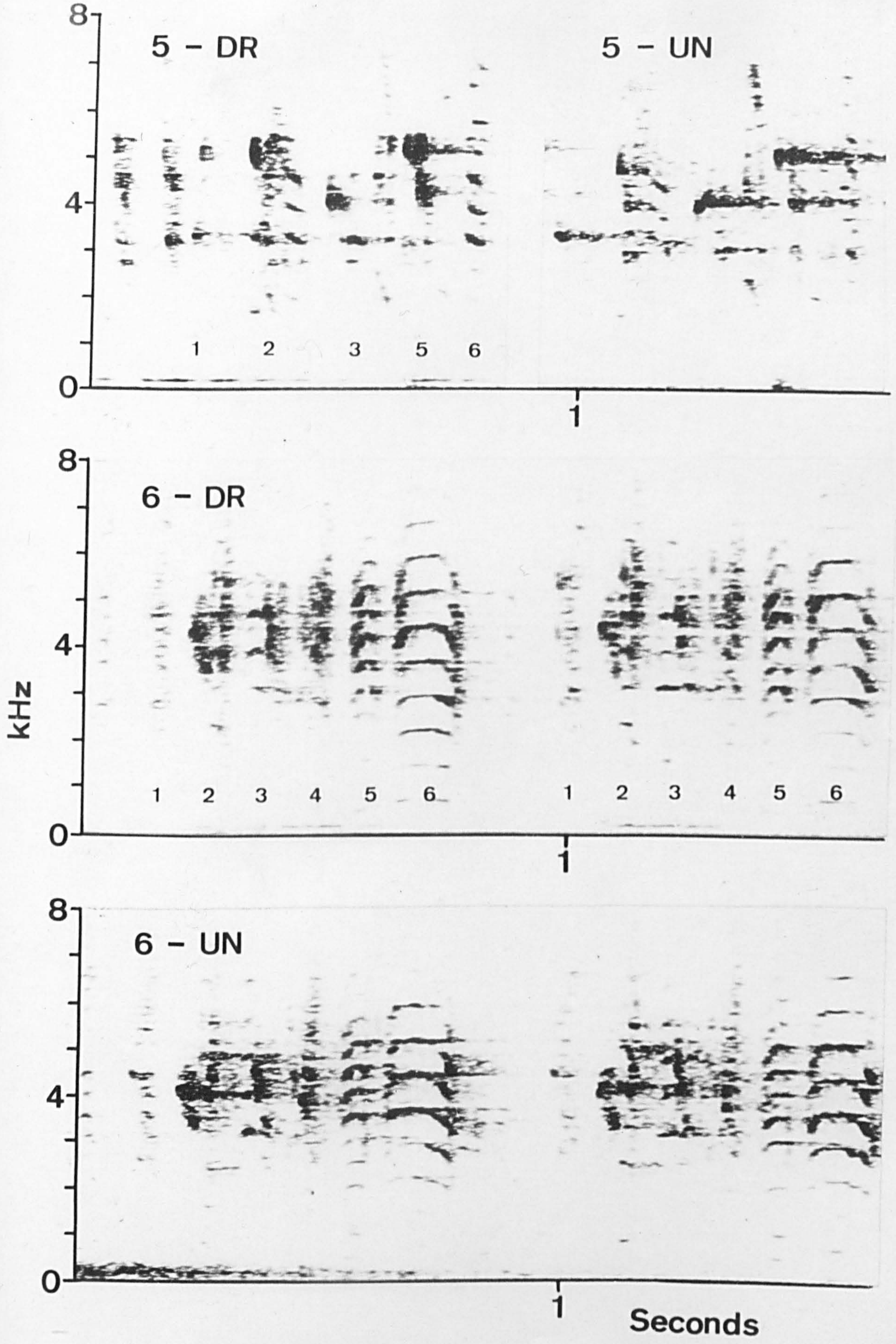
Pl. 9 Male Song



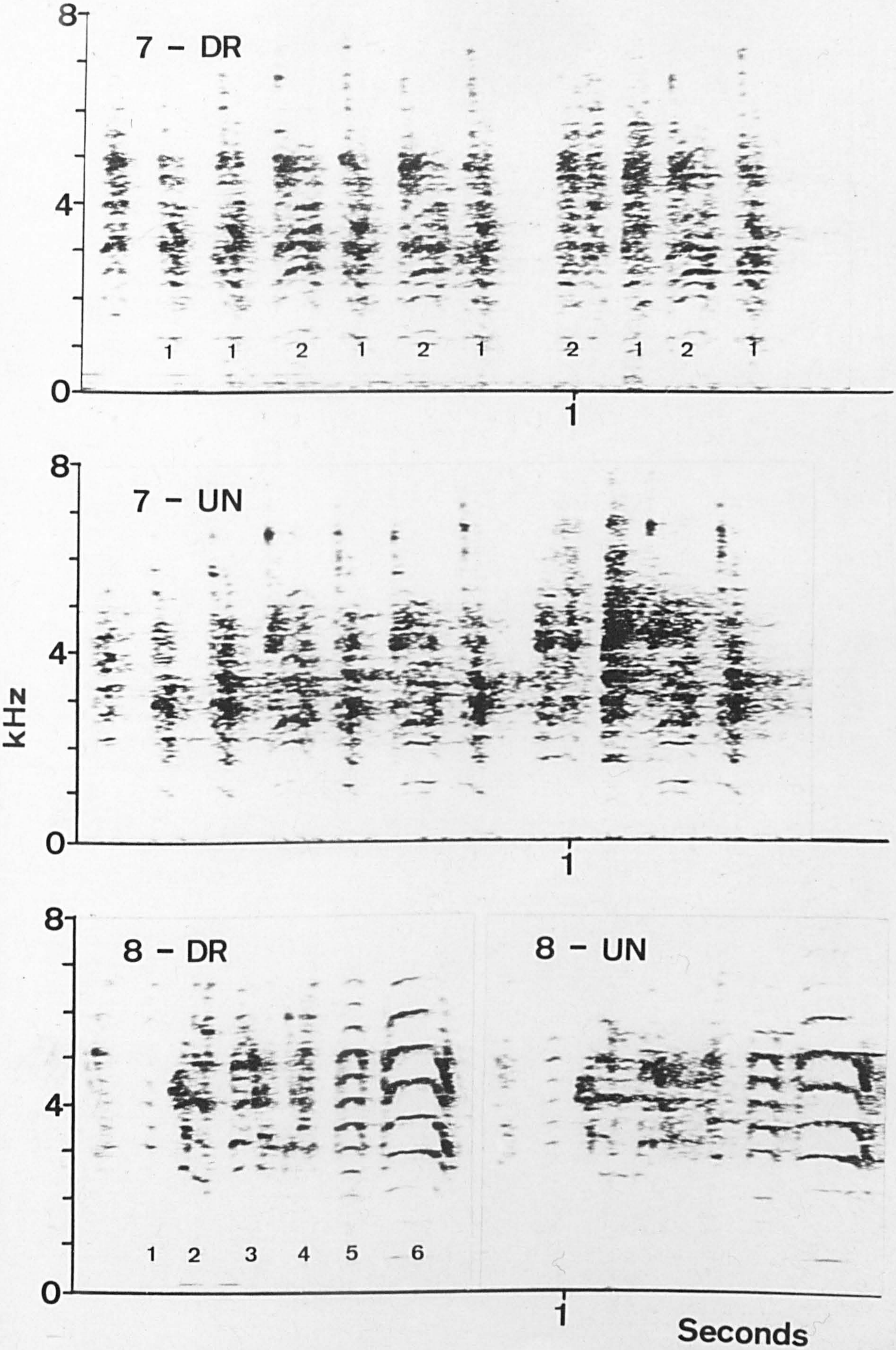
Pl. 10 Male Song



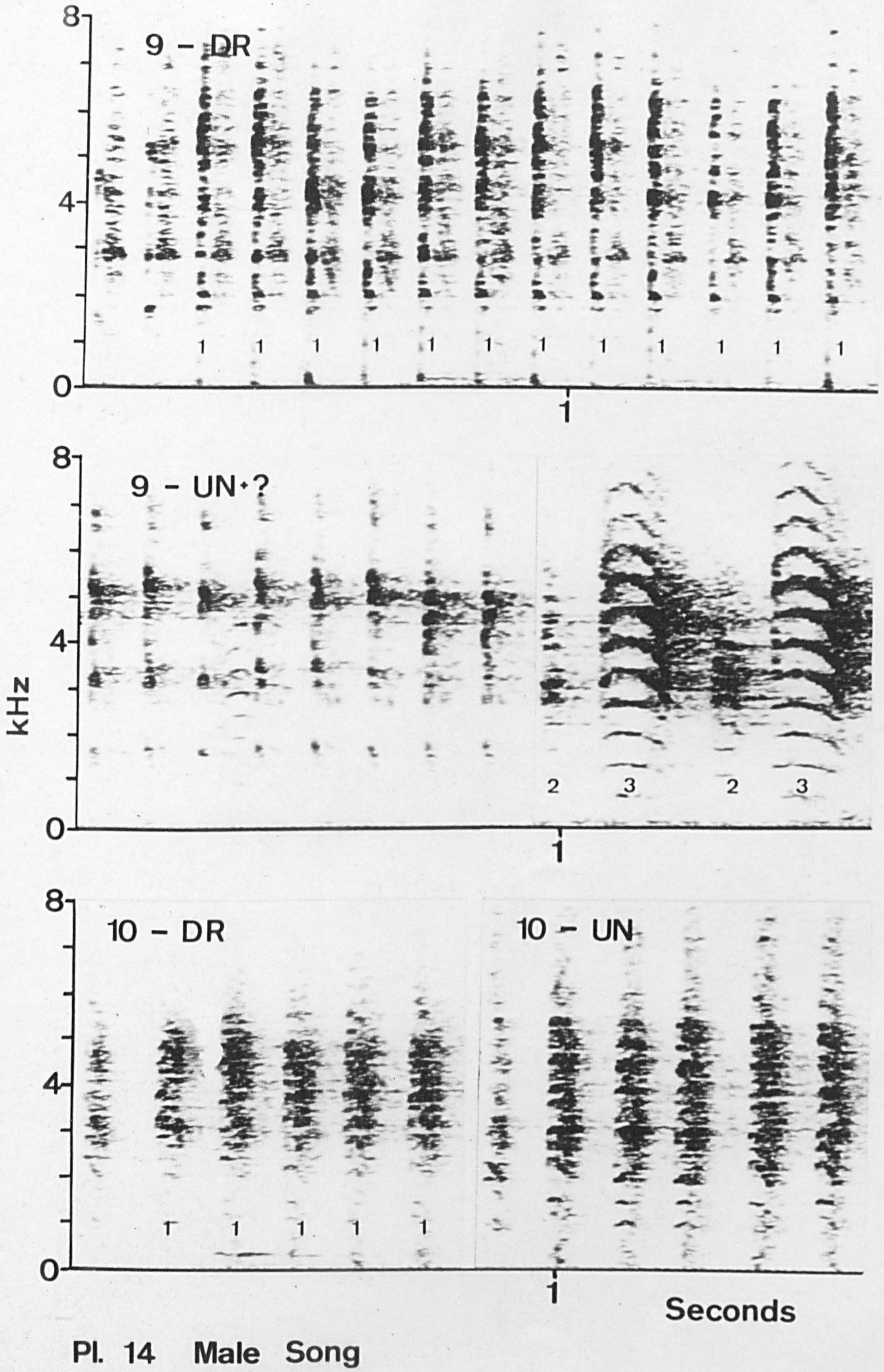
Pl. 11 Male Song



Pl. 12 Male Song



Pl. 13 Male Song



Pl. 14 Male Song

Variations in frequency and duration measures are extremely small (see Appendix IIfor standard error and coefficient of variation scores) and are of the same order as those reported earlier for the calls. The duration measures again show the greatest lability but it is interesting that using Marler and Isaac's (1960) method it can be demonstrated that the timing of the elements is in fact very accurate and the errors involved are of the same order as for frequency measures. This suggests that if the duration of the individual elements in the phrase is being altered then the interval between elements is also altered to compensate for this change and the overall length of the phrase remains the same.

In view of the highly accurate nature of successive song phrase renditions it would seem acceptable to closely compare the songs in order to assess inter-individual variation.

(b) Inter-individual variation

The first impression is of wide disparity between individuals; each male appears to have a unique song with elements which bear little structural relationship to other vocalizations. The sonograms of different males can be readily sorted by eye and the individual songs are quite easily distinguishable by ear. A closer examination, however, reveals some interesting similarities between the songs of different males and one case of a male with two different song phrases! In addition, comparisons between songs and other vocalizations (i.e., calls) shows that many of the song elements are unique in the vocal repertoire of the males (for the calls data see Section 6.1 A).

(i) The songs of males 6 and 8

The subjective impression from the sonograms for these two males is that they sing exactly the same song phrase. The courtship phrase of male 6 can be described as follows;

warm-up note - very short, harmonic soft call,
Element 1 - harsh, tet-like but extended note,
Element 2 - harmonic but with an initial harsh overlying component in the 3.5 - 5.0 kHz range.
Element 3 - this is similar to Element 2 but the initial harsh component is missing,
Element 4 - again similar to 2 but far more tet-like with little evidence of any harmonic structure,
Element 5 - a harmonic soft call,
Element 6 - a harmonic loud call.

Male 8 shares these elements, the measures (Appendix II) are almost identical but there is one marked difference between the two songs. The sonogram for male 8 shows that the warm-up note and Element 1 of male 6's song have exchanged roles.

It is also interesting to compare the calls of these males with the elements of their songs. The loud calls of males 6 and 8 are harmonic but differ both in frequency and duration (male 6, 3.7 - 4.4 kHz, 144 msec.; male 8, 4.1 - 4.9 kHz, 151 msec.). The frequencies of Element 6 of their songs most closely resembles the loud call of male 8 (4.0 - 4.7 kHz) whereas the duration differs in the same way as their loud calls did (i.e., it is 144 msec. for male 6 and 151 msec. for male 8). Thus this loud call-like Element 6 is similar in both birds yet their actual loud calls differ significantly ($p < 0.001$, t test) in both frequency and duration measures.

Element 5 bears no relation at all to the soft calls of either male which is especially interesting as the latter are identical.

Similarly, measures of the harmonics of Elements 2 and 3 are not similar to the soft calls.

Thus, though the harmonic song elements of these birds show similarities to their soft and loud calls they are not identical with them. This may suggest a separate ontogeny or development of these sounds.

(ii) The songs of males 1 and 5

The warm-up notes and elements in the song phrases of these two males are identical with one notable exception. The fourth element of male 1's song is missing from the song phrase of male 5.

The songs consist of few harmonic elements though these are present as components of Elements 2 and 6. The frequency of the 6th harmonic is different in each case but bears no resemblance to the loud or soft calls of either male.

The loud calls of males 1 and 5 are structurally very similar. They share the same harmonic shape, the same low frequency but differ both in highest frequency and duration measures ($p < 0.001$, t test). Their soft calls show similar significant differences.

(iii) The songs of males 9 and 10

These males are similar in that their song has one repeated element only. In each case the element has a harsh, noisy structure with harmonics only partially visible. The attack is much more pronounced in male 9 and, though they share a monotonous delivery rate, the two elements are clearly different. There was no evidence by either male of a tendency to group the elements into phrases within a song bout.

One interesting feature developed in male 9's song. A more musical couplet was used to terminate the song bout on some occasions. This is illustrated and resembles the structure of a male loud call but, interestingly, not that of male 9. This would suggest that the couplet forms part of the song, as an occasional additive, rather than the call repertoire.

(iv) The songs of males 3, 4, and 7

These are dissimilar and are grouped for convenience only. Each song will be discussed only briefly.

Male 3 has a song consisting of four harsh elements. The warm-up notes and Elements 1 and 3 resemble the male's loud call. The normally disyllabic loud call is, however, reduced to a monosyllabic element. Element 4 is unlike any other recorded, it consists of an extended harsh sound of much longer duration than elements produced by the other males.

Male 4 also has four elements. All contain harsh components which overlie succeeding elements. The harmonics visible in Element 4 do not appear similar to the loud or soft calls of this male.

Finally, male 7 is interesting in that only two elements are used in his song but these are arranged in a definite pattern. With the elements numbered 1 and 2, the pattern consists of 112121 which was shortened during bouts of song so that a rhythm of 112121 2121 often occurred.

(v) The use of loud calls to accompany song bouts

On many occasions song bouts were terminated with a series of loud calls. These could be given at the end of a phrase or the male might break off in the middle and begin a rapid rate of calling. There did not appear to be any consistency in the use of these loud calls but the occasional additive couplets of some males (e.g., male 9) may be derived from this tendency. In the case of male 9, it was only after the sonograms were produced that it became clear the couplet did not consist of his normal loud call and hence, it is possible, that other males may also make use of an unusual vocalization in this context.

(vi) The songs of male 2

Finally, the songs of male 2 deserve special attention. At the start of the experiment this male produced a complex song phrase labelled Phrase 1. On some occasions two elements were attached to Phrase 1 as an additive couplet much as was the case in male 9. However, these elements were heard more and more frequently as the experiments proceeded until they were ultimately incorporated into their own song bout and produced without any evidence of Phrase 1. This second song was termed Phrase 2. To complete the confusion, on occasions part of Phrase 1 (Elements 2, 3 and 4) was used as a terminal flourish to a bout of song consisting of Phrase-type 2! Illustrated are examples of Phrase 1, Phrase 1 + 2, Phrase 2 alone and Phrase 2 + 1.

Phrase 1 deserves close scrutiny as all the elements used show resemblences with calls made by male 2;

warm-up note - soft call of male 2,
Element 1 - soft call with emphasised attack and decay components,
Element 2 - loud/soft call of male 2,
Element 3 - similar to Element 1 but with the attack less emphasised and no decay,
Element 4 - loud/soft call of male 2,
Element 5 - similar to 1 and 3 but no attack or decay,
Element 6 - a loud call of male 2 that was not always present.

The elements do differ from their counterparts in the call repertoire of male 2. The loud/soft elements (2 and 4) are structurally the same as loud/soft calls but are of much shorter duration (more than

50%). The soft call-like elements, 1, 3 and 5, neither match with one another nor with the male's actual soft calls. The frequency increases successively and they are all higher than either the soft call or the harmonic part of the loud call. Even Element 6 differs from the normal loud call, its frequency is much increased. Thus, although the elements resemble call-types they are not exact copies.

Phrase 2 consisted of two elements only with warm-up notes;

warm-up note - this was the soft call as in Phrase 1,
Element 1 - this was the same as Element 1 of Phrase 1,
Element 7 - a harmonic sound resembling a loud call but not that of male 2.

The frequencies of Element 7 differ from all male 2 calls and elements; it is apparently a new element. Although the song bouts of this type were of variable length it was noticeable that they did have one consistent feature. They always began and ended with Element 1 which meant that they always included an odd number of elements.

Thus male 2 illustrates a strange phenomenon of Zebra Finch song. The male was adult which suggests that the change in song-type could not be linked with maturation. In any case, Phrase 2 was a reduction from Phrase 1 whereas changes from the juvenile song usually involve an increase in complexity (see Immelmann, 1969).

(c) A comparison of courtship (DR) and undirected (UN) song

The sonograms of undirected song appear visually identical to those for courtship song. The same elements are present in each case and they apparently take exactly the same form. Possible exceptions are males 1 and 5 where the harsh components appear more emphasised in undirected song, and the songs of male 9 which demonstrate an opposite trend. To the ear, the two song types were indistinguishable in all cases.

Measures of frequency parameters revealed that the elements were remarkably similar and the only significant difference appeared in a measure of the duration of the total phrase length. For obvious reasons, this was not apparent in the songs of males 9 and 10(they possessed no phrase) but the undirected song of all other individuals was of longer duration ($p < 0.001$, t test, for all eight males). Changes involved alterations to the elements at the end of the song phrase. Usually the element itself was more prolonged but in some cases the interval between elements was lengthened, for example, male 8 between Elements 5 and 6.

Discussion

(a) Inter-individual variation

The sonograms, and measures from them, reveal a great deal of individual variation in the songs of Zebra Finches. In spite of this the songs of different males are remarkably stereotyped in all the parameters used, including duration. The latter is emphasised as it was shown to alter in some calls and Emlen (1972) found that temporal patterning of songs was very important in species recognition in the Indigo Bunting. No common specific pattern emerged from this Zebra Finch study but it would seem that temporal parameters are important as they vary so little.

The songs could provide ample individual information enabling females to readily recognise their mates. This inter-individual variation is not merely a feature of captive, domesticated birds as Immelmann (1969) found a similar degree of variation within a wild Zebra Finch population. In fact, he concluded that there was as much variation within the population as was found between populations. In addition, the work of Zann (1972) and Güttinger (1973) on wild-caught estrildids (Poephila and Lonchura spp.) revealed large variations within individuals from the same populations.

The songs of the estrildids show some general similarities which hold true throughout the family. Hall (1962) reviewed 24 species sonogramically and, though no data is presented for intra-individual variation, concluded that their songs tended to be soft, simple and usually harsh and toneless, in fact completely lacking in 'musicality'. The song phrases consist of a series of harmonically rich elements with a large frequency range which is rather unique amongst the passerines with the exception of the soft, jumbled song of the carduelines. The sonograms presented here resemble those shown in the literature (e.g., Immelmann and Hall) in that the elements are of comparable structure and the phrase length (around 1 second) is similar. Zann (l.c.) considered that because of this short phrase length, Zebra Finch song was primitive amongst the family. The evolutionary trend, he argues, is towards a longer phrase with more complex, louder elements (e.g., in Poephila the phrase length is about 2.5 seconds).

Returning to the question of the individuality of Zebra Finch song, one is drawn towards the conclusion that they must be important in mate recognition. Immelmann (1968), in spite of a paucity of experimental evidence, felt certain that they aided personal recognition of both mates and flock members. This must include members of a close social unit only as the song is soft and audible only over a short distance (Zann estimates about 5 m). It has been demonstrated in other species that song plays an important role in stimulating ovulation by the female (e.g., Brockway, 1965; Lehrman & Friedman, 1969; Newton, 1972; Putman & Hinde, 1973 and Hutchinson, 1974).

The social Zebra Finch in which, because of the lack of external stimuli (e.g., day length), breeding may occur at any time of the year it will be important for mates to synchronise their particular breeding cycles (see Kunkel, 1974, for further discussion). In this instance, it would be advantageous for a female to recognise her mate's song and be stimulated by that more so than by the songs of other conspecifics. In this way individual pairs could closely synchronise their nest-building and other breeding activities.

(b) Zebra Finches singing the same, or very similar songs

There were two instances of striking similarities in the sample of songs illustrated; in fact, males 6 and 8 had apparently identical song phrases. The history of these individuals is not known for certain but it is likely that Zebra Finches with very similar songs are siblings or, at least, close relatives. This follows Immelmann's (1969) work in which he demonstrated that Zebra Finches learn the songs of their fathers whilst still in the nest and then reproduce them exactly as adults. A similar reliance on the paternal song phrase was reported for the Bullfinch by Nicolai (1959).

This situation, the young learning the song of their father, seems contradictory in that selection appears to favour individuals with very dissimilar songs. However, Nottebohm (1972) appears to have suggested a viable explanation for such phenomena. In his view, there are two advantages; (a) the species song is of low volume in the Zebra Finch and Bullfinch and therefore it is 'better' for the young to learn that which is heard most often and which is most likely to be their own species, and (b) if the female ultimately decides mate selection and she imprints on her parental song type, then she may reject individuals singing this, or similar, song types when she reaches adulthood. This will mean that inbreeding becomes unlikely and gene flow is promoted. The latter would certainly be important in these species in which maturity is reached very quickly and, as Nicolai (l.c.) has shown, temporary sibling bonds may be formed in the nest which are only broken once the juveniles leave the nest and the males begin to sing.

Males 1 and 5 may illustrate that if copying has occurred it is not an accurate one. Arnold (1975) presents sonograms of sibling Zebra Finches and compares these with their father's song. He concluded that, whilst there were great similarities, they still showed large differences. Elements could either be missing or repeated more frequently than in the parental song. Zann (1972) described a similar situation in the ontogeny of Poephila song. Young birds tended to copy their father's song but not exactly and individual differences still existed amongst siblings. In one case, an individual did not use his father's song but instead that of another, nearby male. Presumably, if a male does not sing frequently, for whatever reason, during the early life of his offspring, then they may incorporate features of the songs of other males into their own. Immelmann (1969) demonstrated that Zebra Finches possess an innate preference or auditory template for their species song, in that if they were reared by females only they learned the song of nearby male conspecifics. In the normal development of the song, therefore, the paternal bond must override, or enhance this preference and the father's song is used exclusively as a model. It may be important that there is interaction between the singer of the model and the offspring as Thielke (1970) showed that European Treecreepers would not learn the songs of conspecific from recorded 'tutor' tapes alone.

Thus providing the father sings frequently and interacts with his offspring during their development then one would expect sibling Zebra Finches to produce songs very similar to the paternal one. The copies would not necessarily be exact which may suggest that there is some value attached to individual recognition even of different sibling songs. Güttinger (1973) concluded that in the *Lonchura* spp. the father's song may be modified by his offspring, on some occasions, with learned components from other conspecific songs and individuality could also arise from inaccurate copying of the model. It has certainly been postulated that dialects, in other species with an auditory template but which do not use the father as a model, may have arisen through inaccurate copying of the local song type.

(c) Loud calls and song

An interesting situation emerged when the loud calls given by supposed siblings in this study were compared. In both cases, males 1 and 5 and males 6 and 8, the loud calls of the two individuals shared the same harmonic shape but differed significantly in their frequency parameters. Whether the loud calls are learned or genetically determined, it is particularly interesting to note that they could easily be distinguished from one another whereas the songs were far more similar. This may suggest that whereas siblings can 'afford' to have very similar, or even the same, songs the loud calls must retain individual features. The latter is thought to be an important long distance signal used to maintain contact between mates and flock members as well as warning of danger and alarm situations. To fulfil this role, each male must, presumably, produce a different call.

Loud calls were, on occasions, used in conjunction with the male song. A courtship song bout was frequently terminated by a series of loud calls and, though this was not recorded here, Goodwin (1960) noted Avadavats using loud calls in place of courtship song. Andrew (1961) has pointed out that the main motivation for song in birds is probably the absence of the mate and, as this is also one of the contexts in which loud calls are used, this may explain their incorporation into song phrases. Alternatively, song is considered to have an attracting function in many passerines and, as discussed in the previous subsection, loud calls may also promote contact between mates. This suggests,at least, a similar motivation for both song and loud calls which is presumably sexual, though it is not impossible that the loud calls at the end of a courtship bout are registering alarm or fear on the part of the male. However, Potash (1972) found that in the Japanese Quail 'separation' calls (similar to loud) were related to sexual ones and shared the same motivation.

Male 9 is interesting as the loud calls that he occasionally added to his song were not his own. These elements were an entirely new vocalization for this male and were not recorded at any other time. They could possibly be linked with the loud calling of other males.

(d) The song of male 2

Male 2 produced the most unusual song of all the birds used in this particular sample. He added a second phrase-type to his original song and then actually switched to this new type and sang it exclusively, with the first song-type assuming the role of the occasional terminal flourish.

This situation is remarkable as Immelmann (1969) demonstrated that the Zebra Finch has a well defined critical or sensitive period for the development of song and this period is concluded before the offspring leave the nest! However, Goodwin (1960) reported a "young" Avadavat that could sing a Blue-breasted Waxbill's song as well as its own and, in other species, an extended period in which the song can be modified has been recorded (see Nottebohm, 1969). Arnold (1975) found that the critical period was lengthened by castration of male Zebra Finches and it thus appears to be dependent on androgen levels. The hormonal state of male 2 cannot be assessed but within a few months of these experiments, and still singing song-type 2, he was breeding and rearing young successfully. In addition, the change in song-type involved a drastic simplification rather than an addition or modification of the original song.

(e) The nature of undirected song

A comparison of courtship and undirected song reveals only slight differences in terms of the duration of the song phrases. The elements used were the same in each case but undirected song was consistently longer and Immelmann (1969) noted a similar slower tempo of delivery.

Arnold (1975) has recently shed some light on this state of affairs. He found that castration of male Zebra Finches did not abolish song completely and some song was still given. He noted that this song was different in that it involved a slower rate of delivery and, one can assume therefore, that it was undirected song that continued after castration. Certainly, Prove (1974) in a similar study, showed that courtship song declined and undirected continued in the Zebra Finch.

Thus, undirected song appears to be independent of androgen levels in the body. Arnold (l.c.) found that injection of testosterone into castrates quickened the tempo of their song though, again, it is not clear whether he is referring to all song or merely courtship song. These findings suggest that undirected and courtship song may be influenced differently by the hormonal system of these birds and that they may have different motivation factors. Undirected song continues during the non-breeding season when androgen levels will be low and sexual motivation reduced.

Zann (1972) has listed the proposed functions of undirected song in the estrildids and these include:

(i) It is functionless in the majority of cases and has a social function (promoting contact) in the remaining species (Immelmann, 1968).

(ii) It has a contact function (Morris, 1954, Moynihan and Hall, 1954, and Harrison, 1962) between the members of a pair. In this case it could be useful over short distances only.

(iii) It may be important in group cohesion in those species in which group singing occurs (e.g., Poephila spp.; Zann, 1972).

(iv) It is important during incubation when the female is in the nest and the male sings from outside (Zann, l.c., Birke, 1974). This may 'reassure' the female as to the male's continued presence nearby and could be important in synchronising nest relief ceremonies.

Some, or all of these hypotheses, may well explain features of undirected singing but any, such as (iv), which refer to its occasional use, do not explain why the song is given in such large amounts in the presence of the female and during the non-breeding season. A contact function during these times seems most likely and certainly in species with louder songs it has been shown that females are attracted to and approach a singing male in some situations (e.g., Tinbergen, 1939, Marler 1956, Andrew, 1957a, Payne, 1973). However, the soft nature of Zebra Finch song argues against this function. Another possibility is that of gonadial stimulation both of the female and the male by the sound of undirected song. It is known that the gonads do not regress completely during the non-breeding season of the Zebra Finch (Farner and Follett, 1966) and if male courtship stimulates the female, and song is an important part of this, then the same song given outside of courtship may retain a stimulatory function. It could maintain a tonic state of gonadial development during this non-breeding season in both sexes which would allow sexually motivated (hormonal dependent) activities to continue thus promoting and prolonging the permanent pair bond.

This stimulation hypothesis seems to explain the use of a soft song throughout the non-breeding season. Its independence from high levels of gonadial hormone, as Arnold demonstrated, is an important proviso. Its additional use to promote contact and cohesion between conspecifics is not excluded and presumably there would be an advantage, in both cases, of the female learning, and behaving preferentially to, the song of her particular mate.

SECTION 7. EVIDENCE OF INDIVIDUAL RECOGNITION OF CALLS

Introduction

It has been established in Section 6 that the vocalizations of different Zebra Finches are individually distinct and vary sufficiently to form a basis for individual recognition by auditory means. The following three experimental situations were designed to test whether Zebra Finches actually make use of these differences and, if they do, how this might assist the maintenance of pair bonds. This represents Beer's (1970c) third approach to the investigation of individual recognition in birds (see Introduction to Section 6) and involves experiments to investigate the 'reactions' of birds to the sounds of conspecifics. As was stressed earlier, it is not enough to merely demonstrate inter-individual variation in the vocalizations of a species, it must be shown that birds actually make use of such variations.

In order to assess mate recognition of vocalizations, it must be demonstrated that a preferential response is obtained from a bird when the calls of its mate are heard. This response should be enhanced and greater than that given to a non-mate conspecific giving similar vocalizations. It is in the measurement of the response that difficulties may be encountered (e.g., it may be difficult to describe any preferential behaviour) and, in addition, the Zebra Finch is a social species that feeds in flocks and hence birds can be expected to respond to some extent when any conspecific calls. These problems aside, the experiments that follow used two types of call as stimuli for subject birds. The experiment labelled 7.1 deals with tape recorded loud calls which were played back to individuals and the rate of calling in response to the calls of their mate compared with that in response to a non-mate. In 7.2 and 7.3 calling between mates and non-mates was assessed when birds were in auditory or visual contact and the number of calls given to the subject bird was not controlled by the experimenter in any way. Thus, in contrast to 7.1, these latter experiments demonstrated the responses of individuals to "live", unrecorded calls.

Terminology

In this section a number of terms are used for the first time which could have ambiguous meanings. To clarify the situation a short glossary is provided here.

Subject bird(s) These were individuals in the experimental situation whose responses to the calls of other conspecifics was measured. The Subject bird could either be a male or a female, on different occasions.

Stimulus This term is used in reference to the recorded calls, or calling by a conspecific, to which the Subject bird was expected to respond.

Stimulus calls In 7.1, the Stimulus calls were on tape whereas in 7.2 and 7.3, they were provided by the actual mates or non-mates concerned who could be referred to as Stimulus callers.

Stimulus bird(s) These were the birds used in 7.2 and 7.3, whose calls could be heard by the Subject bird. Their own response was measured and they could either be the 'Stimulus mate' or the 'Stimulus non-mate'.

"Live" calls This term is used in contrast to 'recorded' calls. A subject in 7.1 heard taped calls, whereas one in 7.2 or 7.3 heard calls made by a bird in a 'live' situation.

Successive presentation Stimulus calls of different individuals recorded or live, were presented in turn (i.e. one followed the other).

Simultaneous presentation Calls from Stimulus callers were presented concurrently in an experimental situation. Thus, the subject could hear more than one individual (i.e., both the mate and the non-mate) at the same time.

7.1 Responses to playbacks of recorded loud calls

Introduction

Playback of tape recorded vocalizations has been used extensively in experimental studies of individual recognition in birds (g.v. Beer, 1970c, for a review). They have the advantage of complete control over the stimulus which can be varied at will in terms of both the quality and quantity of calls presented. The opportunities open to the experimentation are thus vast but not without their inherent dangers.

The object of this experiment was to examine the responses of individual birds, of both sexes, to the calls of their mate and to other conspecifics. The measurement of a 'response' was difficult in that a Subject bird might well recognise a call but not respond preferentially towards it in the particular experimental situation used. In addition, the motivational environment of different Subject birds could presumably vary and this will affect their reactions to a stimulus (i.e., they may respond to the situation rather than to the calls). An example of such difficulties was provided by the work of Evans (1970a & b) on the responses of Laughing Gull chicks to the calls of their parents and other adults. He found that reactions to playbacks varied depending on whether different stimulus calls were presented simultaneously or successively. The latter is the simpler situation to set up but Evans was only able to obtain a significant preferential response when the calls were presented simultaneously. Thus the context in which the calls are heard is important and Beer (1970c) went on to suggest that the difference illustrated in this particular gull could be adaptive.

Clearly, any study which involves the use of playback of calls needs careful control of the experimental situation if satisfactory results are to be obtained. The following account, bearing the limitations in mind, deals only with responses to one call type, the loud call, which was shown to be individually distinct in a sample of both male and female Zebra Finches (Section 6.1A). Recorded Stimulus calls of different individuals were presented successively, a context which could arise in the wild when a preferential response to the mate might be expected. The Subject birds response was assessed in terms of both vocal and physical parameters for any indications of a preferential reaction to the calls of the mate.

Methods

In this experiment 10 established pairs of birds were used. These were birds which had been kept as isolated pairs for periods in excess of one month during which time pair formation was assumed to have been completed.

The loud calls of the ten males and females were recorded on a Sony taperecorder. Separation from the mate facilitated the production of loud calls for these recordings; they were thus given in a context in which mate recognition could be expected to be important (i.e., contact promoting). One clear loud call, for each individual, was then chosen and transferred to a second tape recorder from which a series of repetitions of this single call were recorded onto a Stimulus tape. Eight consecutive loud calls, spaced at one second intervals, were produced for each bird and four Stimulus tapes made, two for each sex. In each case a tape held the calls of five different individuals with a two minute gap between each caller. A subject was presented with one of the Stimulus tapes and heard, successively, its own mate's calls together with the calls of four other conspecifics of the same sex as its mate. The particular sequence in which calls were presented to each subject varied as,

	Subject bird	Stimulus Tape I (Females)				
Males	1	(1)	2	3	4	5
	2	1	(2)	3	4	5
	3	1	2	(3)	4	5
	4	1	2	3	(4)	5
	5	1	2	3	4	(5)

( ) = mate's calls

The Stimulus calls (on the Stimulus tape) were presented from a tape recorder situated directly in front of the subject bird and approximately 3m away. Sonograms made of some of the Stimulus calls revealed no unusual auditory phenomena which might have resulted from the recording procedure used.

The experimental procedure involved:

(1) The Subject bird was separated from its mate and placed in the experimental cage. This consisted of a single wire-fronted wooden compartment (40 x 30 x 35 cm) equipped with one horizontal perch and food and water bowls.

(2) The experimental cage was left in the stock room over night (a period of some 15 hours). During this time the mates were in auditory contact but could not see one another.

(3) On the following morning, the experimental cage was transferred to a different room which was well out of earshot of the stock room. Care was taken to disturb the Subject bird as little as possible.

(4) After a 30 minute period, during which the Subject bird was not disturbed, the recording schedule began. This consisted of:

the control period - 2 minutes during which no
Stimulus calls were given,
the calls of Bird 1 - 8 Stimulus calls followed by 2
minutes silence,
the calls of Bird 2 - 8 Stimulus calls followed by 2
minutes silence,
and so on . . . . . . through to Bird 5.

(5) A 10 minute interval then followed before the complete recording schedule was repeated. During this time the tape was rewound.

(6) The recording schedule, in its entirety, was repeated a further two times giving four repetitions, or trials, in all.

Observations were made on the Subject bird live and on videotape recordings. The VTR was described in Section 4 (Methods) and in this experiment the camera was placed 3m from the cage with all but the lens hidden behind a cloth screen. From the videotapes activity and head movements were assessed. The responses measured were:

Vocalizations Each two minute watch was divided into 10 second periods and the number of vocalizations heard during each of these intervals counted. Calls given in response were categorized as loud, loud/soft, soft or tet and any song heard noted in terms of number of bouts and phrases used.

Activity At the start of each ten second interval the behaviour of the Subject bird was sampled. Two behavioural measures were used; "active" denoted any movement on the part of the subject (e.g., flight, hopping, feeding or sitting alert) and "inactive" any periods of immobility and/or sleep.

Head movements This was taken as a measure of searching movements. It might be expected that a Subject bird trying to locate the source of a sound would move its heard through various angles. The number of changes in position of the head (indicated by the direction of the bill) was counted for each 10 second period.

Scores obtained were compared for significance using non-parametric statistics (Siegel, 1956); the McNemar test (McN) and Wilcoxon matched-pairs test (WMP) for related samples and the Mann-Whitney U test (MWU) for independent samples.

Results

(a) The responses of Subject birds to the first calls on the Stimulus tape

This can be determined by comparing the behaviour during the control period with that which took place in the two minutes following the first calls played-back. An assessment of calling, activity and head turning is shown in Table 19.

The males

On hearing the calls males showed a significant increase in calling and head turning ($p < 0.05$, WMP). In addition, they tended to become active in Trial 1 ($p < 0.05$, McN) but not in subsequent trials. Two males showed signs of fear in the experimental situation; male 7 gave no calls in any trial and remained immobile throughout the whole procedure, whereas male 10 gave one call to the first stimulus bird in Trial 1 and thence remained silent.

The females

Responses by females were less pronounced than those of the males and in this case two females (2 & 4) remained silent and

TABLE 19. The behaviour of Subject birds during the control period compared with that after the first Stimulus calls expressed in average scores

		(i) The males		(ii) The females	
Behaviour	Trial	Control	After stimulus	Control	After stimulus
(a) Total calling	1	0.6	13.1	0	1.3
	2	0.8	12.7	1.3	3.7
	3	0.4	7.6	1.4	2.5
	4	0.4	6.6	1.9	3.5
(b) Activity (No. of times active, max. = 12)	1	0	3.4	0.1	0.5
	2	0.2	1.7	0.8	2.8
	3	0.1	1.6	0.4	1.3
	4	0	1.2	1.1	1.6
(c) Head turning	1	72.3	146.4	47.0	74.3
	2	59.5	122.1	66.9	108.6
	3	69.8	106.5	70.4	88.6
	4	65.8	111.9	82.7	86.3

immobile throughout the four trials. Comparing the control period with that after the first calls, the females showed no overall increase in calling during the playback, became more active only during Trial 2 ($p < 0.05$, McN) and showed increased head turning in Trial 1 only ($p < 0.05$, WMP).

(b) Vocalizations (Fig. 16 and Table 20)

The males

The males who answered calls (all but 7 and 10) did so to all the Stimulus females. This was particularly noticeable in Trial 1. Loud calls were predominantly used (96% of all calls given) with the remainder being soft calls. The majority were given actually during the Stimulus calls often at a very rapid rate which reached 3 or 4 calls per second in some cases.

There was no evidence to suggest that males called more to their mates than to non-mates. However, it was clear that within each trial more calls tended to be given to the first stimulus female heard than to the last (Female 5). This reached significant proportions on Trials 2 and 3 ($p < 0.05$, WMP). In addition, the number of calls given to each female showed a significant decline from Trial 1 to Trial 4 ($p < 0.05$, WMP, for each female stimulus). This seems to suggest that the males who responded were habituating to the calls of the Stimulus females in that both within trials, and between successive trials, their vocal responses were reduced. Responses to the calls of the mate in Trial 1 versus Trial 4 showed a similar decline to that towards other female non-mates.

Song was infrequently heard during the four trials and was never given as an immediate response to the stimulus calls of any female.

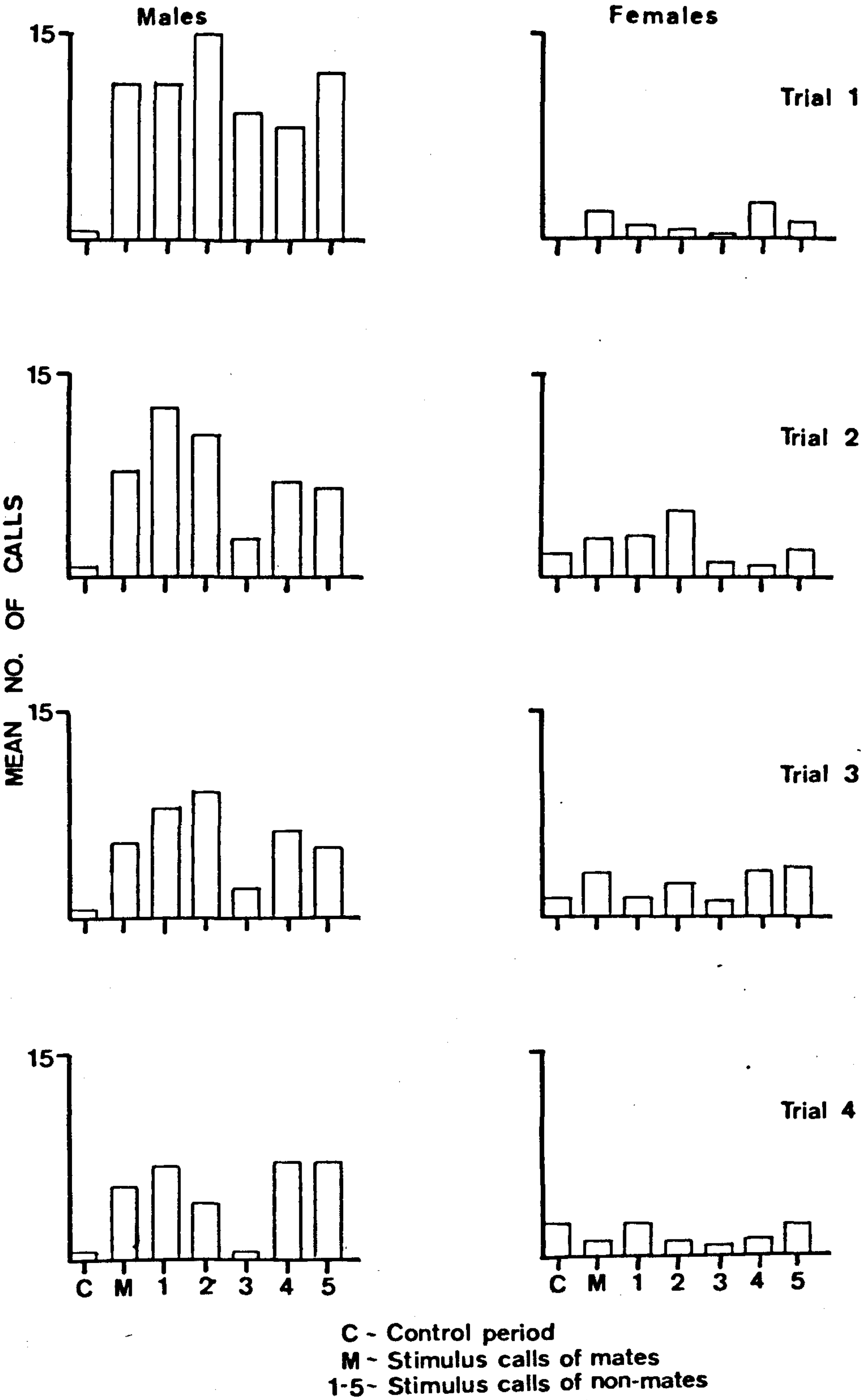


Fig. I6. Calling by males and females in response to the playback of Stimulus calls of their mate and those of other non-mate conspecifics.

TABLE 20. Vocalizations during and after Stimulus calls

Calling by subject to each stimulus bird (average total calls)

				Stimulus birds					Average to non-mates
	Trial	Control	Mate	1	2	3	4	5	
Males	1	0.6	11.4	11.5	15.1	9.3	8.3	13.6	11.5
	2	0.8	7.7	12.6	10.6	3.0	7.1	6.6	8.0
	3	0.4	5.6	8.0	9.3	2.1	6.4	5.1	6.2
	4	0.4	5.3	6.9	3.9	0.4	7.1	7.0	5.1
Females	1	0	1.8	0.9	0.8	0.1	2.5	1.3	1.3
	2	1.3	2.8	3.1	5.0	1.3	1.1	2.0	2.5
	3	1.4	3.1	1.1	2.4	1.1	3.3	3.6	2.4
	4	1.9	1.2	2.5	1.3	0.8	1.3	2.4	1.9

TABLE 21. The number of times subjects were active after Stimulus calls (average scores, possible maximum in each case is 12)

				Stimulus birds					Average to non-mates
	Trial	Control	Mate	1	2	3	4	5	
Males	1	0	2.7	2.4	3.9	4.5	1.9	4.1	3.4
	2	0.2	3.3	2.1	2.8	2.0	1.4	1.5	2.0
	3	0.2	2.0	0.5	1.5	1.7	1.9	1.5	1.4
	4	0	1.7	1.0	0.3	0.2	1.2	1.6	0.9
Females	1	0.1	2.4	0.1	0.3	0.1	1.8	1.9	0.8
	2	0.8	1.5	2.7	2.9	0.5	0.6	0.9	1.5
	3	1.0	1.9	1.1	1.1	0.1	2.2	2.7	1.4
	4	1.5	1.0	1.1	1.0	0.7	1.6	1.3	1.1

The females

The females gave fewer calls than did the males; there were significantly fewer in Trial 1 ($p < 0.01$, MWU). Only one female answered all of the Subject males (female 3) the remainder responded to three or less individuals. The vocalization used was again mostly loud calls (94.4%) with a few soft calls.

The calls by females were too few to bear up to a rigorous statistical treatment but there was certainly no detectable tendency to call more frequently to the mate than to non-mate males. Similarly, there was no evidence of habituation in the four trials, those females who gave answering calls did so in small amounts on each occasion.

(c) Activity (Table 21)

The males

Whilst in the experimental cages few periods of activity were observed in any trial. As noted earlier, only in Trial 1 was significantly more activity seen after the first stimulus calls ($p < 0.05$, WMP). There was no evidence of more activity after hearing the calls of the mate than after hearing the calls of a non-mate.

The females

As in the males, there was no apparent tendency for females to become more active before or after hearing Stimulus calls. If anything, females tended to remain even more static than did the males.

(d) Head turning (Table 22)

The males

Head turning was noticeably more frequent during stimulus calls and the results for this response support the trends seen in the vocalizations of the males. There was a general reduction in the amount of head turning as the trials proceeded and significantly fewer were given in response to female 5 compared to that to female 1 in Trial 4 ($p < 0.05$, WMP).

The females

The females did show head turning as a response to the calls of the Stimulus males but on no occasion were more given after the mate's calls compared to after non-mates. There was similarly no trend towards habituation of this behaviour from Trial 1 to Trial 4.

Discussion

The playback of loud calls induced behavioural and vocal responses in the Subject birds of both sexes. A few individuals remained silent throughout the four trials and they possibly indicate a flaw in the experimental procedure used. Beer (1970c) noted that playback experiments in the past had been most successful when they involved an approach response on the part of young individuals and Payne (1973) had success using a similar technique on adult female whydahs. Whilst accepting that these 'silent' birds throw some doubts on the results obtained, they are still considered interesting enough to be discussed in more detail.

One very interesting feature to emerge is the different responses to the Stimulus calls given by males and females. Males tended to answer all female calls and showed some evidence of habituation with time. The females, on the other hand, were more selective and, though

TABLE 22. The number of head turns by subjects expressed as average scores

				Stimulus birds					
	Trial	Control	Mate	1	2	3	4	5	Average to non-mates
Males	1	72.3	106.0	149.9	129.2	129.5	82.4	135.5	121.3
	2	59.5	126.9	124.8	127.0	104.6	91.2	111.6	110.2
	3	69.8	113.9	103.8	122.6	104.4	110.6	86.6	105.6
	4	65.8	112.3	120.6	104.3	83.0	105.5	85.4	99.8
Females	1	47.0	100.0	59.9	84.3	73.9	87.4	94.9	80.1
	2	66.9	105.9	95.4	128.4	72.4	58.9	94.3	89.9
	3	70.4	104.5	63.3	111.4	76.6	99.8	103.8	91.0
	4	82.7	95.2	83.9	107.5	100.9	93.5	78.3	82.8

they did not answer their mate's calls preferentially, they did not answer all the male stimulus calls equally. In both cases, males and females tended to answer like with like, that is, they answered loud calls with loud calls of their own.

This difference in the responses of the sexes is interesting when one recalls the differences found between the structure of male and female loud calls. Those of the male were more stereotyped and carried predictable clues as to the identity of the caller whereas, the female loud calls tended to show less individual variation and could be altered in at least one of the parameters measured (i.e., duration). Thus, the structural differences which suggest a possibly different function for the calls of the two sexes, are born out by the results of the behavioural responses to the calls. It would be interesting to ascertain how males and females react to the calls of their own sex, but this is outside of the scope of the present thesis.

Immelmann (1968) is certain that Zebra Finch mates recognise one another by their loud calls and Güttinger (1970) suggests a similar situation in the African estrildid, Odontospiza. However, neither of these authors provides any experimental proof to back up their statements and this experiment suggests that it is not a simple phenomenon to demonstrate in the laboratory situation. In fact, the male's responses suggest that he will answer any female he hears irrespective of whether a sexual bond exists between that female and himself. The fact that the link between calls and the responses of birds is complex is not necessarily unexpected. The Zebra Finch is a highly social species and each individual must strike a balance between recognition of, and responses to, the calls of their mate with the recognition and response to the calls of members of the social flock.

It is clear that this experiment does not demonstrate preferential responses by isolated individuals to the calls of their mates. This does not mean, however, that it does not exist in other contexts and what is apparent from this study is that males and females respond differently to the loud calls made by conspecifics of the opposite sex.

7.2 Responses of subject birds to the "live" calls of their mates and non-mates

Introduction

The use of playback of calls allowed the responses of individuals to a constant stimulus to be compared. However, it is unlikely that a similar situation would arise in the normal use of calls by the Zebra Finch when calling by a Stimulus bird would be expected to alter after replies from the subject were received. Such alterations might, in turn, cause a further change in the Subject bird's calling rate and so on and thus involving a dynamic exchange of vocalizations. It can be postulated that mutual stimulation of calling rates could occur and the experiments that follow attempt to discover whether in such a situation of "live" calls, not playbacks, mates will call more to one another than they do to a conspecific non-mate. Presumably this would be advantageous to a pair of birds in that continuous vocal contact would assist in maintaining proximity particularly whilst both birds were active.

Zebra Finches are social and are frequently found in groups away from the nest site (see Section 3). It is unlikely, therefore, that in the wild calling between mates would occur in the absence of other calls from nearby conspecifics. In this situation recognition of the mate would be at a premium and in order to assess how non-mate calling may affect the vocal responses of mates an experiment was designed in which two Stimulus birds could be presented to an individual simultaneously. In other words, the context in which the calling between mates and non-mates occurred was altered from one of isolation to a possibly more typical situation in which both calls could be heard at the same time.

These two experiments 7.2(A) and 7.2(B), were termed successive presentation and simultaneous presentation respectively. They were both conducted with the calling birds in auditory contact only (i.e., they could not see one another). In this situation it seems logical that calling between mates would be enhanced. In order to test this suggestion the final experiment involved a simultaneous presentation of two Stimulus birds (a mate and a non-mate) but, this time, whilst in visual, as well as auditory, contact. (experiments 7.2(C)).

In addition to vocal responses of Subject and Stimulus birds other behavioural reactions were monitored such as synchronisation of activities by mates and non-mates. These are explained in more detail in themethods.

Methods

All the birds used in these experiments were members of established pairs (i.e., had been kept as isolated pairs in excess of one month). Three separate experimental situations were employed. The original sample size was 10 pairs but during the second experiment (7.2 B) one individual died and the results for that pair were excluded. This meant that the sample size in experiments 7.2(A) and 7.2(B) was 9, in 7.3(C) a replacement pair was used bringing the total to 10 pairs. The methods involved in each experimental situation will be outlined in turn below before any results are discussed.

7.2(A) Successive presentation of Stimulus birds (mate and non-mate)

Subject birds were tested with a stimulus bird when out of visual contact. The stimulus was either a mate or, on a different occasion, a non-mate. Males and females were tested, as subjects, in turn and the following procedure adopted in each case.

(1) Both the subject and the two Stimulus birds (mate and non-mate) were transported and tested in small wooden, individual compartment cages (40 x 30 x 35 cm). Each cage was equipped with a standard wire front, a single horizontal perch and food and water bowls.

(2) Tests were carried out in the mornings (between 9.00 and 12.00 hours) and the afternoon prior to the test the Subject bird was placed in the experimental room. This involved separation from the mate and once in the experimental room no vocal contact was possible with any conspecific. The two Stimulus birds were placed in a second room in separate cages. They were in auditory, but not visual, contact with one another but well out of earshot of the subject bird.

(3) On the morning of the test the subject was observed for a 10 minute control period without stimulation.

(4) The first Stimulus bird was then brought into the room and its cage placed 1 metre away from the subject. The birds were not in visual contact and the test began after the first calls were heard. The test period was 10 minutes and, in practise, calling usually started soon after the Stimulus bird was brought in.

(5) The Stimulus bird was removed at the end of the test period and a one hour interval allowed before the second Stimulus bird was brought into the experimental room. 10 minute control and test periods were observed as for the first stimulus bird.

(6) With successive subjects the order in which the two Stimulus birds were presented was reversed, that is:

Subject bird 1 - Stimulus mate, followed by, the Stimulus non-mate,

Subject bird 2 - Stimulus non-mate, followed by, the
Stimulus mate, and so on. The males were used as subjects first.

Observations were made directly (i.e., live) and from videotape recordings (equipment described in Section 4) on the subject bird only. The following records were made:

(a) The initial response to calls from the Stimulus birds

The subjects immediate responses to these calls were described for the first 30 seconds of the watch. Notes taken consisted of a subjective impression of the behavioural activity shown.

(b) Vocalizations

The number of calls and undirected singing bouts per minute of the observation period, were tabulated for both the Subject and Stimulus birds. No attempt was made to categorise the vocalizations other than into song and calls. The experimenter was seated behind and between the two cages at a point where he was unlikely to disturb the test birds and binaural comparison of the calls rendered the identification of the calling bird easier.

(c) Activity

The Subject bird's behaviour was sampled at 20 second intervals. At these times its behaviour was categorised as either active (including sitting alert, hopping, flighting and feeding) or inactive (sitting drowsily, preening and sleeping).

(d) Head turning

This was taken as indicative of searching movements, as it was in Experiment 7.1. The number of head turns made by the subject in the first 10 seconds of each minute of the control and test periods were counted.

All of the measures, with the exception of (b), were taken from videotape recordings.

7.2(B) Simultaneous presentation of two Stimulus birds (mate and non-mate)

In this experiment the subject and the two Stimulus birds were tested at the same time. This demonstrated the ability for mates to communicate with one another when a conspecific was calling nearby. A three compartment cage was employed with a single horizontal perch and solid wooden partitions separating the individual units. The Subject bird was placed in the centre compartment and the two Stimulus birds in the compartments to either side. They were thus completely out of visual contact.

The same procedure as described above for 7.2(A) was adopted with a few modifications. The period of acclimatisation for the Subject bird in the experimental room was greatly reduced and the subject placed in the cage 45 minutes before recording the control period. The Stimulus birds were housed in individual cages in a separate room as before. After the control, they (the Stimulus birds) were brought in and placed in their separate compartments of the experimental cage and the test began from the first calls heard. The position of the Stimulus mate was switched with successive subjects (i.e., with one Subject bird the mate was on the left, the non-mate on the right, with the next the mate was now placed on the right and so on).

Recordings were made for 10 minutes and the same measures taken as above. The activity of all three birds was monitored so that synchrony in behaviour between mates (as a result of calls) could be compared with levels between non-mates. Measures of head turning were no longer possible as the camera had to be focused on a wider image and movements could not be seen in sufficient detail.

7.2(C) Simultaneous presentation of two Stimulus birds (mate and non-mate) in visual contact

Experiments in (A) and (C) concentrated on calling between birds in auditory contact only and in this experiment the effect of visual contact was assessed. Exactly the same procedure was used as in 7.2(B) but in this case the solid wooden partition was replaced with ½ inch wire mesh.

Results

7.2(A) Successive presentation of Stimulus birds

(a) The initial response to calls from the Stimulus birds

Descriptions of the first responses of both male and female subjects suggested that calls made by the Stimulus bird induced an increase in certain activities. These impressions were confirmed by a statistical comparison of the control and test periods. There was an increase in;

(i) the rate of calling (if the subject had been silent calls were initiated and none of the birds remained totally silent throughout the test period),

(ii) the number of head turns,

(iii) activity (hopping and flight) was induced, ($p < 0.05$, WMP, in each case).

(b) Vocalizations (Fig. 17 and Table 23)

(i) The behaviour of males

The total number of calls given by male subjects was greater when calling to the Stimulus mate than to the Stimulus non-mate

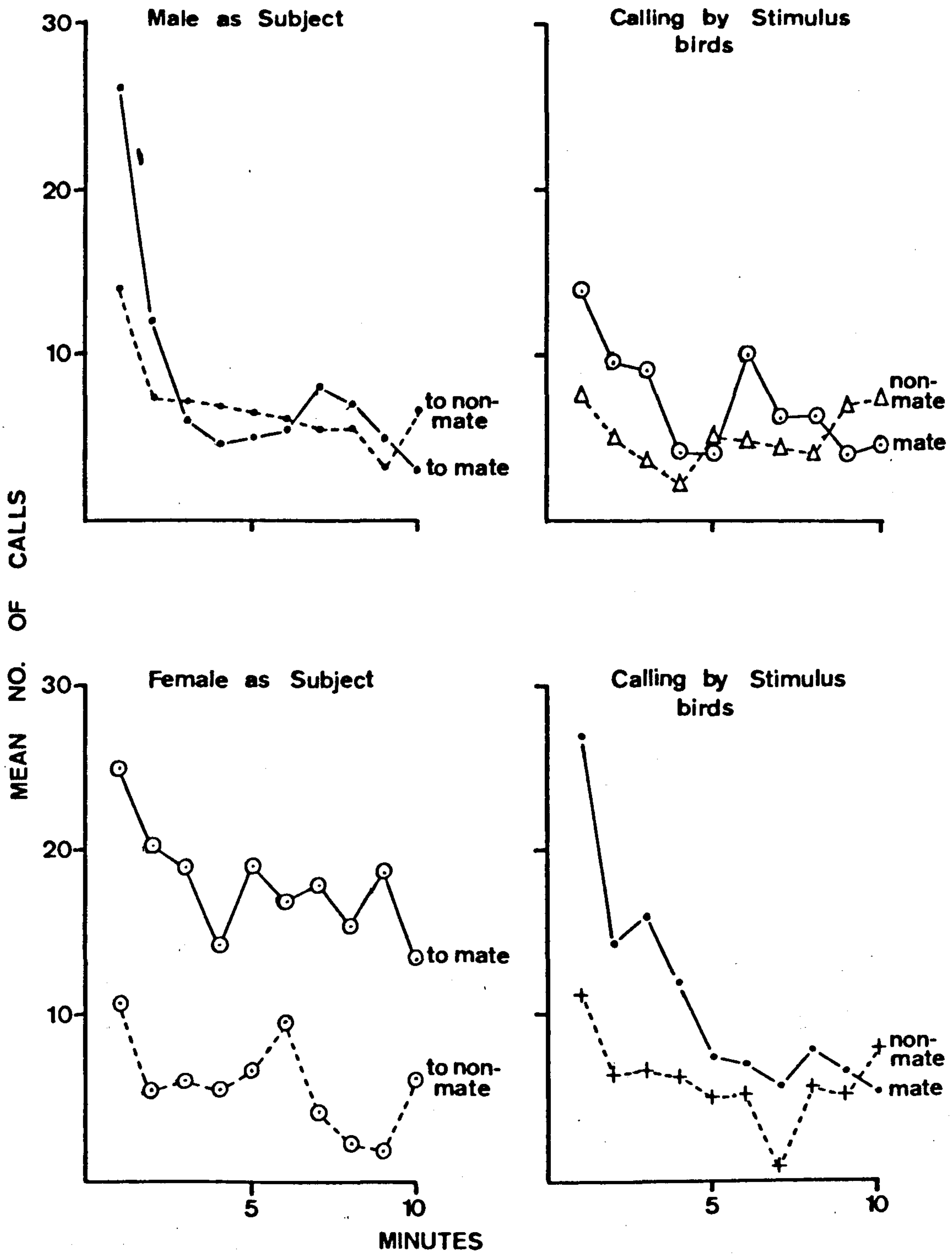


Fig. I7. The number of calls given by the subject and the Stimulus birds during the successive presentation of two Stimulus birds (the mate and a non-mate).

TABLE 23. Measures of vocalizations, activity, and head turning during the Successive Presentation of Stimulus birds (No. of subjects = 9)

						STIMULUS BIRDS	
BEHAVIOUR	SUBJECT	CONTROL	RESPONSE TO MATE	CONTROL	RESPONSE TO NON-MATE	RESPONSE BY MATE	RESPONSE BY NON-MATE
CALLS (Mean no.)	Males	11.3	81.2	14.3	69.6	70.1	54.1
	Females	4.5	179.2	6.2	57.2	127.4	54.6
SONG (Mean no. of bouts)	Males	0	12.4	0	12.0	-	-
	Females	-	-	-	-	1.4	9.6
ACTIVITY (Mean no. maxm = 30)	Males	2.4	20.8	9.4	18.5	-	-
	Females	7.1	22.5	6.2	12.2	-	-
HEAD TURNING (Mean no.)	Males	62.5	107.7	58.2	92.0	-	-
	Females	41.0	124.9	38.4	92.1	-	-

suggesting some recognition on their part. However, the amount involved did not reach significant proportions. Undirected singing bouts were given on occasions (Table 23) and significantly more were heard during the test period than during the control ($p < 0.05$, WMP). However, similar amounts of singing were recorded for both the Stimulus mate and non-mate.

When used as a Stimulus bird the males behaved similarly to when a subject and gave similar amounts of calls. However, the amount of undirected song was reduced.

(ii) The behaviour of females

There was evidence of the females recognising their mates as they gave significantly more calls when the Stimulus bird was the mate than when a non-mate ($p < 0.05$, WMP). Taking the total number of female calls overall the females still gave fewer calls than did the males ($p < 0.05$, MWU).

Comparing the calling of the females as Subject birds with that when they were used as Stimulus callers it was clear that they gave fewer calls in the latter situation ($p < 0.05$, WMP).

(iii) The correlation of calling rates by mates and non-mates

As well as giving more calls to a Stimulus mate it is possible that mated birds tend to answer one another more than they would a non-mate conspecific. This tendency was looked for in the results by calculating Spearman Rank Correlation coefficients for Subject and Stimulus bird calling rates. This is a comparison of the closeness of fit of the number of calls given in each minute of the test period and a positive correlation indicates that the two birds concerned were calling at the same times and, therefore, probably answering one another.

The correlation scores obtained are presented in Table 24 and with the male as subject, calling between mates showed positive correlation in all cases and significantly so in 8 out of the 9 possible pairs. Positive r_s values were obtained for calling between male and non-mate but in this case only 4 reached significant levels. The r_s values obtained for the females as subjects showed fewer significant positive scores (only 4 from 9) but remained at similar levels for non-mates (3 cases). Bearing in mind that the females gave more calls to their mates when used as a subject than when as Stimulus birds, the correlation scores suggest that they called less with their mate in this situation. When used as a stimulus, females gave fewer calls but, more often, at times when the mate was also calling.

(c) Activity (Table 23)

Both the male and female subjects tended to become active on hearing Stimulus calls and the females showed a significant increase in activity when the stimulus was her mate rather than a non-mate ($p < 0.05$, WMP). This supports the evidence from the vocalizations results and suggests that females were correctly identifying their mates on the basis of their calls.

(d) Head turning (Table 23)

There was an increase in head turning movements by all Subject birds during the test period but there was no evidence to suggest that more of these searching movements accompanied mate calls.

7.2(B) <u>Simultaneous presentation of two Stimulus birds</u>

(a) The initial response to calls from the Stimulus birds

As in 7.2(A), it is clear from a comparison of the control and test periods that both male and female subjects increased their calling rates and became more active on hearing Stimulus calls ($p < 0.05$,

TABLE 24. The Spearman Rank Correlation coefficient values (r_s) for the successive presentation of Stimulus birds (mate and non-mate)

(a) The males as Subject birds

Pair No.	Male and mate calling		Male and non-mate calling	
	r_s value	p value	r_s value	p value
1	0.647	0.05	0.579	0.05
2	0.275	N.S.	0.680	0.05
3	0.659	0.05	0.592	0.05
4	0.818	0.01	1.000	0.01
5	0.876	0.01	0.074	N.S.
6	0.997	0.01	0.289	N.S.
7	0.928	0.01	0.084	N.S.
8	0.759	0.01	0.450	N.S.
9	0.745	0.05	0.196	N.S.
$\bar{X}$	0.745		0.439	

(b) The females as Subject birds

Pair No.	Female and mate calling		Female and non-mate calling	
	r_s value	p value	r_s value	p value
1	0.537	N.S.	-0.104	N.S.
2	0.107	N.S.	0.745	0.05
3	0.642	0.05	0.771	0.01
4	-0.151	N.S.	-0.159	N.S.
5	0.564	0.05	0.215	N.S.
6	0.239	N.S.	0.486	N.S.
7	0.830	0.01	0.563	N.S.
8	0.251	N.S.	0.693	0.05
9	1.000	0.01	0.324	N.S.
$\bar{X}$	0.447		0.393	

N.S. = Not significant

WMP, in each case).

(b) Vocalizations (Fig. 18 and Tables 25 & 26)

(i) The behaviour of males and females

There was evidence to suggest that recognition of mates by their calls was occurring when both a mate and a non-mate were calling at the same time. When the male was the Subject bird it was possible to compare calling by the mate and a female non-mate (i.e., the two Stimulus birds) in response to the males calls. The non-mate female gave significantly fewer calls than the Stimulus mate in this situation ($p < 0.05$, MWU) which indicates that the mated female could recognise her male's calls. With the female as subject, the two Stimulus males (mate and non-mate) did not show a significant difference in their total calling but the male mate did give more calls, on average. These differences are evident in Fig. 18.

In the previous experiment, 7.2(A), the females gave fewer calls when used as a Stimulus than when a Subject bird. This tendency was not apparent here and, like the males, females gave the same number of calls in both situations. This suggests that some feature of the Stimulus bird situation in 7.2(A) may have inhibited female calls. Undirected singing appeared to be reduced in this experimental set-up. Only three males gave any at all when used as subjects and none when they were Stimulus birds. This represents a possible difference between successive and simultaneous presentation of Stimulus callers.

(ii) The correlation of calling rates by mates and non-mates

r_s scores prepared for the calling between mates and non-mates are shown in Table 26 and in this case, unlike 7.2(A), it was possible to test for the correlation of calling between the two Stimulus birds

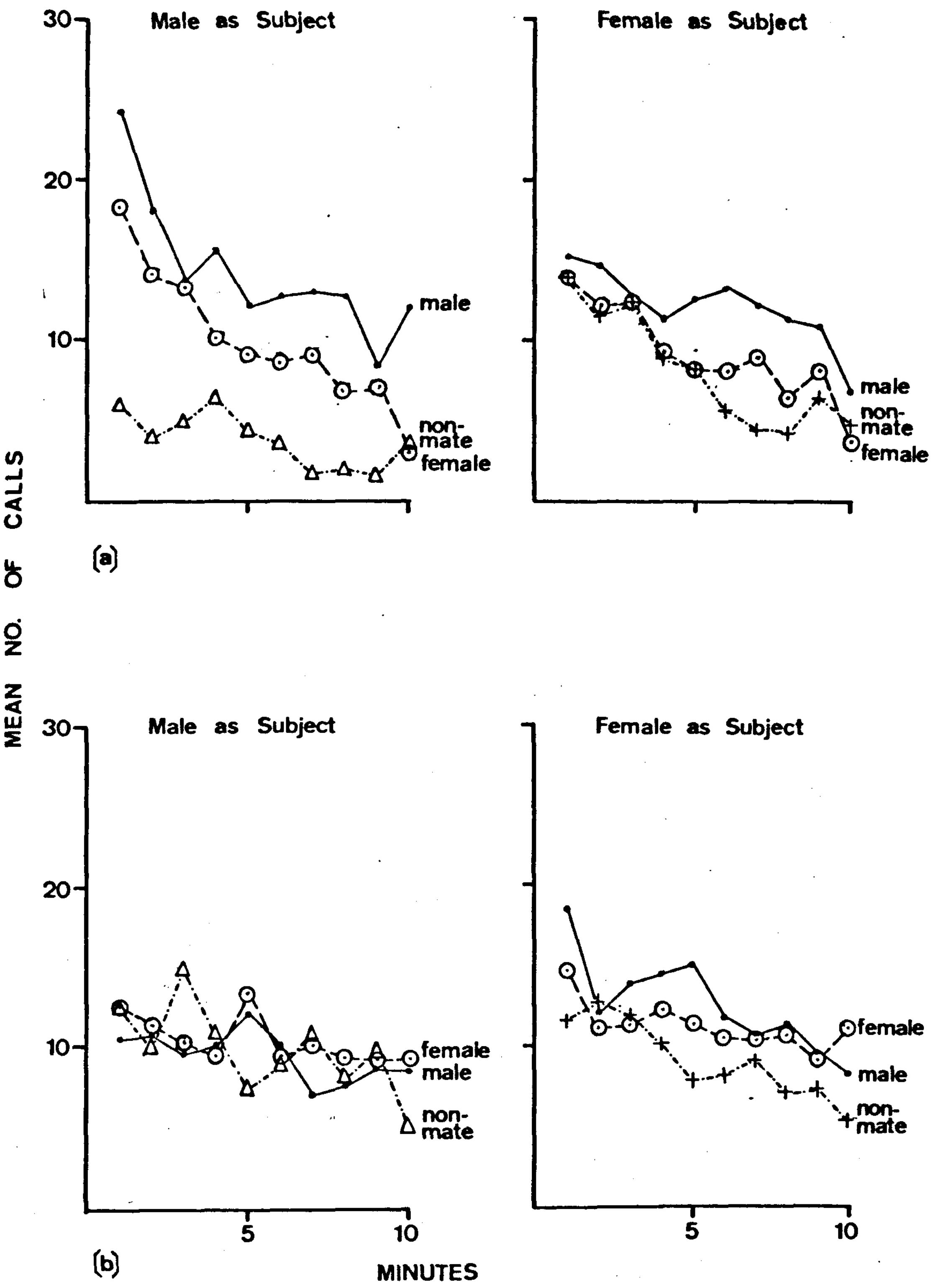


Fig. 18. The number of calls given by the subject and the Stimulus birds during the simultaneous presentation of two Stimulus birds. (a) Experiment 7(B) - in which birds were in auditory contact only. (b) Experiment 7(C) - in which birds were in both auditory and visual contact.

TABLE 25. Measures of Vocalizations and Activity during simultaneous presentation with the callers out of visual contact. (No. of subjects = 9)

				STIMULUS BIRDS	
BEHAVIOUR	SUBJECT	CONTROL	RESPONSE BY SUBJECT	RESPONSE BY MATE	RESPONSE BY NON-MATE
CALLS (Mean No.)	Males	74.2	140.0	91.8	33.0
	Females	22.1	94.6	125.1	82.3
SONG (Mean no. of bouts)	Males	0	5.1	-	-
	Females	-	-	0	0
ACTIVITY (Mean no, maxm = 30)	Males	11.7	26.0	21.6	15.4
	Females	7.4	20.7	21.7	21.9
SYNCHRONY	Males			14.8	13.1
	Females			18.2	12.1

TABLE 26. The Spearman Rank Correlation coefficient values (r_s) for the simultaneous presentation of two Stimulus birds

(a) The males as Subject birds

Pair No.	Male and mate		Male and non-mate		The 2 Stimulus females	
	r_s value	p value	r_s value	p value	r_s value	p value
1	0.790	0.01	0.000	N.S.	0.000	N.S.
2	0.186	N.S.	-0.329	N.S.	-0.137	N.S.
3	0.576	0.05	-0.075	N.S.	-0.073	N.S.
4	0.463	N.S.	0.117	N.S.	0.527	N.S.
5	0.874	0.01	0.765	0.01	0.766	0.01
6	0.811	0.01	0.494	N.S.	0.576	0.05
7	0.537	N.S.	0.101	N.S.	0.294	N.S.
8	0.336	N.S.	-0.192	N.S.	0.060	N.S.
9	0.353	N.S.	0.387	N.S.	0.456	N.S.
$\bar{X}$	0.548		0.142		0.275	

(b) The females as Subject birds

Pair No.	Female and mate		Female and non-mate		The 2 Stimulus females	
	r_s value	p value	r_s value	p value	r_s value	p value
1	0.992	0.01	0.588	0.05	0.702	0.05
2	-0.480	N.S.	0.160	N.S.	-0.056	N.S.
3	-0.121	N.S.	0.412	N.S.	-0.237	N.S.
4	0.840	0.01	-0.161	N.S.	0.048	N.S.
5	0.214	N.S.	0.117	N.S.	-0.014	N.S.
6	0.994	0.01	0.340	N.S.	0.327	N.S.
7	0.459	N.S.	0.481	N.S.	0.204	N.S.
8	0.282	N.S.	0.480	N.S.	-0.295	N.S.
9	0.841	0.01	0.841	0.01	1.000	0.01
$\bar{X}$	0.447		0.362		0.187	

as well. The tendency revealed in the results is for correlation of calling between mates when both the male and the female were Subject birds. In the former, all of the mates showed positive correlation with 4 (from 9) reaching significant values. The females showed a similar 4 significantly positive values but two negative scores were obtained indicating a tendency for the two birds concerned to call at different times rather than together. In contrast, calling between non-mates resulted in only one significant positive value when the male was the subject and two in the case of the female. Thus as well as tending to call more to mates birds with a pair bond tend to answer one another or, at least call at the same times.

Calling by the two Stimulus birds in these experiments were positively correlated in some cases (2 when males were subjects and 2 when females were subjects) indicating that calling by any two conspecifics may be correlated on some occasions.

(c) Activity and synchrony (Table 25)

Both the males and the females became active on hearing the calls of Stimulus birds and a measure was taken of synchrony of behaviour between mates and non-mates. This involved counting the number of times the subject bird and its mate were engaged in the same activity at the same time and comparing this figure with that for the subject and non-mate. This does not necessarily result in an accurate measure of synchrony but provides a suitable method of comparing the amounts shown. The data revealed that when the female was a subject she synchronised her behaviour more with that of her mate than a non-mate male ($p < 0.05$, MWU). On the other hand, when the male was a Subject bird this tendency was not evident indicating that it was the female who altered her responses as a result of recognising her mate's calls. If the male recognised the calls, his response did not affect the level of synchronisation of activities by mated birds.

7.2(C) Simultaneous presentation of Stimulus birds in visual contact

(a) The initial response to calls from the Stimulus birds

Changes in behaviour recorded were similar to those outlined in 7.2(A) and (B) but in this situation the males could now court the females through the wire barrier which separated them.

(b) The Vocalizations (Fig. 18 and Tables 27 and 28)

(i) The behaviour of mates and non-mates

The evidence that females called more to their mate than to a non-mate, as found in 7.2(A) and (B) disappeared when the calling birds were in visual contact. With the male as subject both Stimulus females, mate and non-mate gave similar numbers of calls and the mates showed no signs of a preferential response. However, both the Stimulus mate and non-mate females increased the number of calls they gave when compared to the levels heard during the previous experiment when the birds were out of visual contact ($p < 0.05$, WMP).

When the females acted as Subject birds there was, similarly, no evidence that mates called more to one another. The female subject's calling did increase over the level recorded when the birds were out of visual contact ($p < 0.05$, WMP) but the two Stimulus males continued to give comparable amounts. Finally, courtship song given by the males was directed at both mate and non-mate females such that no preference could be detected from the results.

(ii) The correlation of calling rates by mates and non-mates

The r_s values calculated are shown in Table 28 and for the first time significant negative correlations were measured. This would

TABLE 27 Measures of Vocalizations and Activity during simultaneous presentation of callers in visual as well as auditory contact (No. of subjects = 10)

				STIMULUS BIRDS	
BEHAVIOUR	SUBJECT	CONTROL	RESPONSE BY SUBJECT	RESPONSE BY MATE	RESPONSE BY NON-MATE
CALLS	Males	75.7	94.7	102.7	99.2
(Mean no.)	Females	30.3	111.9	124.8	88.4
SONG	Males	0	8.4	-	-
(Mean no. of bouts)	Females	-	-	2.2	2.4
ACTIVITY	Males	6.0	23.4	20.7	19.1
(Mean no. Max = 30)	Females	7.4	24.8	25.9	27.0
SYNCHRONY	Males			18.3	15.3
	Females			20.9	15.9

TABLE 28. The Spearman Rank Correlation coefficient values (r_s) for the simultaneous presentation of the Stimulus birds in visual contact

(a) Males as Subject birds

Pair No.	Male and mate		Male and non-mate		The 2 Stimulus females	
	r_s value	p value	r_s value	p value	r_s value	p value
1	-0.163	N.S.	-0.234	N.S.	0.059	N.S.
2	-0.163	N.S.	0.069	N.S.	-0.798	0.01
3	0.425	N.S.	-0.241	N.S.	-0.776	0.01
4	-0.445	N.S.	0.153	N.S.	-0.238	N.S.
5	0.111	N.S.	-0.573	0.05	0.387	N.S.
6	0.966	0.01	0.730	0.05	0.770	0.05
7	-0.167	N.S.	-0.487	N.S.	0.375	N.S.
8	0.959	0.01	-0.499	N.S.	-0.375	N.S.
9	0.171	N.S.	-0.202	N.S.	-0.718	0.01
$\bar{X}$	0.239		-0.153		-0.173	

(b) Females as Subject birds

Pair No.	Female and mate		Female and non-mate		The 2 Stimulus males	
	r_s value	p value	r_s value	p value	r_s value	p value
1	0.059	N.S.	0.353	N.S.	0.334	N.S.
2	0.574	0.05	0.126	N.S.	0.020	N.S.
3	0.561	N.S.	-0.245	N.S.	-0.202	N.S.
4	0.606	0.05	-0.708	0.05	-0.160	N.S.
5	0.370	N.S.	0.073	N.S.	-0.213	N.S.
6	0.172	N.S.	-0.424	N.S.	0.747	0.01
7	0.046	N.S.	0.105	N.S.	-0.279	N.S.
8	0.349	N.S.	-0.019	N.S.	0.365	N.S.
9	0.272	N.S.	0.414	N.S.	0.580	0.05
$\bar{X}$	0.334		-0.014		0.132	

suggest that in these cases birds were calling at distinctly different times rather than together. In addition, the results show that with visual contact the correlation of calling between mates was reduced over the levels seen in the previous experiments. When the male was the Subject bird there were only 3 cases of significant positive scores for the mates and one for non-mates. The female as subject results show a similar three significant results with none of the positive values for non-mates reaching significance.

The birds which showed significant negative values were all non-mate pairings. One was for male subject and a Stimulus non-mate whereas the other four scores were all in cases where the calling of the two Stimulus females (mate and non-mate) was compared. This suggests that the females, when they could see one another together with a Subject male, chose to call at different times. The two male Stimulus birds were different in that their r_s values indicate positive correlation on 5 occasions with 2 of these reaching significance.

(c) Activity and Synchrony (Table 27)

As in 7.2(B), the mates showed significantly more synchronisation of their activities than did the non-mates in the male as subject situations ($p < 0.05$, WMP). This suggests that the female mate was adapting her behaviour to match that her mate was engaged in by both auditory and visual cues. Non-mates did show synchrony but not to the same degree.

Discussion

Beer (1970c) has reviewed the evidence for birds using calls as the basis for individual recognition. There are many field observations quoted with some of a more experimental approach. Notable amongst the more recent papers are Tschanz (1968) on Guillemots, Beer (1970a & b) on the Laughing Gull, Stevenson et al (1970) on the Common Tern, Evans (1970) on the Black-billed Gull, White (1971) on the Gannet and Burger (1974) on gulls; all of these stress the importance of vocalizations to birds nesting in colonies. Evidence in the estrildids is far more subjective; Zann (1972) notes that in Poephila more loud calls were given when mates were separated than were heard when two conspecifics from the same flock called to one another. Immelmann (1965) has described the behaviour of Zebra Finches in the wild and includes the observations that, (a) nesting neighbours 'know each other' by their calls, (b) nest relief of paired birds occurs outside of the nest (i.e., recognition must initially take place out of visual contact), and (c) the larger a flock of these birds becomes the more vocalizations are heard. These suggest that recognition of vocalizations made by the mate is important in the Zebra Finch but demonstrating such a preference experimentally is another matter.

The results presented here argue that mate recognition of calls, whilst out of visual contact, does occur. There were no instances of birds remaining silent throughout the experimental period and thus this is possibly a better situation for studying mate recognition than that described for the playback experiment in Section 7.1. In both successive and simultaneous presentation of Stimulus birds males and females called more to their mate than to a non-mate. However, it is notable that only in the females does this difference reach significant proportions. It would appear, therefore, that the onus for mate recognition of calls lies with the female rather than the male member of the pair bond. This suggestion is supported by the data for activity and synchrony as it was only the females in both experiments who showed any preference for the mate and in 7.2(B) synchronised their behaviour with his when out of visual contact.

(a) The effects of successive and simultaneous presentation of Stimulus birds

The comparison of calling rates in the two experiments revealed that the females were affected more by the successive presentation procedure than by the simultaneous one. In the first, females showed less calling when used as a Stimulus bird than when the subject of a trial but this difference disappeared when the mates and a non-mate were calling simultaneously. The males, on the other hand, called at approximately the same rates throughout. This seems to suggest that the calling rates of the females may be affected by environmental influences more readily than can the males and this may obviously affect the ability of mates to maintain contact at different times.

Beer (1970c) notes a similar difference in the responses of Laughing Gull chicks to the calls of their parents and of neighbouring adults when they were successively presented as opposed to simultaneously. In the former case, the chicks showed no preference for parental calls and responded just as readily to the neighbour's calls whereas, in the latter (simultaneous), they only approached the speaker which emitted the parental calls. Beer suggests that this is adaptive in that during successive presentations the chick must approach other adults in the hope that it may be fostored as, for all it knows, its parents may be lost and not returning. In simultaneous presentations this quandary on the part of the chick is no longer taking place and the parental calls take precedence.

Presumably, a similar strategem could operate in the responses to calls made by mated Zebra Finches. In the prolonged absence of a partner it might be more advantageous for a bird to call to a non-mate than when there is vocal evidence of the mate's presence. If this were the case one would expect the subject birds during successive presentation to call quite readily to non-mates which is in fact what occurred. It is interesting that the females still exhibited a preference for calling to the mate but this does not explain why they (the females) called more as a Subject bird than as a Stimulus. Possibly, in the latter situation, the chance to call to the other Stimulus bird during separation from the mate reduced the effect of that separation period. Certainly, Beer's explanation of the strategy of Laughing Gull chicks provides one possible explanation for the calling between non-mate Zebra Finches.

(b) The effect of visual contact on the calling rates of birds

It seems very likely that a change in context will affect the way in which mated Zebra Finches use vocalizations. Hence, it is interesting to compare calling between birds in visual contact with that when they were in auditory only. Beer (1970c) notes that there was good evidence of individual recognition by calls in bird species that lived in colonies or in dense vegetation. In these contexts there would probably be many occasions when an absence of reliable visual clues would make identification difficult. Such contexts could easily arise in flocks of Zebra Finches in the wild whereas on the small nesting territory such problems would be less likely and calls would be exchanged when birds were in visual contact.

Beer also noted an interesting observation concerning gull colonies. Alarms often caused birds to take flight and, in the absence of vocal clues from the mate on the nest, there was much hostility as individuals attempted to land. Smith and Bird (1963, 1964) found that auditory stimulation was enhanced when it was accompanied by visual signals in eliciting an approach response of domestic chicks. Similarly, Ingold (1973) noted that recognition of the parent by young Razorbills was more effective in cases where both auditory and visual signals were provided by the adult.

In the present experiments it was noticeable that the preferential calling to the mate showed by females disappeared when visual contact was provided. In fact, calling by both the mate and the non-mate female was increased compared to that seen during auditory contact only. The activities of the female mate were still more synchronised with their males than was the non-mates, however, and this would be expected from two birds with an established pair bond (as shown in Section 4). Thus, visual contact with other Zebra Finches induces the females of this species to call more readily than when they can only hear the calls of a mate or conspecific. In other words, it is again the females rate of calling which is affected whereas the males apparently call at roughly the same rate in either context.

(c) Correlation of calling by mates and non-mates

The information for the correlation of calling between mates and non-mates adds support to the findings discussed above. It provides evidence to suggest that even in the visual situation, mates called more to one another than did non-mates. However, it must be noted that this is not necessarily an accurate assessment of correlation but only reflects a tendency by two birds to give the same number of calls in each minute of the observation period.

A possibly better method would involve a sonogramic analysis to see whether individuals were actually replying to each others calls.

Mated birds do seem to answer one another and Immelmann (1965) has noted this tendency in the wild. There is thus the possibility that a rather loose form of duetting occurs between paired birds such that calls may be answered in turn. Kilham (1972) found that this appeared to occur between mated Nuthatches as they moved around in their habitat and the suggestion that Zebra Finches make use of a similar technique will be explored more fully in the following experiments (section 7.3).

7.3 Vocalizations after separation and on introduction of mated and non-mated birds

Introduction

It is worth recalling the importance of individual recognition by mates before the last experiments in this section are described. As Thorpe (1968) suggested, it seems that in colonial bird species the efficiency and success of breeding will depend, in large part, on the individual recognition of members of the family. One could add, that recognition and continual contact between mates will be paramount in a social species such as the Zebra Finch in which pair bonds are prolonged. The difficulty for the experimenter, if 'difficulty' is the right word, is that there is an advantage for individuals to keep in vocal contact with other members of the social flock as well. Any measures of possible responses to calls must therefore take into account two conflicting tendencies, (a) to answer the calls of the mate, and (b) to answer the calls of other familiar conspecifics. One could also argue that there might even be interspecific exchanges as the Zebra Finch is known to form mixed-species feeding flocks.

Calling between Zebra Finches does not apparently show a simple relationship with the establishment of pair bonds. This has been shown in the previous experiments in which results suggest that a paired female is likely to adjust her rate of calling to that of her mate. A mated male, on the other hand, replies to any conspecific with equal fervour.

The two experiments described in this section examine more closely the vocal responses of mated birds. If birds do alter their calling rates depending on the conspecific they are calling to, then there should be at least two times when this may be observed: (a) the calling response between two birds should change as they form a pair bond; (b) calling to a mate should differ from calling to a non-mate. Both of these situations were examined in Section 7.2 but in this study two different types of calls will be distinguished. There are those designated 'Loud' calls (which include loud and loud/soft calls) and those termed 'Soft' calls (Soft and tet together). In addition, calling in two contexts was observed. These were, (i) calling whilst separated (out of visual contact) from a conspecific, (ii) calling after introduction following the separation period. Experiments of 7.2 showed that visual contact affected calling rates.

Methods

7.3(A) Calling by males and females before and after their pair formation

12 males and 12 females were used and care was taken to ensure that these individuals had not met in a pair formation situation prior to this experiment.

The experimental cage was housed in a separate room well out of earshot of the stock cages and consisted of a two compartment cage. A single horizontal perch was provided and a solid wooden partition separated the two compartments. The partition could be removed by means of a length of cord attached to its leading edge with minimal disturbance to the Subject birds. The experimenter and the recording equipment, were situated some 3m from the cage and hidden from the subjects by a large screen. This allowed considerable movement without the risk of disturbance which might have elicited calls.

Birds were brought directly from a stock cage and a male and a female placed one on either side of the solid partition. Males were placed alternately to the right or left of the partition in successive trials to eliminate any extraneous variables. Observations were made for 30 minutes after the first calls were exchanged. The partition was removed and a further 30 minutes monitored after introduction.

After each trial the male and female used were placed in an individual cage in the stock room and left for a period of seven days. At the end of this period the same experimental procedure was repeated as before with the, by now, paired birds.

7.3(B) Calling between 'established' mates and between non-mates

10 pairs were used. Each had established a pair bond in individual cages over periods in excess of one month. The experimental procedure followed that described above but in this case calling in three different diads was compared;

i) The established mates calling to one another during separation and then on introduction.

ii) The mated male calling to a non-mate female during separation from her and then on their introduction.

iii) The mated female calling to a non-mate male in the same two situations (as above). There was a period of at least 5 days, during which birds were housed in stock cages with their mates, between the use of each individual (both mate and non-mate) in the experimental situation.

Behavioural measures

The number of calls given by each bird in one minute intervals of the observation time, were counted. They were divided into;

(a) 'Loud' calls (loud plus loud/soft calls), and (b) 'Soft' calls (soft plus tet calls).

On introduction courtship song occurred but this has been described elsewhere (Section 5) and was excluded here. Undirected song, when it occurred, was counted in terms of number of singing bouts.

Results

7.3(A) Calling by males and females before and after their pair formation

The results are shown in the form of histograms of the mean number of calls given per minute (Figs. 19 and 20). The assessment of the correlation of calling between birds, the Spearman Rank Correlation r_s values, are shown in Table 29, which should indicate to what degree birds were replying to one another.

The total amount of calling given between paired birds did not differ from that given between the same individuals on their introduction (as strangers) in both the auditory and the visual contact situations. Similarly there were no obvious changes in the correlation of these calling rates for the birds in these situations.

There were, however, other differences which can presumably be associated with the processes of pair formation. First, females in auditory contact with their partner gave more 'soft' calls after pairing than before it ($p < 0.05$, WMP). Second, both males and females showed decreased tendencies to make 'loud' calls on their re-introduction ($p < 0.05$, WMP); there was a corresponding increase in the number of soft calls given by both sexes in this situation (significant in the females, $p < 0.05$, WMP).

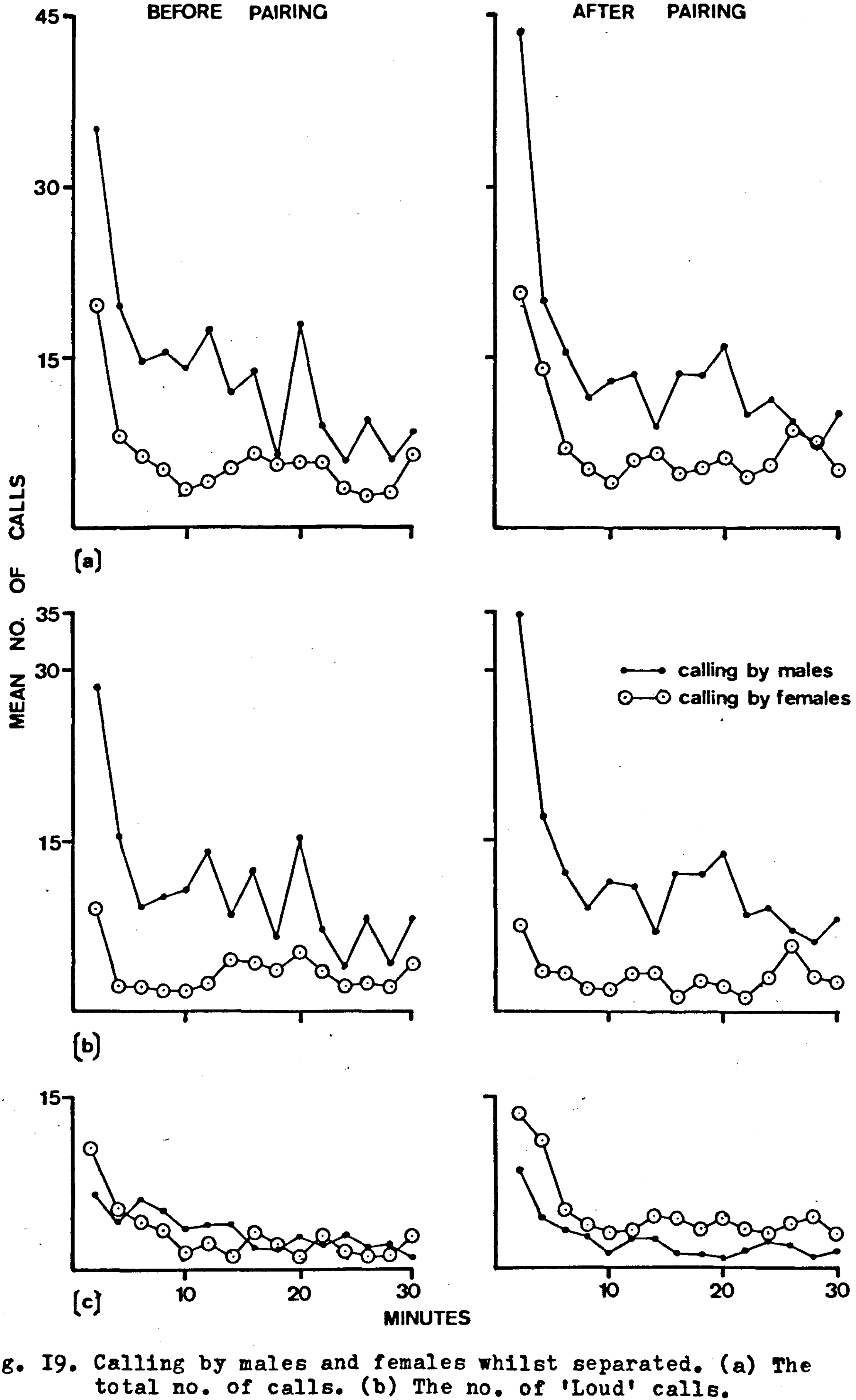


Fig. I9. Calling by males and females whilst separated. (a) The total no. of calls. (b) The no. of 'Loud' calls. (c) The no. of 'Soft' calls.

TABLE 29. The Spearman Rank Correlation coefficients for Calling by males and females, before and after their pair formation

(a) Calling during separation

Pair No.	Total Calling		Loud Calls		Soft Calls	
	Before	After	Before	After	Before	After
1	0.519*	0.813*	0.920*	0.816*	-0.072	0.810*
2	0.460*	0.762*	0.088	0.756*	0.164	0.500*
3	0.746*	0.913*	1.001*	0.800*	0.666*	0.443*
4	-0.147	0.348*	-0.349*	0.337*	0.246	-0.307*
5	0.726*	0.236	0.765*	-0.143	0.498*	-0.167
6	0.608*	0.888*	0.800*	1.000*	0.721*	0.888*
7	0.438*	0.249	0.581*	0.111	-0.207	0.289
8	0.687*	0.516*	0.495*	-0.013	0.029	0.397*
9	0.631*	0.467*	0.201	0.000	0.464*	0.388*
10	0.817*	0.735*	0.686*	0.557*	0.649*	0.853*
11	0.467*	0.565*	0.379*	0.257	0.609*	0.706*
12	0.215	0.438*	-0.163	-0.224	-0.167	0.195
$\bar{X}$	0.514*	0.578*	0.451*	0.355*	0.300	0.417

(b) Calling after Introduction

Pair No.	Total Calls		Loud Calls		Soft Calls	
	Before	After	Before	After	Before	After
1	0.837*	0.728*	0.348*	-0.041	0.856*	0.728*
2	0.105	0.151	1.000	-0.043	0.010	0.045
3	0.670*	0.588*	0.428*	-0.041	0.550*	0.558*
4	0.539*	0.313*	0.313*	0.000	0.695*	0.493*
5	-0.423*	0.233	0.059	0.000	0.503*	0.262
6	0.397*	0.472*	0.897*	No Calls	0.080	0.472*
7	0.302	0.691*	0.752*	-0.162	0.520*	0.505*
8	0.365*	0.728*	0	No calls	0.389*	0.728*
9	0.707*	0.735*	0	0.000	0.729*	0.735*
10	0.233	0.689*	-0.076	No calls	0.233	0.689*
11	0.378*	0.063	-0.076	0.107	0.378*	0.122
12	-0.244	-0.149	0.473*	No calls	-0.115	-0.149
$\bar{X}$	0.291	0.437*	0.344*	0.319*	0.403*	0.433*

* = $p < 0.05$

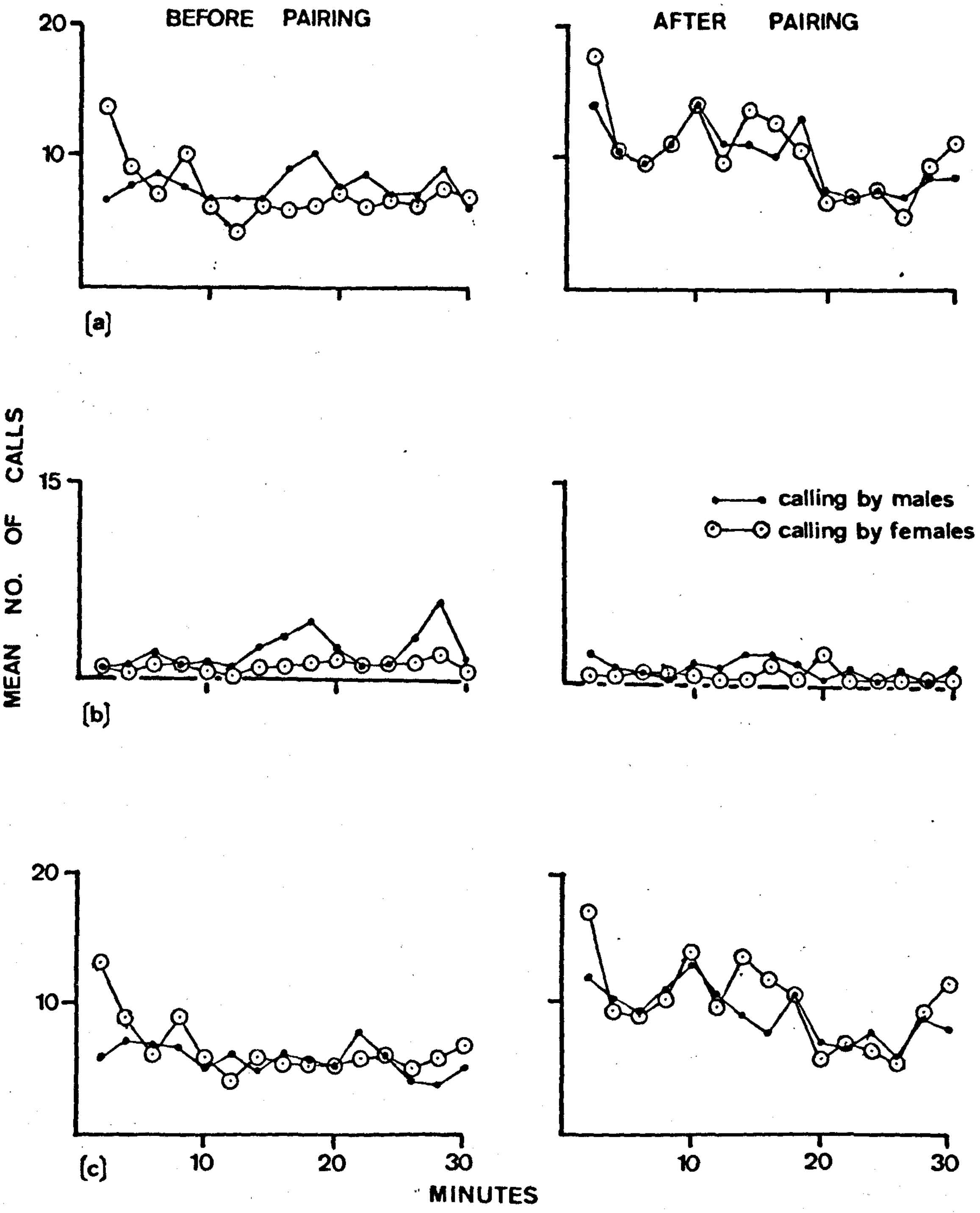


Fig. 20. Calling by males and females after introduction. (a) The total no. of calls given. (b) The no. of 'Loud' calls. (c) The no. of 'Soft' calls.

7.3(B) Calling between 'established' mates and between non-mates

In each situation (i.e., during separation and after introduction) comparisons were made of the calling between mates, that between the mated male and a non-mate female and those for the mated female and a non-mate male. The calls, their total rates and the numbers of loud and soft are shown in Figs. 21, 22 and 23. The correlation coefficient values (r_s) appear in Appendix III.

The established mates tended to give more calls to one another than to a non-mate but the differences did not reach significant proportions. The correlation coefficient values (r_s) for total calling show no evidence of mate duetting.

The use of loud and soft calls, however, appeared to be altered by both males and females when they called to different individuals. The number of loud calls given by males and females did not differ during separation from the mate or a non-mate but they did after introduction. Both sexes gave more loud calls on introduction to a non-mate than they did to the mate ($p < 0.05$, WMP, in each case). The soft calls showed a difference when out of visual contact (during separation) and the number given by a male or female to a non-mate was reduced, significantly, over the amount given to the mate ($p < 0.05$, WMP, for both sexes). Similarly, the correlation of soft calling in this situation showed fluctuations. 6 mated pairs showed significant positive r_s values compared with only 3 of the male with non-mate and 4 of the female with non-mate diads (the difference between the male's correlation scores with his mate and those with a non-mate is significant, ($p < 0.05$, WMP).

The number of soft calls given by mated birds also differed after introduction to a mate or non-mate. Both males and females produced fewer calls when introduced to a non-mate ($p < 0.05$, WMP)

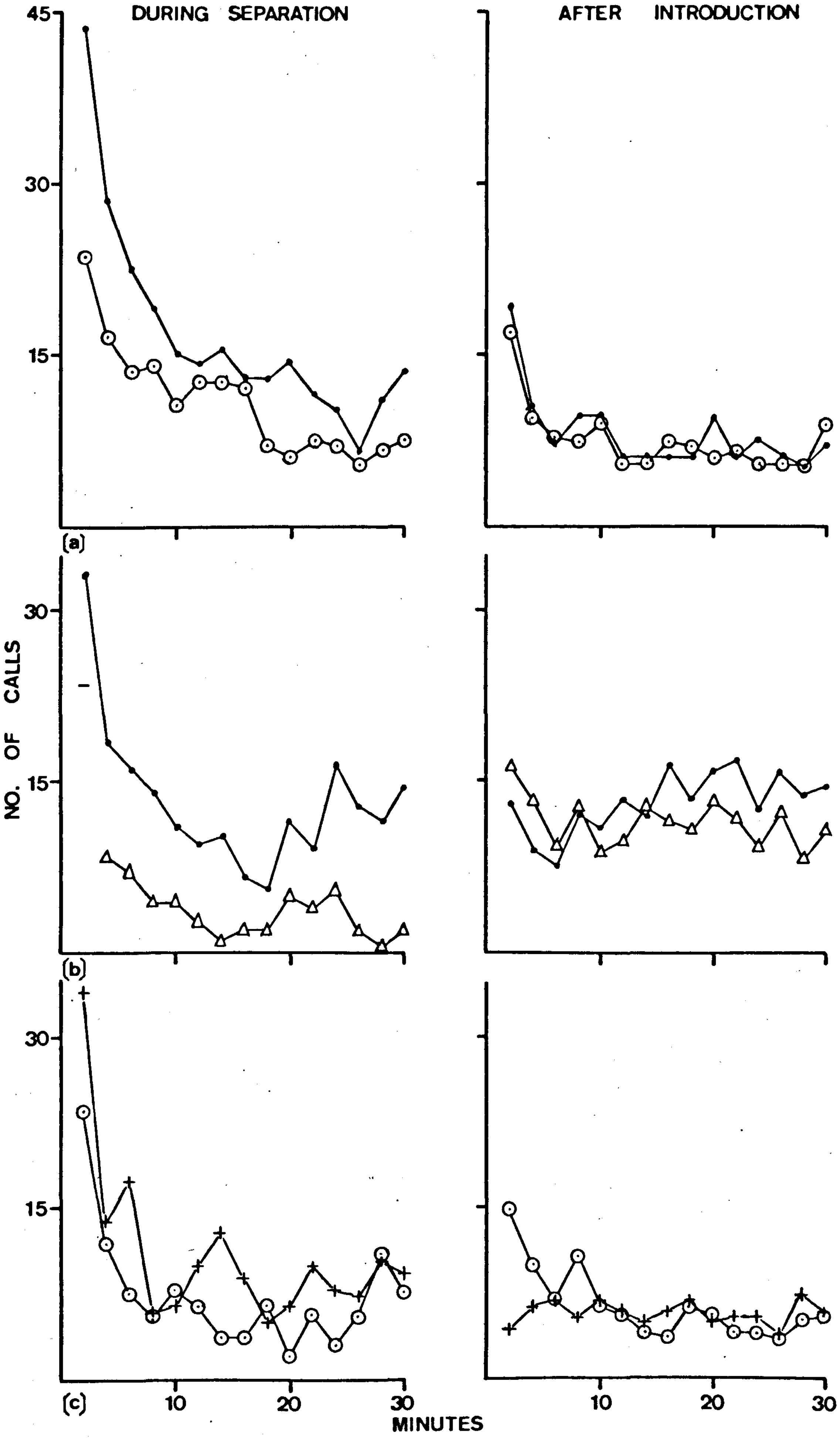


Fig. 2I. The mean (total) number of calls given by males and females during separation and after introduction. (a) Between established mates. (b) Between the male and a non-mate female. (c) Between the female and a non-mate male.

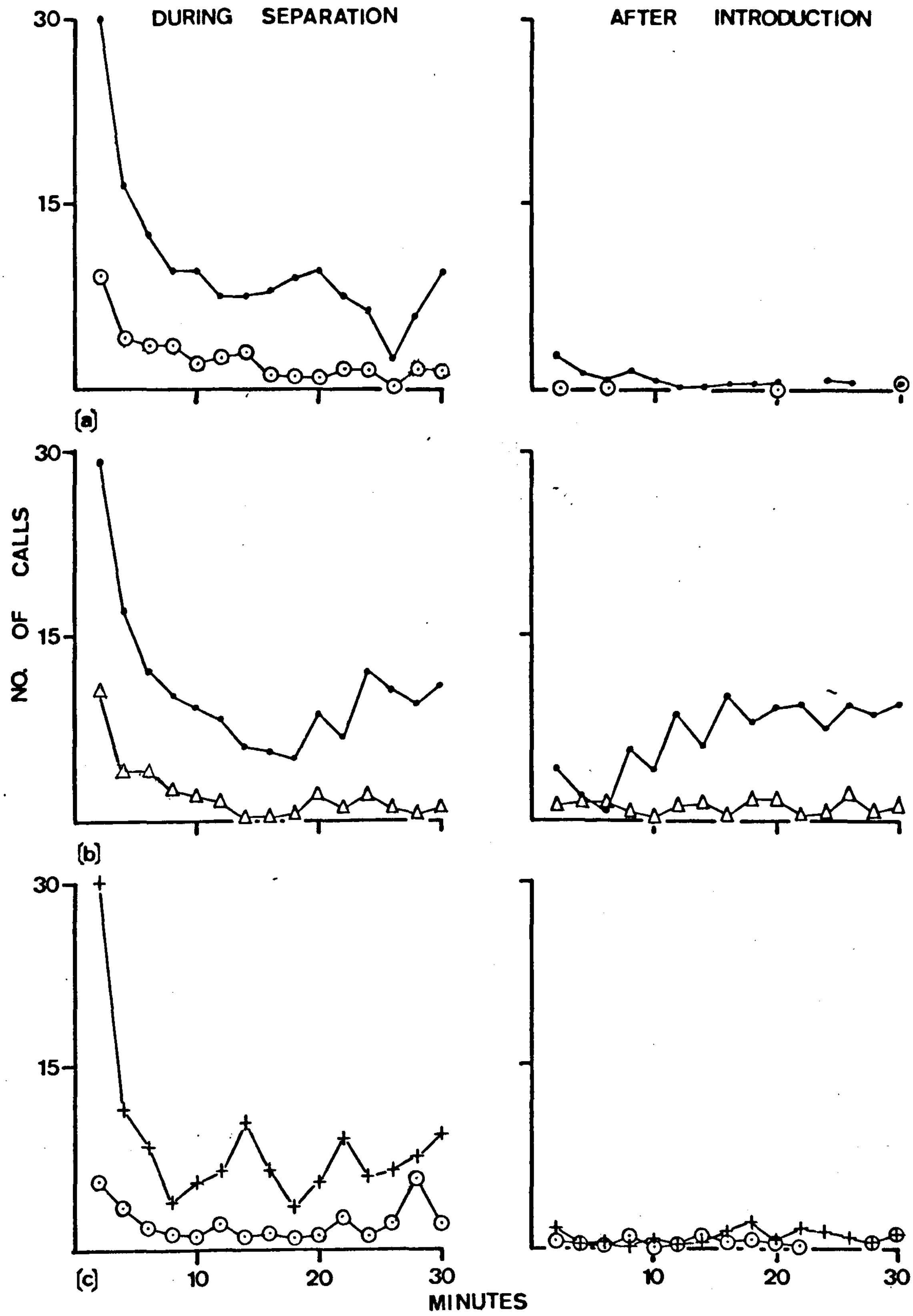


Fig. 22. The mean number of 'Loud' calls given by males and females during separation and after introduction. (a) Between established mates. (b) Between the male and a non-mate female. (c) Between the female and a non-mate male.

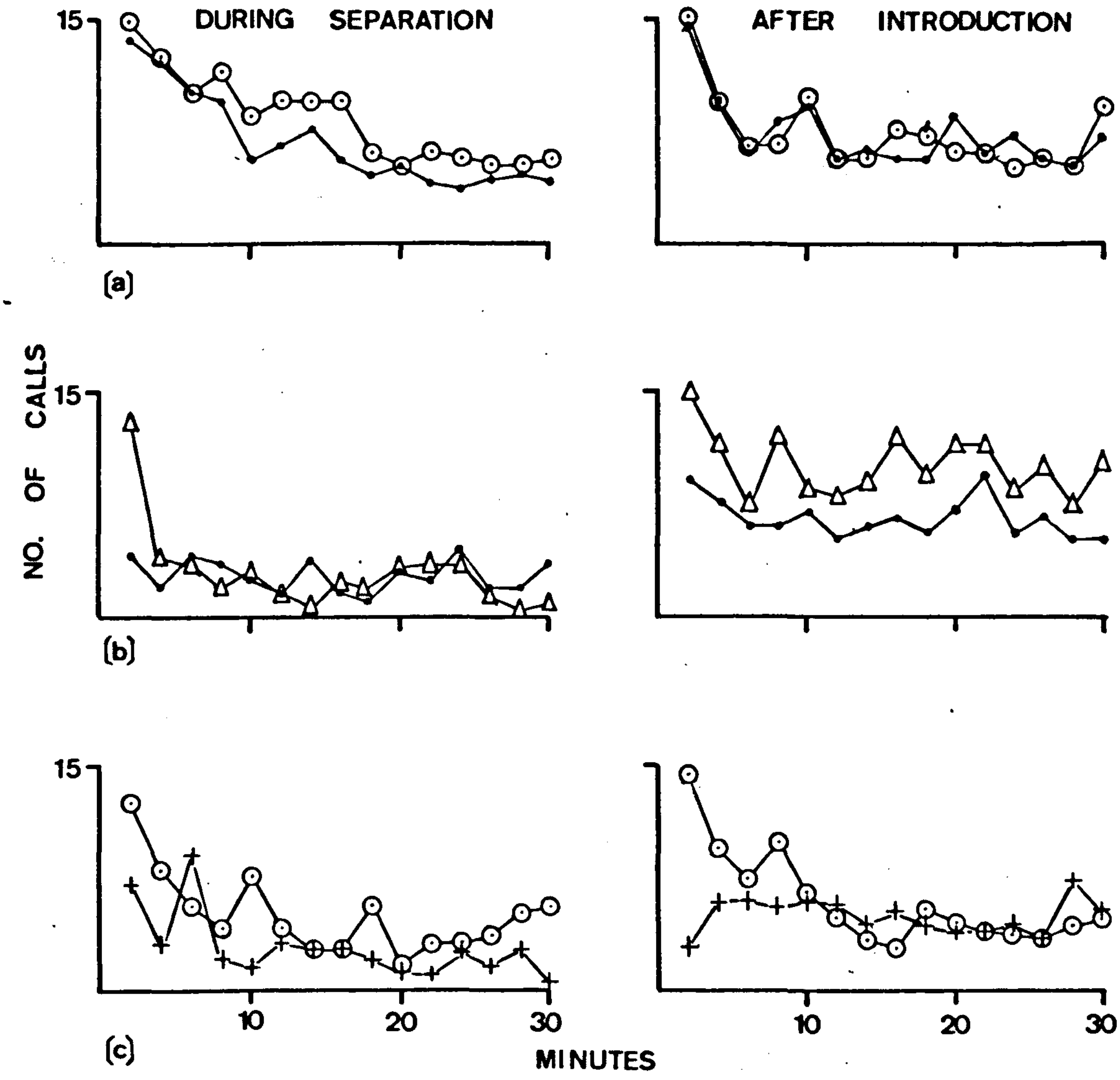


Fig. 23. The mean number of 'Soft' calls given by males and females during separation and after introduction. (a) Between established mates. (b) Between the male and a non-mate female. (c) Between the female and a non-mate male.

and the calling between mates showed more cases of significant positive correlation than did the calling between non-mates (9 for mates, 4 for male with non-mate, and 4 for female with a non-mate; ($p < 0.05$, Fisher Exact Probability Test).

Discussion

One might expect changes in the vocal responses of a Zebra Finch, both when calling to a conspecific and to the mate, as a result of pair formation. Experiment 7.3(A) suggests that calling between a male and a female which are separated changes only slightly as those two birds form a pair bond. The only measurable difference was in the number of soft calls given by the female which were increased after the pairing process. On introduction (i.e., visual contact) the male and female gave less loud calls than whilst separated and pair formation induced a further decrease in the number of these calls given, particularly in the female. However, soft calls were increased with visual contact so that overall birds gave as many calls after introduction as they did during separation. Pairing influenced the number of soft calls used, again, particularly in the female, and these were increased.

Thus the changes observed involve an alteration in the use of loud and soft calls. Most loud calls are given whilst birds, either mated or unmated, are separated and the effect of introduction is to reduce the number used. Zann (1972) noted that in Poephila spp. loud calls were particularly used when mates were separated or a bird removed from its flock. It appears that the pair bonding process induces a further reduction in the use of loud calls by both sexes. As discussed earlier (Section 6.1(C)), loud calls are used in the Zebra Finch as both a 'lost' call and to signify alarm situations. These results suggest that after pair formation, introduction to the mate suppresses the use of loud calls probably as a result of familiarization with the partner. In other words, the partners presence induces less anxiety on the part of a mate.

Soft calls show an opposite trend. On introduction of two birds more are used than were heard when they were separated. In this case, the effect of a pair bond is to enhance this effect such that birds now give more soft calls when in visual contact with their mate. It is possibly interesting that in both these changes, loud calls and soft calls, the female's response is more marked than the males.

The results of the 'established' mates versus non-mates study support these suggestions. On separation, both the male and the female of the pair gave loud calls in response to conspecific calls and, as in the successive presentation experiments of Section 7.2, the same number were given to a conspecific as to the mate. However, soft calling did show a change with the mate as more were given than when separated from a non-mate. With visual contact loud calling was reduced between mates but both the male and the female gave loud calls when introduced to a non-mate. Similarly soft calls were prevalent between mates after introduction but reduced between non-mates.

It seems that the use of soft calls is reserved largely for vocal responses between mates (i.e., they are a feature of the pair bond). These calls (soft and tet) are individually distinct (see Section 6.1) and the evidence here suggests that mates can recognise each others calls whilst out of visual contact. The loud calls (loud and loud/soft) on the other hand, are used apparently for calling to any conspecific that is out of visual contact and no preferential response to the mate could be demonstrated. Loud calling does differ, however, once birds are introduced. When mates are involved less loud calls are given than when non-mates are introduced. Such calls could therefore be termed 'separation' calls (after Potash, 1972) in this context and their use when introduced to a non-mate, by both sexes, may be indicate of attempts to locate the mate.

Thus loud calls are used in a variety of contexts with presumably different motivational factors. Their use when separated from the mate, or in alarm situations when the mate is present are unlikely to involve the same tendencies although one could postulate that fear, a registering of alarm, is the key factor.

Data for the correlation of calling is difficult to interpret in this study. However, soft calling between mated as opposed to non-mated birds, did differ both before and after introduction. These calls did appear to be given at the same time by the mated male and female. It remains to be seen whether this calling involves a duet, that is, has a temporal relationship unique to the pair as Thorpe (1963) found in the antiphonal singing of *Lanarius erythrogaster* and Thompson (1969) demonstrated in the Common Crow. The latter showed that the duration and intervals between the calls of pairs of crows were individually distinct. Certainly Sasvári (1973) has found that the repetition rates of calls are important in eliciting responses in the Great Tit and the results here, in which mates tend to call together, suggests that repetition of the mate's vocalizations may be inducing calling by the partner.

Finally, one must remember that not only vocalizations are important in the recognition process. Visual characteristics can substitute for vocal ones as Tinbergen (1963) showed in the Herring

Gull. Even when birds are out of visual contact there may be other cues operating than just vocal ones. For example, the location of a particular song post may be constant, the calls may be given only at the nest and so on. These experiments on the Zebra Finch demonstrate that the relationship between the pair bond and calling and answering rates, in this species, is not a simple one and differs when different calls are considered in different contexts.

SECTION 8. FACTORS IMPORTANT IN PAIR FORMATION

Introduction

It has been demonstrated so far that various behavioural factors may be associated with the pair formation process. Contact-promoting behaviour (e.g., clumping and courtship), aggression directed away from the mate, synchronisation of activities, and vocalizations have all been implicated in the complex process by which a male and female Zebra Finch establish a link, or bond, which separates them behaviourally from the remainder of their flock. In this section of the study an attempt was made to assess the relative importance of these different activities in the pairing of birds. For example, is the sight and sound of a potential mate 'enough' to allow bond formation or must physical contact be experienced? Indeed, is it possible to form a bond through only auditory contact with a conspecific and no actual sight of this potential mate?

In attempting to answer some of these questions three different situations were compared; pairing of a male and female in auditory contact only; pairing in which both auditory and visual contact was possible but no physical interactions were allowed (such as clumping, allopreening and copulation); normal pair formation in which complete contact between potential mates was permitted. In each case a period was allowed for pair formation to occur, in isolation, followed by observations, of the by now possibly paired birds, in group situations in which the presence or absence of bonds could be assessed.

It was possible, in this study, to compare the relative importance to the pairing process of auditory experience, visual contact and actual physical interactions. It was not possible to determine the strength of any resulting bonds by the methods used but only whether the two birds behaved as a pair at the end of the experimental period.

Methods

The sample size, in each of the experimental situations, was 12 males and 12 females (72 individuals in all). Birds paired together had no previous experience of their partner in a pairing situation and each pair was housed in a separate two compartment cage.

8.1 Pairing occuring with complete contact (CC)

The two compartments of the experimental cages were both available to the male and female, no partition was used.

8.2 Pairing occurring in auditory and visual contact (A+V)

The two compartments of the experimental cages were separated by a perspex partition which was completely transparent. Black vertical lines were drawn on the perspex at 5 cm intervals to ensure that birds were aware of its presence.

8.3 Pairing occurring in auditory contact only (AO)

The perspex partition of Experiment 8.2 was replaced with ones made of solid ¼ inch plywood so that no visual contact was possible between the male and female in the two compartments.

Experimental procedure

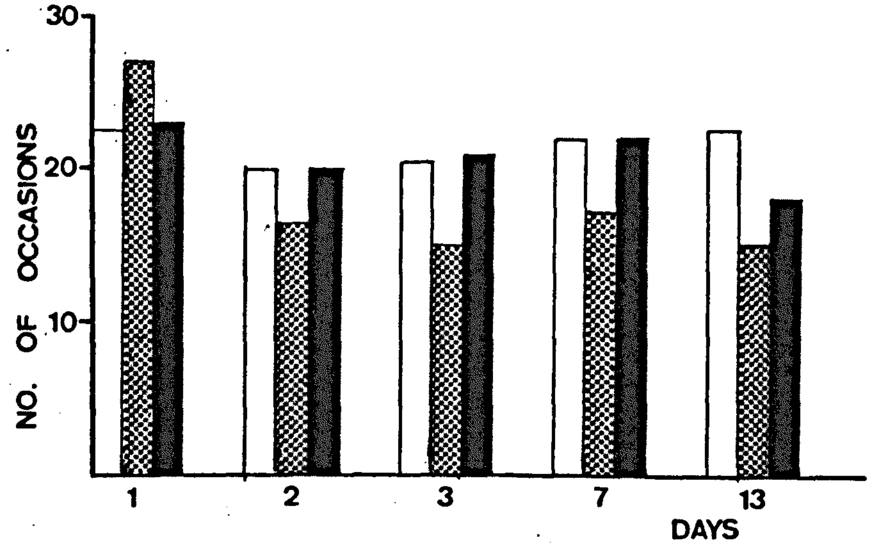
In each situation, the birds were left in the two compartment cages for a period of 14 days. During this time observations were made on all individuals for one hour on the mornings of Days 1, 2, 3, 7, and 13. This was to discover whether pair formation appeared to be taking place. Measures of settled distance (between the male and female) and the amount of synchronisation of behaviour were taken at two minute intervals. Both of these behavioural changes were observed during pair formation in earlier work (see Section 4) and similar methods of assessment were used here.

On the fourteenth day birds were introduced into two large indoor flights measuring 6' x 3' x 4', in groups consisting of 12 individuals (i.e., 6 males and 6 females in each flight). Individual birds could be recognized, with little difficulty, by coloured leg rings and plumage variations. Nevertheless the first observation period (immediately after introduction on Day 14) was very hectic. Observations lasted for one hour and were also made on Days 15, 16, and 20, these three later watches being in the afternoon. Persistent clumping was chosen to indicate the formation of a bond between two individuals (as it was in Section 4) and at two minute intervals the identity of clumping individuals was noted.

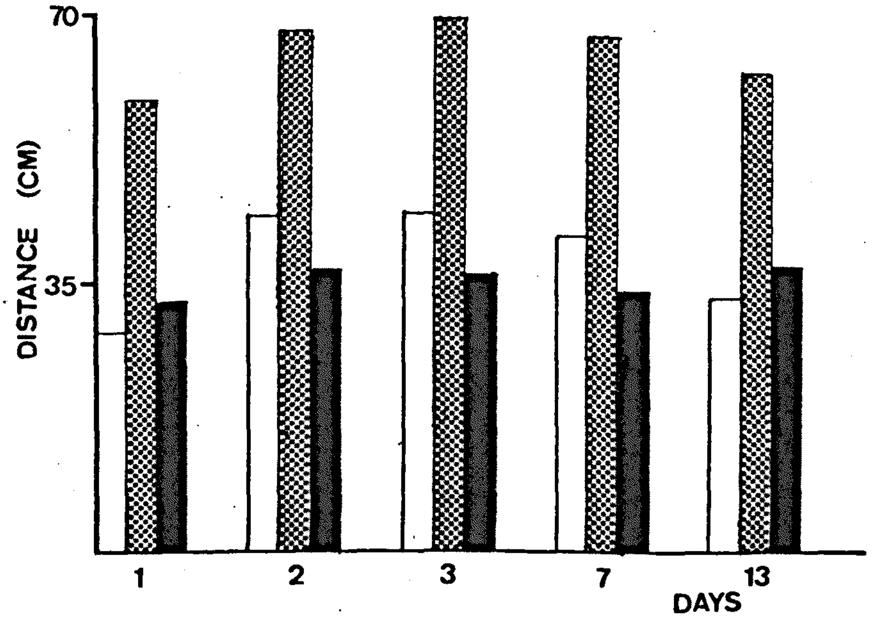
Some of the other behaviour prevalent in the groups is presented in the results but not in detail. This was noted whilst collecting the clumping data and indicates the numbers of courtship bouts, allopreening bouts and supplanting attacks by different individuals.

Results

In discussing the results behaviour between 'potential' mates will be described. These are males and females who were paired together in the experimental situations (Days 1 to 13) and their behaviour towards one another is shown both in the two compartment cages and the groups. In the latter situation, the behaviour between non-mates (i.e., birds meeting for the first time on Day 14) is also presented.



(a) Synchrony scores



(b) Settled distance

Fig. 24. Behaviour in the two compartment cages between potential mates. (a) The synchrony scores. (b) the settled distance. For explanation of the shading - see Fig. 25.

Behaviour in the two compartment cages between potential mates (Days 1 to 13)

The results are presented in Figure 24 and the measures of behaviour taken suggest that pair formation was occurring in the complete contact and auditory plus visual birds but not in the auditory only situation.

(a) Synchrony

The amount of synchronisation of activities was very similar on all days for the birds in complete contact (CC) and auditory plus visual contact (A+V) and only varied significantly on Day 13 when more was apparent in the CC situation ($p < 0.05$, MWU). The auditory only (AO) pairings showed their highest levels of synchrony on Day 1 but in subsequent watches they fell well below the levels seen in either CC or A+V. The level in AO is significantly less than that in CC on Days 3 and 7 ($p < 0.01$, MWU, in each case).

(b) Settled distance

The CC and A+V situations again proved to be similar. They showed comparable scores for the average distance maintained between the males and females whereas in AO the distances involved were much greater on all days (significantly so on Days 1, 3 and 13; $p < 0.01$, MWU).

Behaviour in the groups between potential mates and between non-mates (Days 14 to 20)

Behaviour in the groups is shown in Fig. 25.

(a) Numbers of pairs seen clumping

Much more clumping was observed between potential mates after the CC situation than after A+V or AO which suggests that these

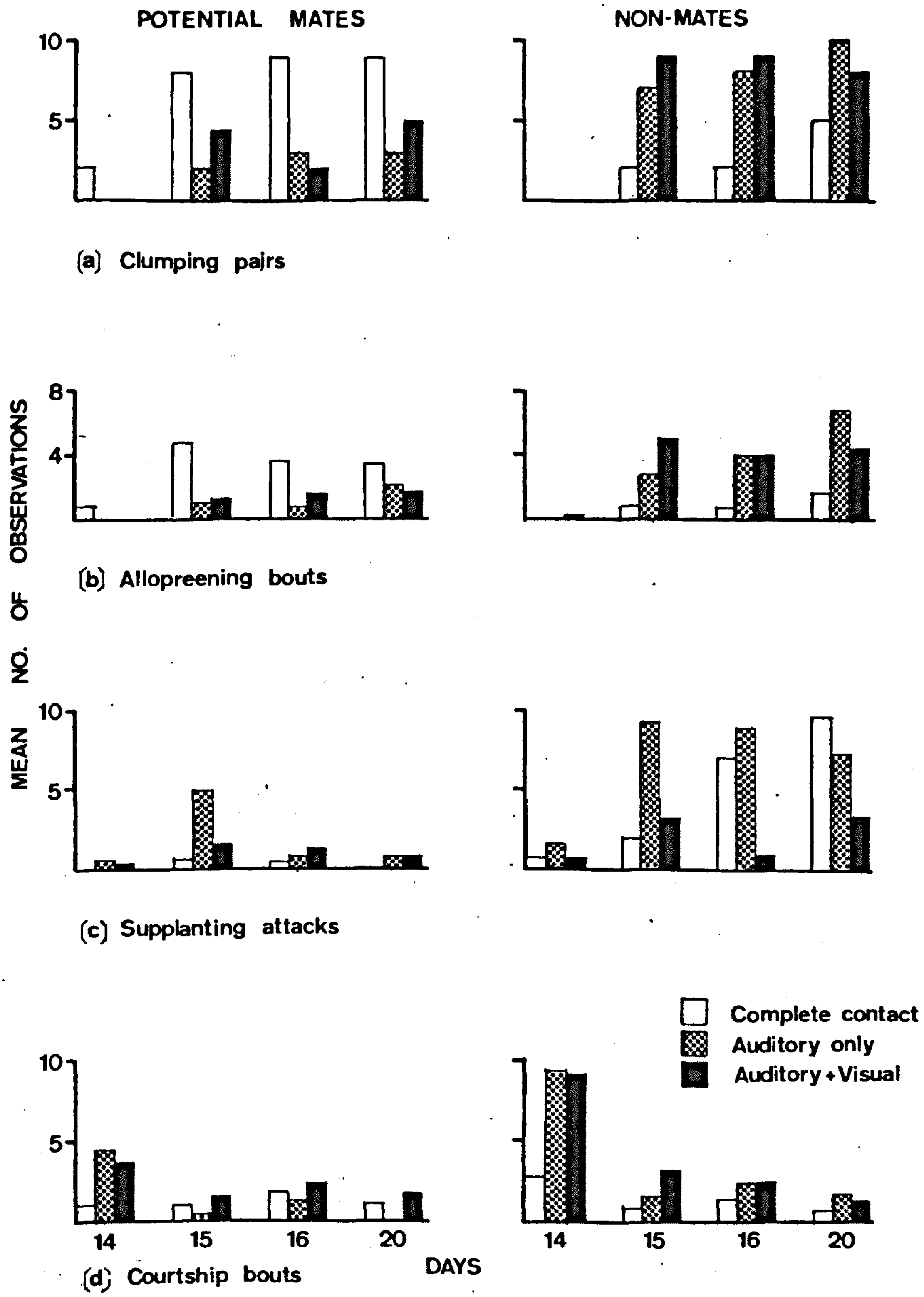


Fig. 25. Behaviour in the large flights (a group situation) between potential mates and non-mates.

birds had formed bonds in the two compartment cages. The difference in the number of pairs seen clumping on Day 15, CC versus A+V and CC v AO, are significant in both cases ($p < 0.05$, Fisher Exact Probability Test). As a corollary much more clumping was seen between non-mates on the A+V and AO groups as birds who had not met until the group situation began to form bonds.

(b) Allopreening bouts

The data for clumping is supported by results for allopreening as more bouts of allopreening were observed between potential mates after complete contact than either A+V or AO situations ($p < 0.05$, WMP, on Day 3), and less between non-mates.

(c) Supplanting attacks

Aggression between birds during pair formation was found to be very infrequent in the experiments described in Section 4. It is thus interesting to note that aggression between potential mates was lowest after CC. This was most marked on Day 15 in all three cases ($p < 0.05$, WMP) and aggression between non-mates increased from Day 14 to Day 20.

(d) Courtship bouts

High levels of courtship were found to be associated with pair formation (Section 4) and in this experiment the highest levels of courtship were observed between both potential mates and non-mates in A+V and AO birds. The lower levels recorded for CC birds suggest that pair formation had already occurred in the experimental cages.

Discussion

The results suggest that pair bonds were most likely to be formed after a period of complete contact without any hindrances provided by the experimental situation. There were some instances of bonding when birds were kept in auditory and visual contact but the numbers involved never reached significant levels. Cases in which only vocal contact was allowed during the pair formation period provided no signs of paired birds suggesting that visual signals, as one might expect, are very important in the bonding process.

It appears from these experiments that physical contact is important in the formation of bonds, at least in the time permitted for pair formation here. They suggest that experience of the behaviour possible in complete contact is necessary in addition to familiarity with the visual appearance and vocal repertoire of an individual. Thus, the bond emerges as a relationship dependent on the performance of all the overt behaviour exhibited by paired birds and which is less likely to be maintained if any of these activities are prevented.

Courtship and proximity were maintained by individuals in auditory plus visual contact, in most cases, yet few bonds resulted. What was not possible in this situation was the so-called contact behaviour (allopreening and clumping) which may therefore assume an important role in pair formation. It could be, as Harrison (1965) suggested, that such behaviour allows the outlet of aggression during proximity and thus without it aggressive tendencies remained in the group situations and no pair bond resulted. Wood-Gush and Rowland (1973) showed that the situation is possibly more complex than this, at least in domestic fowls. They found that allopreening could not be linked directly with the amounts of aggression shown by individuals. However, the importance of allopreening or mutual (social) grooming in promoting proximity and facilitating bond formation has been suggested in many species, including the primates (Eibl-Eibesfeldt, 1971).

Courtship was possible in the auditory plus visual situation but not copulation which raises the question of whether consummatory behaviour is involved in the bonding process. The act of copulation could well be reinforcing to the male, and possibly the female, as Peretti and Brummel (1973) demonstrated was the case in rats. Certainly many bird species, including the Zebra Finch, copulate on more than one occasion and in some cases even up to and including the incubation period. For example, Buckley and Buckley (1972) described copulation occurring between mates throughout incubation in Royal Terns and Burger (1974) noted copulation during nest relief ceremonies in Franklin's Gull. It can be suggested, therefore, that copulation may have a 'bond-servicing' function (McBride, 1969) which, when absent, leads to the formation of, at most, weak, unstable relationships.

The difficulty in this study involved the assessment of whether bonds had been formed in the experimental situations. Observations there, on Days 1 to 13, were not conclusive and the group situations may have been too disruptive. Craig et al (1965) and King (1965) showed that in the domestic fowl, behaviour learned and established in an individual situation did not always carry over into subsequent group arrangements. A clearer more empirical method of detecting bond formation, something on the lines of Butterfield's (1970) learning situation, would be an invaluable asset in this line of study. It may well be that pair bonds formed in individual situations are different (possibly less stable) to those in which birds learn and are conditioned to one another in a group context. In the present work it might be more suitable to to refer to the formation of "pair bonds which are evident in group situations."

Finally, bird pairings were chosen at random in these experiments and it is possible that incompatibility between potential mates could account for some of the cases in which bonds were not formed. Work described in Section 4 showed that two "likely" individuals did not always form a bond but there was no evidence from the two compartment cages to suggest that this could account for all the evidence presented here.

These experiments thus suggest the importance of contact behaviour and possibly copulation, in the bonding process. Clearly, in conditions where such behaviour is prevented pairs formed will, at best, possess weak, unstable bonds which are unlikely to be maintained in group situations. It is interesting that copulation is implicated as this is an example of sexual behaviour taking on a bond maintenance function. Perhaps, the soliciting (tail quivering) of _Poephila_ spp. when greeting conspecifics (Zann, 1972) is another example. Eibl-Eibesfeldt (1971) has suggested that pair maintenance appears largely to be due to aggressive and fear tendencies and their subsequent release. These are certainly important but the results of this study suggest that sexual behaviour may also be involved.

SECTION 9. FACTORS IMPORTANT IN PAIR MAINTENANCE

Introduction

In the previous sections I have concentrated on the behaviour seen between Zebra Finches during the time pair bonds are being formed. In this, the last section dealing with experimental data, behaviour between birds with long-term, well-established bonds was examined. Once a bond has been initiated it is subject to a wide variety of stresses which may lead to a weakening of the relationship at different times, or even breakdown of that bond. For example, there will be numerous occasions when bonded birds may become separated whilst feeding, flighting or incubating and rearing the young and there could well be unmated conspecifics in the vicinity. In the face of these potentially unsettling influences one would expect bonded birds to exhibit behaviour which would serve to prolong the bond. Such activities have been called pair maintenance behaviour.

It is important to stress that in dealing with bond maintenance we are not embarking on a new topic but rather extending and re-examining the work done to date. In observing how the bond may be disrupted, and renewed after such disruption, it is hoped that additional information will be gleaned as to the nature of the pair formation process and the importance of this phase in the life of the birds. If choosing a "good" partner is important during pair formation then any resulting bond between two individuals should be resistant to breakdown. There are other reasons why bonds should show resistance but if this feature were to be lacking then it would certainly alter the importance placed on mate selection in the earlier work. Indeed, pair bonding would emerge as a phenomenon which, at best, merely increased the likelihood of two individuals staying together without being necessarily binding on the parties concerned.

For the work on pair maintenance described here pairs of birds were used who were judged to have established 'strong' bonds over a considerable time span; they had been kept as pairs in individual cages for at least three months. There were two series of experiments which used the same 12 pairs of birds. The object of the first series (Experiments 9.1) was to investigate the possibility that pair bonds formed in isolated pairs were retained in the same birds when they were introduced into a large flight cage with other pairs. In other words, they had the chance to re-pair in these flight cages if their original bond were to be disrupted. In addition, experiments were carried out in which mates were separated for a period and then examined in the large cages for any signs of bond disruption and those in which mates were separated and given a new partner whilst absent from their mates. In the latter situation the effect of a new pairing relationship on the original bond could be assessed.

The object of the second series of experiments (9.2) was to see if re-pairing (the formation of a new pair bond) was a possibility and if so whether incomplete contact with the former mate prevented the acquisition of new relationships. Three situations were employed, (a) a new partner was presented and no contact was allowed with the established mate, (b) a new partner was presented but established mates were in auditory contact, and (c) a new partner was presented whilst established mates were in both auditory and visual contact. In each of these situations birds and their partners were assessed for evidence of having formed pair bonds and then the males and females were allowed to choose between maintaining their new relationships or reverting to the former, more established ones. In this way it was possible to determine the relative importance of auditory and visual cues in preventing the disruption of pair bonds.

9.1 The effects of separation on the maintenance of established pair bonds

Methods

In this series of experiments three separate rooms were used. Two of these housed sectional cages which could be split into double or single units and they were far enough apart to ensure that birds in one room could not be in auditory contact with those in another. The third room housed two large indoor flight cages (6' x 4' x 3') which could each accommodate 6 pairs quite comfortably.

12 pairs of birds were used which had been allowed to establish long-term bonds over a minimum period of 3 months. During this time they were housed in single compartment cages and will be referred to as the 'established pairs' or the 'established mates'.

The established pairs were first placed in the two experimental rooms for each of the situations used and then introduced into the large flights. Four experimental situations were used;

(A) After 1 week of complete contact (CC) between established mates in single compartment cages they were introduced into the flights (6 pairs in each).

(B) The established pairs were allowed a further week of complete contact (CC2) and again introduced into the flights (the same 6 pairs in each). This acted as a control period in that it examined the effect of being introduced into the group situation and allowed some habituation to the experimental set-up. Without this second period of complete contact it would have been more difficult to interpret results from the two following experimental procedures.

(C) The established pairs were separated and the mates isolated (S) in two separate rooms for 1 week (i.e., no contact was allowed). This meant that the males were housed in individual cages in one room and the females in the other. They were out of ear shot and as far as each bird "knew", their mate had ceased to exist. They were then reintroduced in the large flights in groups of six pairs.

(D) The pairs were separated and housed in individual cages in separate rooms, but this time they were given a new conspecific (SN) with whom they could form a pair if they so "wished". After 1 week the established mates were reintroduced to their former mates in the large flights.

Thus in situations (c) and (d), bond maintenance activities were interrupted and the effect of this disruption on the established bond was assessed in the large flights where the group situation allowed evidence of bond disruption to be observed.

Measures taken Recordings were made on birds in the large flights only (i.e., the group situation). The first watch constituted a 30 minute period immediately after the introduction of the pairs into the large flights. Subsequent watches lasted for one hour on the morning and afternoon of the day of introduction (denoted Day 1 (AM) and Day 1 (PM))and on the following afternoon (Day 2 (PM)). Birds with plumage variations were chosen so that it was possible to identify individuals readily.

During the first watch (30 minutes following introduction) the experimenter concentrated on recording the incidence of four particular activities. These were;

(i) The number of courtship bouts by each male and the female to whom they were directed.

(ii) The number of beak fencing encounters in which each individual was involved.

(iii) The number of supplanting attacks made by each individual.

(iv) The number of allopreening bouts in which each individual was involved.

In the remaining watches, Days 1 (AM), 1 (PM) and 2 (PM), the number, and the identity, of the clumping pairs observed was sampled at two minute intervals. This was in addition to the measure described above.

The results concentrate on the behaviour observed between established mates after each experimental situation. The behaviour between non-mates of opposite sexes is also shown as if a bond has broken down a male or females behaviour towards non-mates will also alter.

Results

The results suggest that separation and isolation of mated birds does not result in the break down of pair bonds. Bonds formed in isolation are retained in groups of birds but separation, whether with a new partner or not, enhances certain behavioural traits observed on the reunion of mates.

Behaviour immediately following introduction (the first watch) (Fig. 26)

Behaviour on introduction was similar on all occasions. There

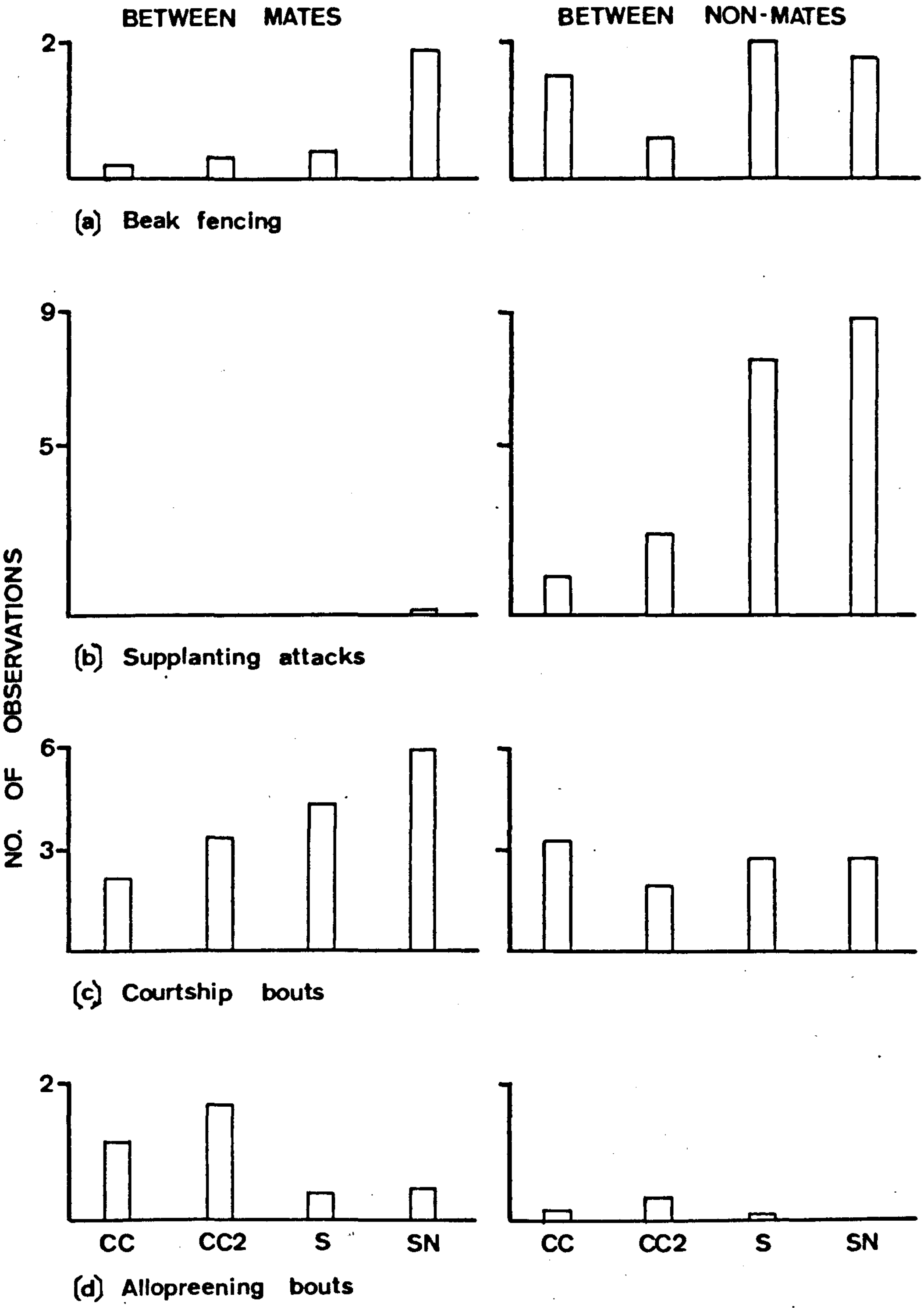


Fig. 26. Behaviour in the first 30 minutes between mates and non-mates on introduction to the large flight cages.
CC - After a week of complete contact between mates.
CC2 - After a second week of complete contact.
S - After a week of separation of the mates.
SN - After a week of separation with a new partner.

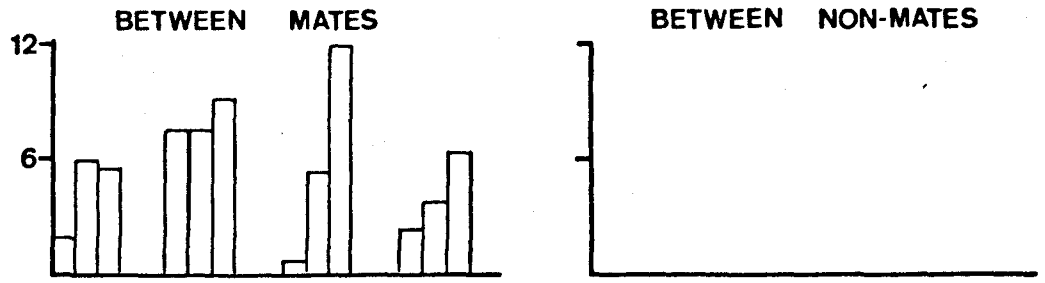
was great activity during which courtship, agonistic encounters and allopreening attempts were prevalent. Clumping was not seen until the later recording sessions.

It is clear that even at this stage there was little aggression between mates with the highest amounts recorded for beak fencing after separation with a new conspecific (SN) ($p < 0.01$, WMP). The amounts of courtship between mates showed greater variation; they were most frequent after separation (both S and SN situations) when more bouts were recorded than after either of the periods of complete contact (CC1 or CC2) ($p < 0.01$, WMP, in each case). The number of allopreening bouts were the same in each case.

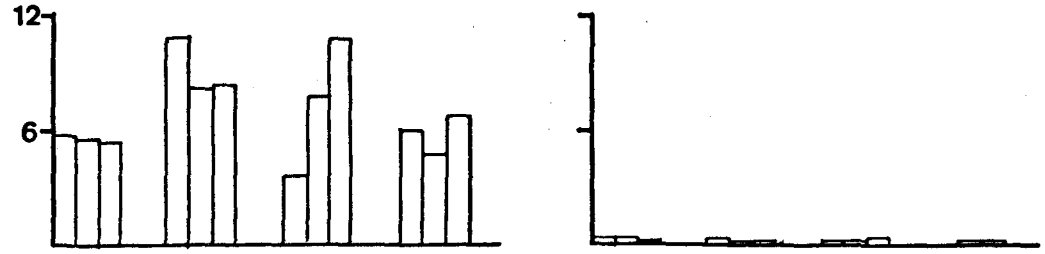
Thus the only evidence that bonds had been disrupted at all by the experimental situations came after the separation of mates. This is supported by the data for the behaviour between non-mates. Beak fencing was significantly reduced after the second period of complete contact (CC2) over the levels seen after the first period ($p < 0.05$, WMP) and the highest incidences of supplanting attacks were incurred after separation from the mate (S and SN). These peaks lacked significance but indicated that aggression between non-mates had been affected and this is reflected in the fact that the highest levels of male-male supplanting attacks occurred after S and SN conditions ($p < 0.01$, WMP) - see Fig. 28.

Behaviour in the later recording sessions of Day 1 and Day 2 (Fig. 27)

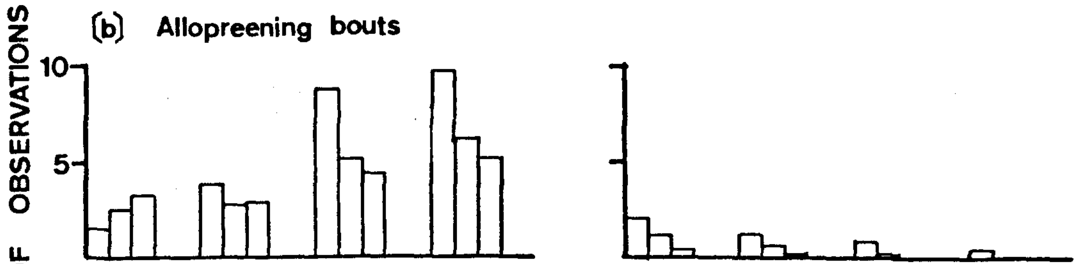
Clumping was observed in these watches and this is a good indicator of bond formation between individuals (see Section 4). The results support those quoted above as no clumping between non-mates was recorded after any of the experimental situations. Therefore none of the bonds were in fact broken. However, fewer



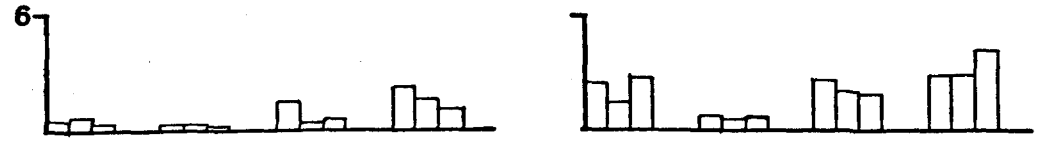
(a) Clumping pairs



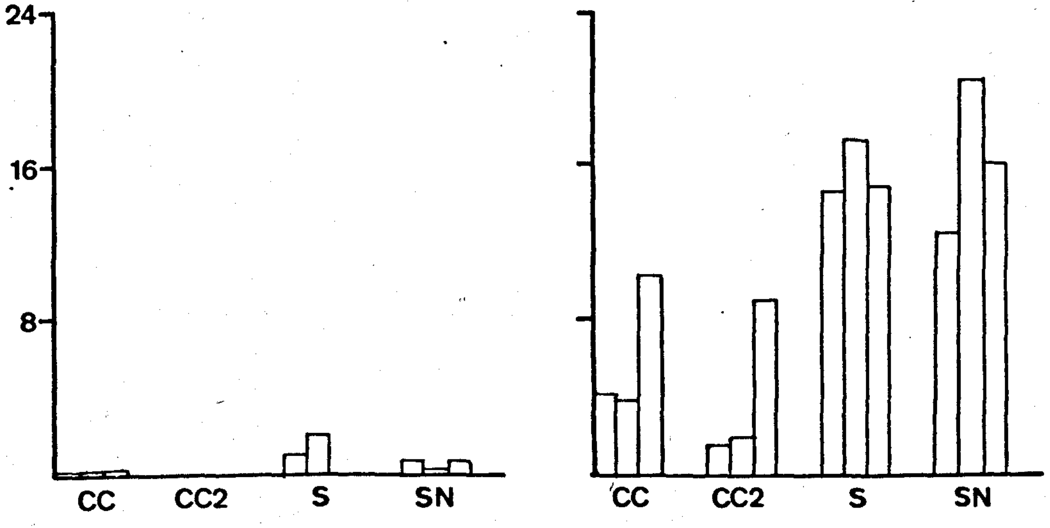
(b) Allopreening bouts



(c) Courship bouts



(d) Beak fencing



(e) Supplanting attacks

Fig. 27. Behaviour in the large flight cages in the later watches on Days I(AM), I(PM) and 2(PM). For an explanation of the abbrieviations - see Fig. 26.

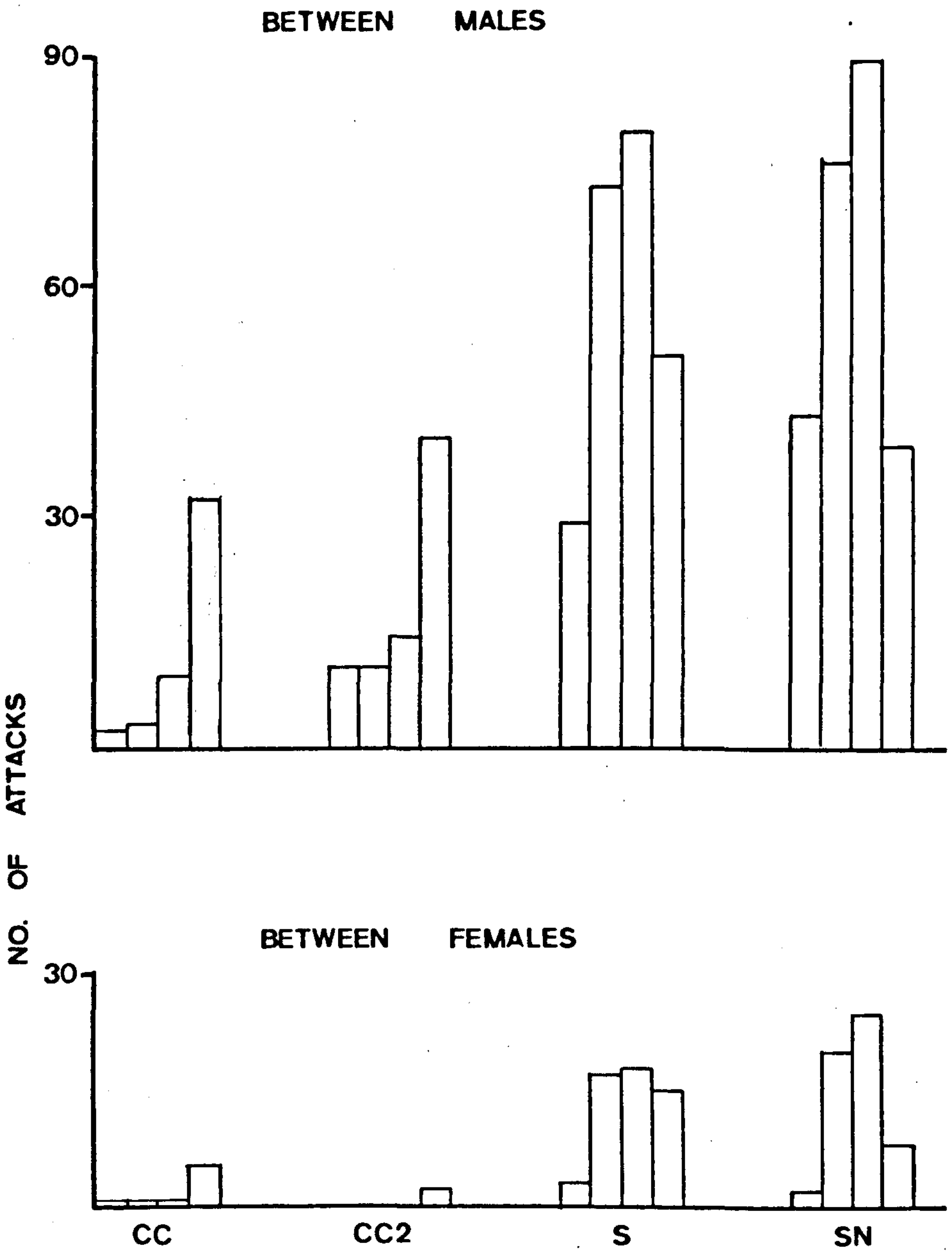


Fig. 28. Male-male and female-female supplanting attacks between birds in the large flight cages.

established pairs were seen to clump on Day 1 (AM) after separation from the mate, S and SN, and the highest amounts of clumping were recorded after the CC2 situation ($p < 0.01$, WMP).

The difference in courtship of the established mate after S and SN, which was noted in the first 30 minute watch, was retained in these later watches until Day 2 (PM) ($p < 0.01$, WMP). By this watch it had fallen to a level comparable to that seen in the CC and CC2 birds. Similarly the tendency for more non-mate aggression after S and SN conditions was confirmed as many more supplanting attacks were counted between these birds on Days 1 (AM) and 1 (PM) than after either of the complete contact treatments ($p < 0.01$, WMP). The lack of significance on Day 2 (PM) is due to an increase in fighting by the CC and CC2 birds rather than a decline by S and SN non-mates. Finally male-male aggression, shown in Fig. 28, indicates an increase by the S and SN birds ($p < 0.01$, WMP) with some individuals reaching over 400 attacks in a single hour. Female-female aggression shows similar tendencies though these are less marked as fewer individuals were involved.

Discussion

Erickson (1973) worked on the bonding processes of the Ring Dove and noted that there were various factors capable of interfering with the maintenance of a pair bond. Earlier, working with Morris (1972), he had shown that birds separated from their mates would readily re-pair with unfamiliar conspecifics. He quoted examples from the literature of other species in which pairs broke down in the winter months, the non-breeding season. This suggests that the bond is either broken down completely or modified in some way so that birds are capable of re-pairing if continuous access to the mate is denied. In addition, behaviour prevalent in the breeding season appears to be important in the maintenance of pair bonds.

In Section 5 it was demonstrated that male Zebra Finches separated from their mates will court unfamiliar females. Presumably, in the continued absence of their mate a pair bond would have resulted in these cases. An observation of breeding birds made by the author may serve as an example of the way in which the bond ceases to be apparent once mates are separated. An established pair had built a nest and were sharing the incubation of five eggs when the female died. Within three days the male had deserted his old nest, built a new one and with a replacement female was busily incubating a single egg. Thus individuals who in the presence of the mate show great fidelity, are apparently capable of immediately re-pairing once access to the mate is denied. This suggests that behaviour between mated individuals acts as a reinforcement of the bond, and that this reinforcement must be continuous throughout the duration of the bond.

In the experiments carried out here it was clear, however, that a short period of separation and isolation of established mates did not result in bond breakdown. The lack of bond reinforcement behaviour did not destroy the attachment between the two birds or, if it did, it could be very readily re-established on reunion. The effect of isolating the mates on their existing bond was to increase the amount of courtship directed at the mate and enhance the amounts of aggression towards non-mates when birds were reintroduced. The chance to re-pair during the period of isolation had similar effects on reintroduction. Ring Doves can also recognise their mates after periods of separation of similar length (Morris and

Erickson, 1971; Erickson and Morris, 1972) and courtship is again enhanced on reintroduction of former mates. Erickson and Morris (l.c.) concluded that recognition of the mate presented no problem but the basis for this recognition remained unclear. They thought that males might be reacting to subtle changes in the behaviour of their females and that the onus for recognition was therefore, on the female. They could not identify these changes and, though they could be important in the first encounters after reunion, they do not explain the male's subsequent fidelity. It seems likely that the males and females possess 'central specifications' in the central nervous system, a phrase coined by Andrew (1972), by which they can readily recognise one another without continuous behavioural reinforcement.

The changes in behaviour due to separation of the mates

On reunion of mates after complete separation, either with or without a new partner, there was an increase in courtship directed at the mate and aggression directed towards non-mates (particularly male-male aggression). This is reminiscent of pair formation as it was described in the group situation in Section 4 in which individuals were meeting for the first time, and differs from the reactions seen after complete contact before reunion (i.e., CC and CC2). It is as if pair formation is re-occurring and it suggests that the behaviour seen in the earliest stages of a bond are particularly important in establishing and re-establishing a preference for a particular individual.

The increase in courtship between mates after separation (also described in Section 5) would appear to be due to an increase in the "sexual attractiveness" of the female which in turn is dependent on the separation period. This was discussed earlier in some detail.

The changes in aggression, on the other hand, are similar to those noted by Maier (1964) in the dominance relationships of 'pairs' of domestic fowl. These relationships were allowed to become established and the birds separated, though still in auditory and visual contact, for a period of three weeks. On reunion there was an increase in the amount of aggression and this was explained on the basis of a lack of reinforcement of the original relationships. It would seem that dominance relationships are learned and reinforced by the interactions that take place, without these interactions, the relationship is lost. Presumably, a similar argument holds for Zebra Finch relationships, although in the present context, it was aggression directed outside of the pair which was affected. In the groups, therefore, it became necessary to re-establish dominance relationships after the intervening period of separation.

Clearly, however, the pair bond affects this dissolution of dominance relationships within the groups. If it was merely the lack of reinforcement of learned relations then one would expect the same amount of aggression after each of the experimental situations. Yet, in this study, isolation of the mates during the separation period leads to a further increase in non-mate aggression suggesting that it is this isolation which results in enhanced aggression for whatever reason. Possibly males and females are reasserting their pair bonds as well as re-establishing the group dominance relationships.

9.2 <u>The importance of auditory and visual reinforcement in preventing the breakdown of established bonds</u>

Methods

The same 12 pairs of birds were used as in Experiments 9.1. They were housed for a period of two weeks in single unit cages to ensure that all bonds were re-established after the earlier experimental treatments.

The three rooms were used with the same experimental cages and flights. The different situations involved allowing established mates to re-pair with a new partner over a period of two weeks and then testing them with this individual in the large flights to see if a bond had been formed. Following this the established pairs were reunited and given the choice between their old, established mate and the new partner. Two weeks was allowed with the established mate between each experimental situation to ensure that their bonds were present before the next treatment.

The three experimental situations used were;

(A) Re-pairing in birds which were isolated from, but still in auditory contact with, the established mate (referred to as AO)

The established mates were separated by a solid wooden partition in a two compartment cage. The male and female were each given a new partner with which to form a new pair. In this way auditory contact would be maintained between the established mates but they could not see one another.

(B) Re-pairing in birds which were isolated from, but still in auditory and visual contact with, the established mate (A+V)

The established mates were separated by a clear perspex partition in a two compartment cage and given a different conspecific with which to re-pair. Black vertical lines, 5 cm apart, were drawn on the perspex to ensure that birds could see the partition.

(C) Re-pairing in birds which were completely isolated (both visually and auditorily) from the established mate (CI)

In this, the last situation considered, the males and females were isolated in different rooms and then given a new partner (again, the new conspecific was different to that used in (A) and (B)). They could thus re-pair without either auditory or visual contact with the established mate.

Measures taken First, males and females with their new partners were assessed for evidence of having formed a bond. They were examined in two contexts;

(i) The experimental cages Whilst the birds were in the two compartment cages, for each situation used, observations were made on the mornings of Days 1, 2, 3, 7, and 13. Each watch lasted for 30 minutes and the behaviour recorded indicated whether bond formation was taking place whilst in incomplete or complete isolation form the established mate. Behaviour assessed was;

Agonism - The number of beak fencing encounters and supplanting attacks occurring between the male and female and their new partners were counted.

Courtship - The number of times the male courted his new partner or, in A+V (i.e., situation (B)), the established mate, was recorded.

Clumping - The number of pairs seen clumping during the watch was noted.

Synchrony - The amount of synchronisation of activities shown by the new pairs was assessed by noting their behaviour at one minute intervals (see Section 4).

In the AO and A+V situations it was possible to compare synchrony between the new partners with that between the established mates through the intervening partition.

Settled distance - The distance between individuals was noted at one minute intervals. The perches were marked at 5 cm intervals and by recording the distance from the partition it was also possible to compute the settled distance maintained by established mates in AO and A+V.

ii) <u>The large flight cages</u> As in the previous experiments (9.1) the presence of pair bonds was assessed in groups of birds in the large flights. Males and females and their new partners were placed in groups of six pairs in each of the two flights. Their established mates were not in the same group. Records were made for one hour periods on the morning after introduction in the flights, Day 14 (AM), on the afternoon of that day, Day 14 (PM), and on the following afternoon, Day 15 (PM). Behaviour recorded concentrated on those activities most likely to indicate the presence of a new bond between members of new pairs. These were,

Courtship - The number of courtship bouts by each male and the identity of the courted female were noted.

Clumping - The number of pairs seen clumping, and their identity, was sampled at 2 minute intervals.

Allopreening - The number of allopreening bouts between different individuals was counted.

Second, males and females from the established pairs were reunited in the presence of their new partners in a double compartment cage. They were thus given the choice between re-establishing their former bonds or continuing with the new relationship they had formed after the experimental situations. Observations were made for 30 minutes following reunion, Day 16 (AM) and for a similar period on the following morning, Day 17 (AM). The behaviour noted was:

Courtship - The number of bouts directed at the established mate and the new partner was compared.

Agonism - The number of beak fencing and supplanting attacks by different individuals was recorded.

Clumping - The amount of clumping between the different pairs was sampled at one minute intervals.

The results are presented as in Section 9.1. First, behaviour in the experimental cages between males and females and their new partners is presented. Where applicable, behaviour between established mates in this situation is also shown. Second, in the large flights, the behaviour directed towards the new partner is shown with that towards non-mates of the opposite sex. Finally, on reunion, the behaviour between the new partners is contrasted with the reactions of birds to their established mates.

Results

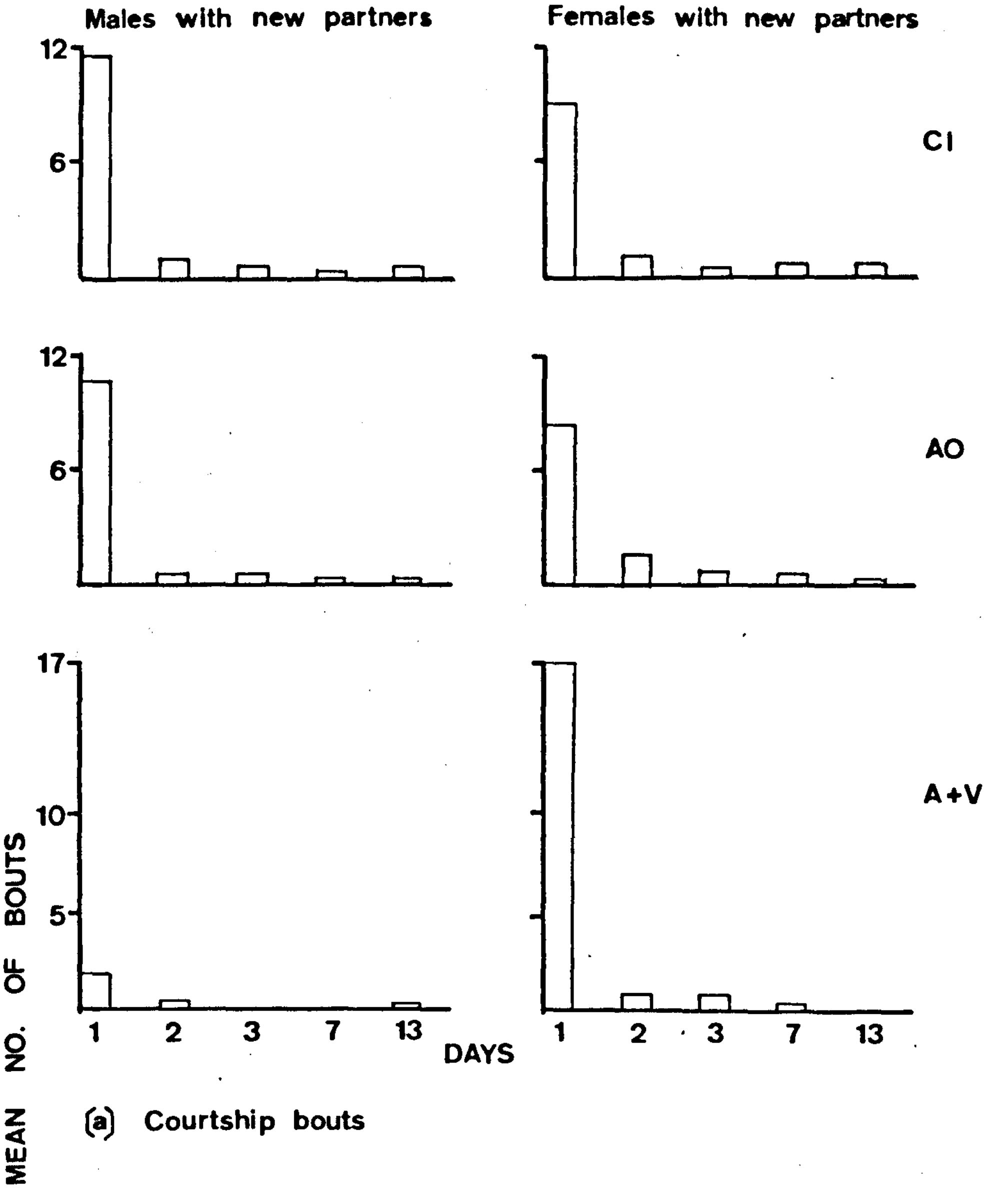
Evidence for the formation of new pairs (i.e., re-pairing)

The results of observations in the experimental cages and the large flights indicated that new bonds could be formed when birds were completely isolated from their established mates (CI). When auditory and/or visual contact was allowed between the mates (AO and A+V) the new partners were rejected and the established bond retained. The clearest evidence of rejection came when visual contact was permitted (i.e., A+V).

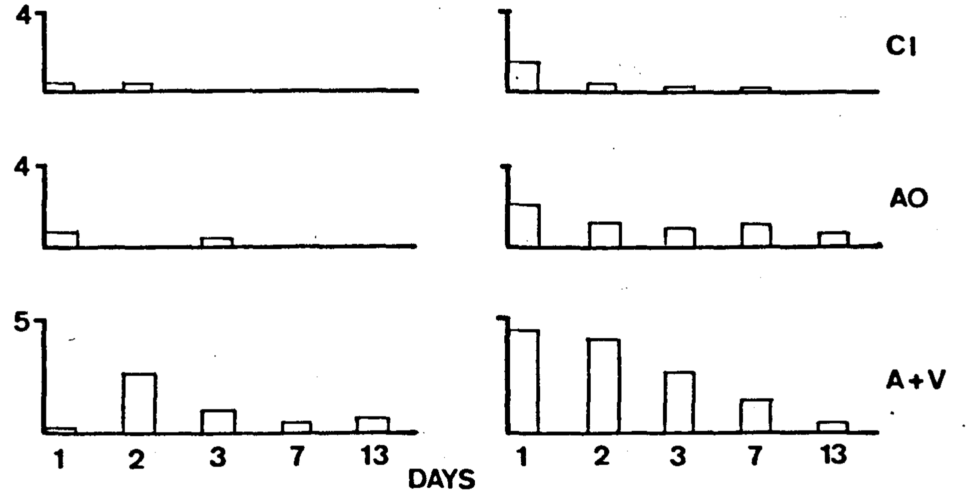
(i) Behaviour in the experimental cages (Figs. 29-32)

Male courtship of their new partners occurred frequently on Day 1 (Fig. 29(a)) but there was significantly more courtship when the established mates were completely isolated (CI) or in auditory contact only (AO), than there was when they were in both auditory and visual (A+V) contact ($p < 0.05$, and $p < 0.01$, WMP, respectively). In addition, in the A+V situation the males remained faithful to their mates in that they began to court them through the intervening perspex partition and they did so significantly more often than their new partners on Days 3 and 7 ($p < 0.05$, WMP).

Aggression was most prevalent when some contact was allowed with the established mate and, unlike courtship, auditory contact was enough to elicit this differential response. Fig. 29(b) shows that beak fencing with the new partner was unusual during isolation from the established mate (CI) whereas, with auditory contact it was quite common with the female showing more than their males (significant on Day 2, $p < 0.05$, MWU). The highest scores, however, were during visual contact (A+V) with the females again showing more and the results for supplanting attacks of the new partner show similar trends (Fig. 30(c)). For the males, comparing CI with A+V and AO, there was significantly more fighting in A+V on Days 2 and 3 ($p < 0.05$, WMP) with AO showing intermediate amounts. The females rejected their new partners even more vehemently than did the males with both AO and A+V showing scores much higher than the CI birds. A+V is significantly higher on Days 3, 7 and 13 whereas, AO scores do show significance on Day 3 ($p < 0.05$, WMP, in each case). Thus, both males and females actively rejected their new partner although the AO females showed a reduction in the amount of fighting from Day 3 to Day 13 ($p < 0.05$, WMP). This was not apparent in the A+V

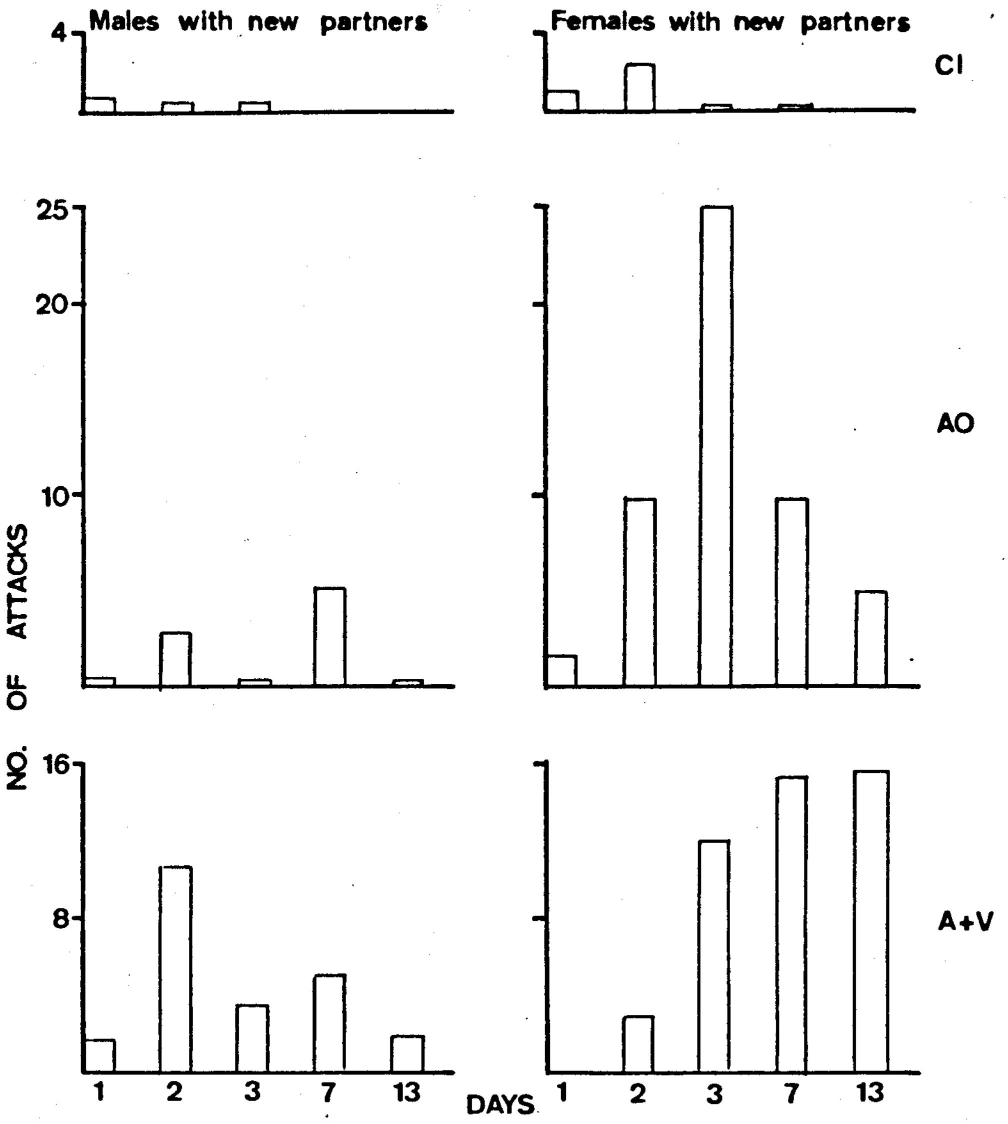


(a) Courtship bouts

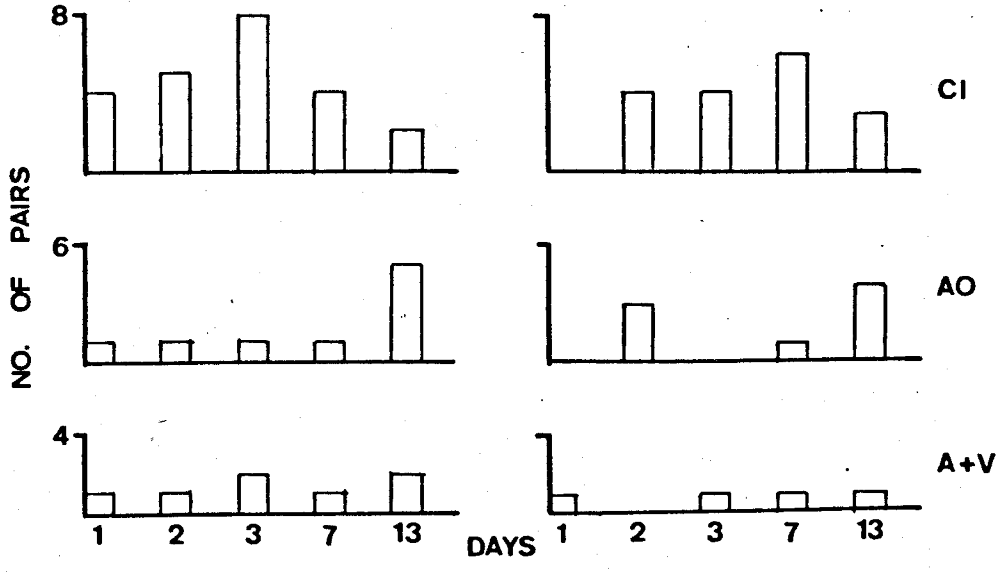


(b) Beak fencing

Fig. 29. Behaviour of the new pairs in the single unit cages.
CI - During complete isolation of the established mates.
AO - During auditory contact between established mates.
A+V - During visual contact between established mates.

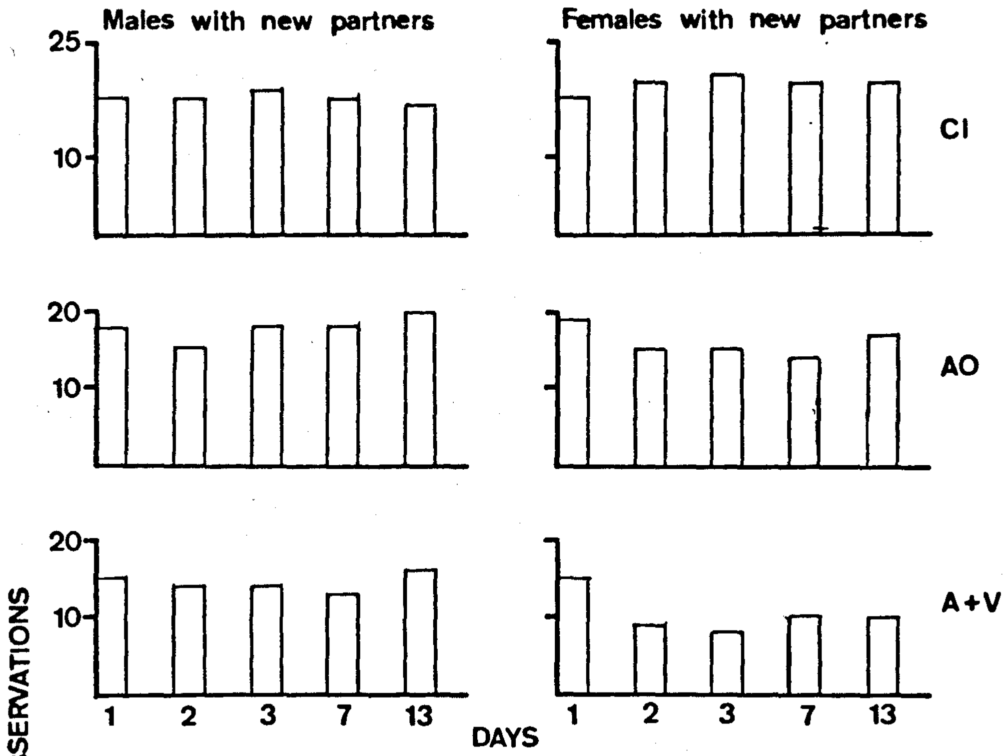


(c) Supplanting attacks

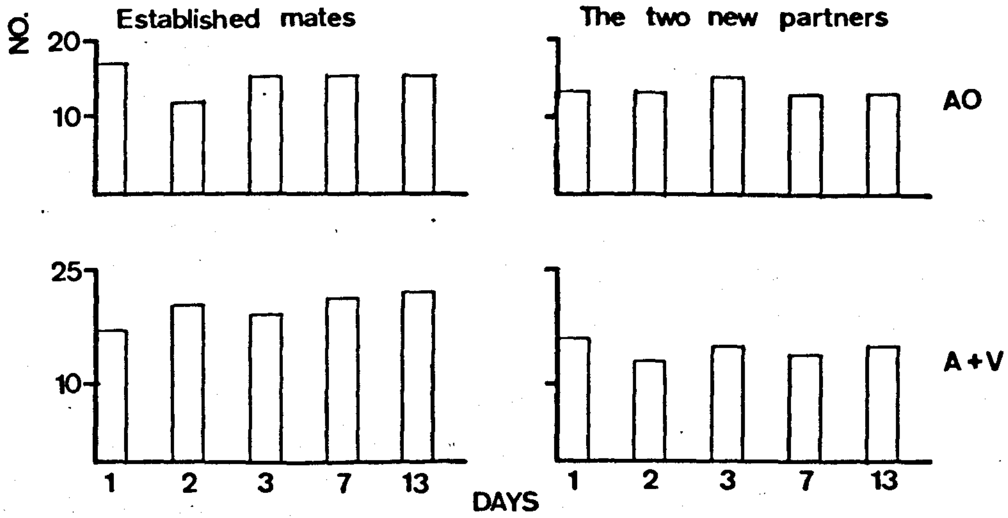


(d) Clumping

Fig. 30. Behaviour of the new pairs in the single unit cages (continued).

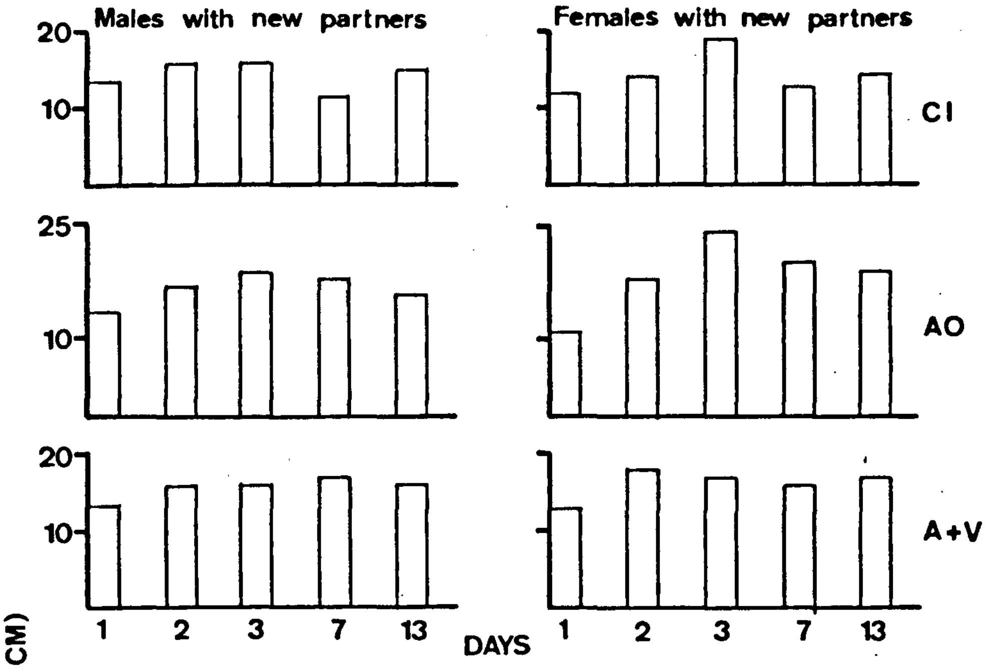


(e) Synchrony scores

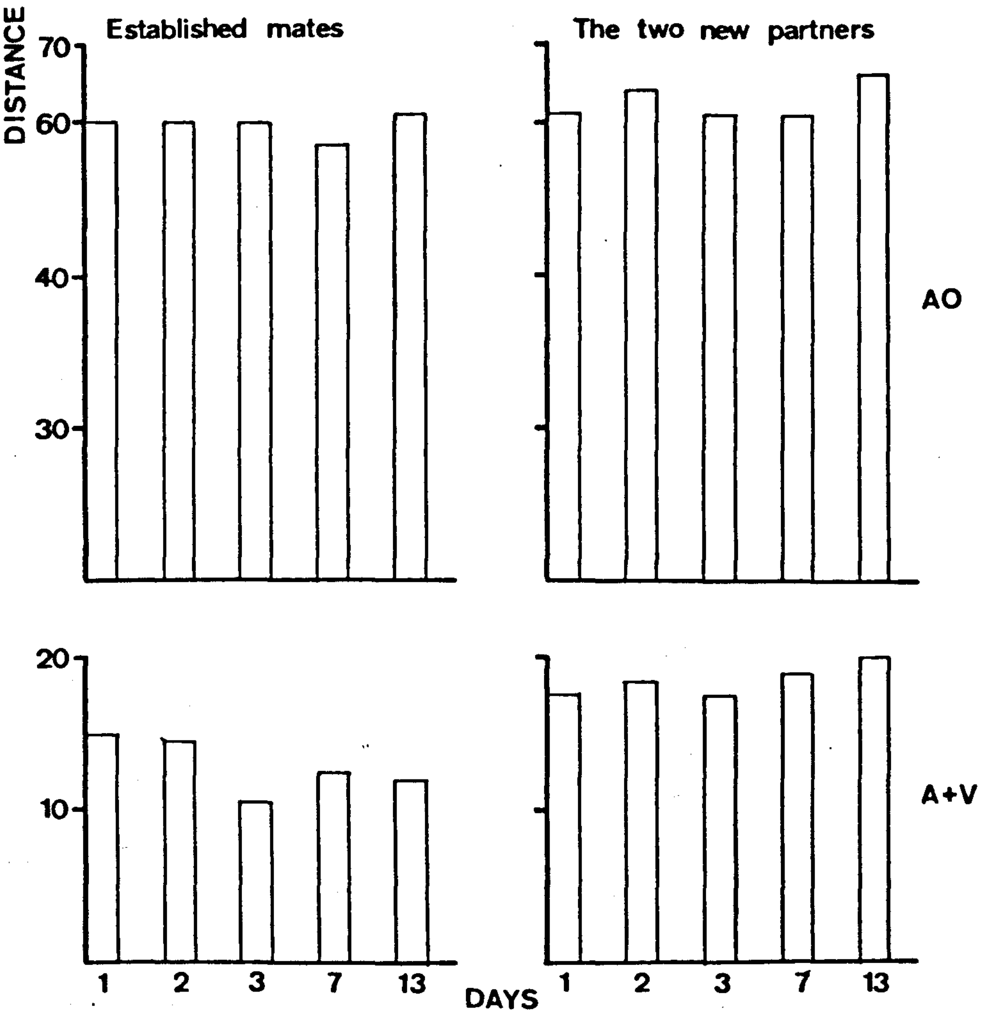


(f) Additional synchrony scores

Fig. 3I. Behaviour of the new pairs in the single unit cages (continued).



(g) Settled distance



(h) Additional settled distance scores

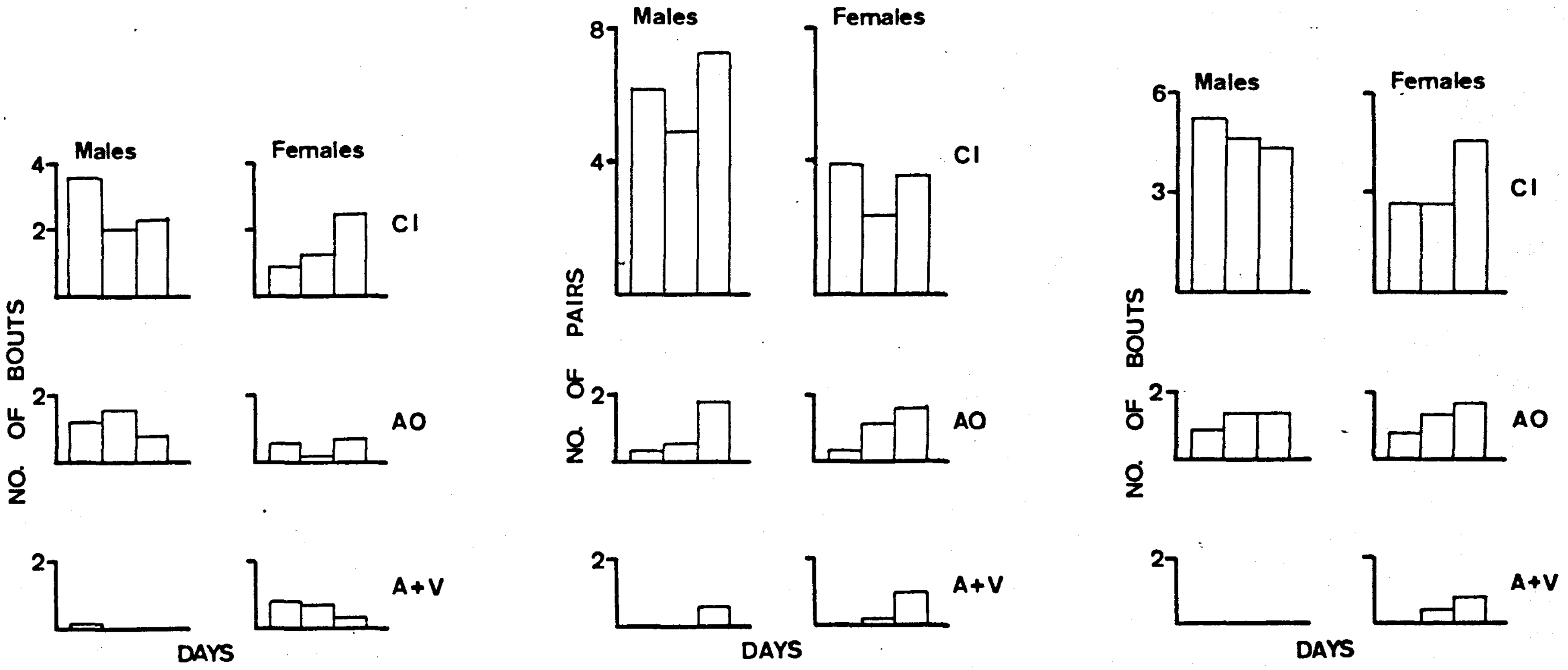
Fig. 32. Behaviour of the new pairs in the single unit cages (continued).

birds and could indicate that auditory contact with the mate was not maintaining the established bond as strongly as when visual contact was permitted. In complete isolation, the mates appeared to be unfaithful to one another.

The remaining observations on birds in the experimental cages support these suggestions. The number of new pairs seen clumping was highest in the CI situation, significant on Day 3 (CI $>$ AO and A+V, $p < 0.05$, Sign Test). Again, the AO birds tended to show an increase in clumping by Day 13 in both sexes but this did not reach significant proportions. Behaviour by the new pairs tended to be synchronous in all situations (Fig. 31) but the lowest scores for birds with a new partner were recorded during A+V situations. In addition, Fig. 31 shows that in A+V and AO situations the established mates showed synchrony in spite of the partition between them. However, there was significantly more where the mates could see one another, A+V, in all watches except Day 1 ($p < 0.05$, WMP). Finally, the settled distance scores (Fig. 32) showed that in the A+V situation the established mates maintained close contact through the perspex partition. Distances between the new partners did not vary appreciably.

(ii) Behaviour in the large flights (Fig. 33)

These results were examined for evidence of the males and females having formed pair bonds with their new partners. As in the experimental cages it was apparent that pair bonding occurred only after complete isolation from the established mate (CI). This was shown in the courtship activity directed towards new partners in the large flights in which a peak was observed in the CI Birds immediately after their introduction on Day 14 (AM) (CI $>$ AO and A+V, $p < 0.01$, WMP). The lowest courtship scores between new pairs



(a) Courtship (b) Clumping (c) Allopreening

Fig. 33. Behaviour between males and females and their new partners in the large flight cages. Observations were made on three days in each case; Days I4(AM), I4(PM) and I5(PM).
CI - After complete isolation from the established mate.
AO - After auditory contact between established mates.
A+V - After visual contact between established mates.

were obtained after A+V conditions and these are significantly lower than the CI bird scores in all watches ($p < 0.01$, WMP). In addition, the numbers of clumping pairs show the highest scores in the case of CI birds as do the results for the amount of allopreening seen between members of new pairs ($p < 0.05$, WMP, in each case).

Behaviour on reunion with the established mate (Fig. 34)

The results show that in all cases birds chose to reform their established pair bonds. Even the CI birds, who showed evidence of having formed new pair bonds in the experimental situation, returned to their former relationships although with possibly more reticence than the AO and A+V birds. For example, the males directed their courtship at the established mate rather than their new partner on reunion (Day 16 (AM)) and the difference was significant in the AO and A+V birds ($p < 0.01$, WMP). A similar preference was evident in the CI birds but did not reach significant proportions.

Very little aggression was seen between established mates but supplanting attacks directed at the new partner were frequent in the AO and A+V birds. Again the CI birds showed less evidence of rejection of the new partner and there were significantly fewer attacks during the watch on Day 17 (AM) than were seen in the A+V birds ($p < 0.01$, WMP). The number of established pairs seen clumping on Day 16 (AM) was higher in the A+V and AO birds than in the CI individuals ($p < 0.05$, Sign Test) but this difference had disappeared by Day 17 (AM) which indicates that the CI birds were finally settling into their established bonds in the majority of cases.

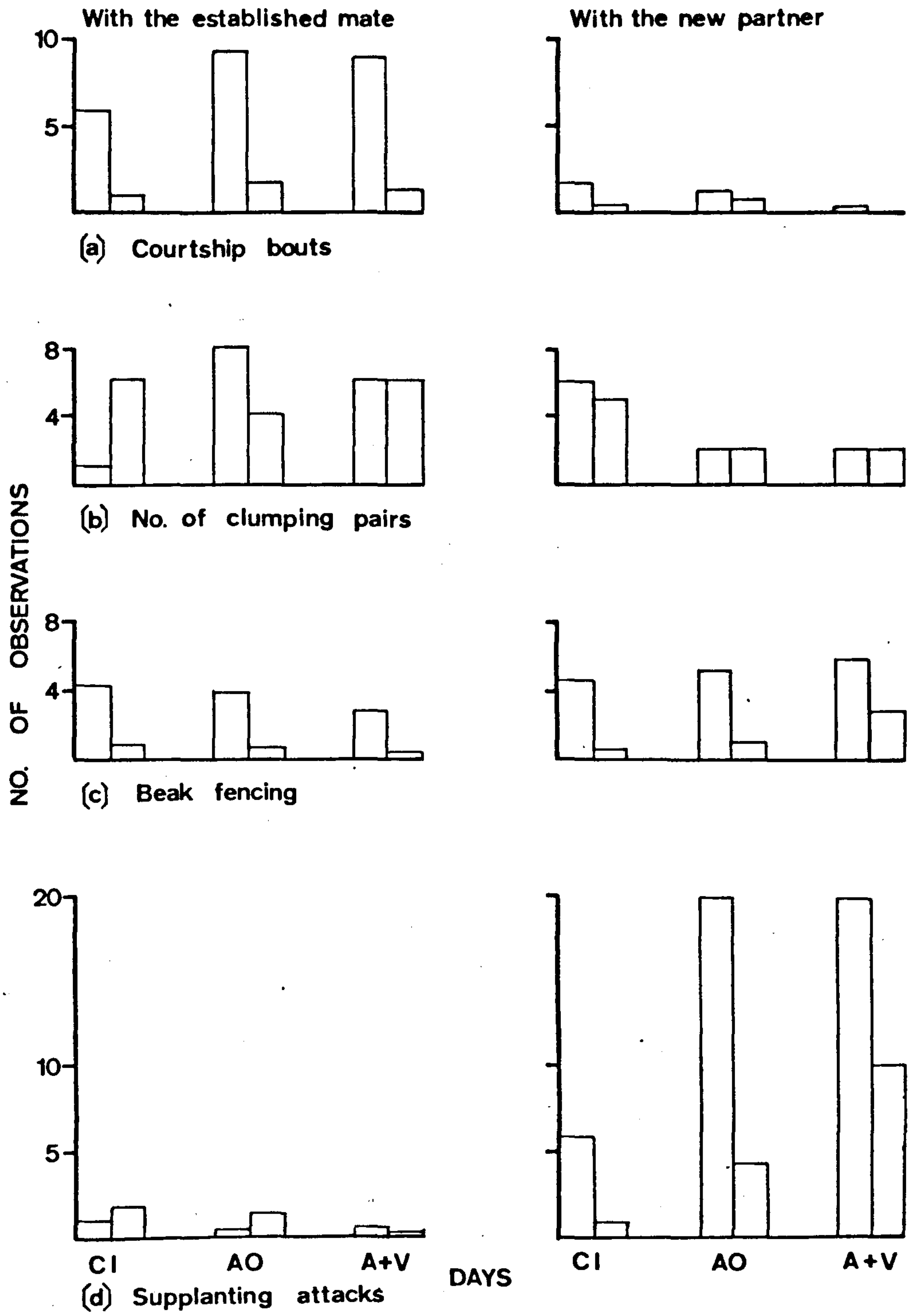


Fig. 34. Behaviour on the reunion of birds after the three experimental situations. Observations were made on two days in each case, Day 16(AM) and Day 17(AM). For an explanation of the abbrieviations - see Fig. 33.

Discussion

Pair formation appears to involve a learning process during which the mate becomes, as Thorpe (1961) put it, a fundamental part of the "key environmental situation". In other words, continued interactions with the mate have a consummatory function and it is this perception of the environmental situation, with the mate in it, that is the "goal" of a searching individual. The imprinted response of young birds has been shown to have a similar basis (e.g., Hinde, 1961). Young moorhens, imprinted on a variety of objects, show a waning of the following response unless an object they are familiar with is presented. This extinction of the response resembles that seen in conditioning experiments and was regarded by Hinde as due to the "absence of consummatory stimuli presented by the familiar model which normally act as a reinforcement." That sight of the mate may be reinforcing in the Zebra Finch (at least in the males) was demonstrated by Butterfield (1970) and thus the results of these experiments will be discussed in terms of the pair bond as a learning and reinforcing situation in which perception of the mate may play an important part.

When contact was allowed with the established mate, reinforcement of the bond was possible and both males and females actively rejected a new partner and seemed resistent to the formation of a new bond. This was most evident when visual contact between the established mates was allowed whereas with only vocal contact the rejection was less marked in some cases. Thus visual reinforcement, assisted by that due to vocal stimulation, appears to be effective in preventing re-pairing and thus maintaining the existing bond. It is unfortunate that equipment was not available to test the visual <u>without</u> auditory contact situation (e.g., sound proof cages) but it can be concluded, without these results, that vocal reinforcement occurs and probably accentuates that due to visual components. Without this reinforcement new bonds may be formed, but this does not mean that the first bond is necessarily destroyed. Reunion with the established mate showed that in the majority of cases the bond was 're-forged' and the new partner rejected.

The nature of pair bond reinforcement appears to revolve around the visual displays of the Zebra Finch with their vocalizations playing a supportive role and this ties in with the evidence presented in the literature. Beer (1970c) in his review of vocal recognition by birds, concluded that visual characteristics might support vocal ones in the recognition of individuals. Indeed, in some species they might substitute for vocal cues and he quotes the Herring Gull and Ruff as examples. In an imprinting context, Miller and Emlen (1975) showed that adult Ring-billed Gulls would attack their own chicks if the latters plumage had been altered, but not if the chicks vocal patterns had been changed. Both Evans (1972) and Ingold (1973) proposed that visual stimuli enhanced the responses of birds to both species-typical and individually distinctive vocalizations. Lastly, it has been suggested that during imprinting sounds may assist the process by which attachment to a visual stimulus is initiated by creating a "higher degree of arousal" (Smith and Bird, 1963 and 1964). It seems likely, therefore, that in the attachment process involved in pair bonding, vocal stimulation may play a similarly supportive role to a predominantly visual learning and reinforcement situation. Certainly in the Estrildids, Kunkel (1974) remarked on the predominance of visual components in their displays with duetting, seen in a few species, the only example of an elaboration of their vocal contact.

Aggression in the defence of an existing bond

Contact with a former mate tended to prevent the formation of a bond with a different partner and in many cases described here, aggression was used in 'defence' of the relationship. Supplanting attacks and beak fencing were noted in both the males and the females. Caryl (1975) was able to demonstrate that male-male aggression in the Zebra Finch could be increased by the sight of a female, and even more so if that female were mated with one of the males. On the basis of this, he suggested that it was the sexual attractiveness of the female which decided the amount of male aggression and, one would expect, formation of a bond enhanced the attractiveness of the mate. Again, this reflects the learning components involved in the processes of bond formation. The individual characteristics of the mate can be recognised easily and become the principle releasers for all aspects of courtship, aggression and breeding behaviour. This enhancement of male to non-mate aggression was discussed more fully in Section 5.

Caryl (l.c.) was able to demonstrate an increase in female aggression due to the sight of the mate as was observed here and first noted in Section 5. It would certainly seem to be of benefit in bond maintenance for the female to behave aggressively towards encroaching non-mates. However, beak fencing and supplanting attacks appear less frequently and are given by fewer individuals which suggests that the threshold level for aggression is somewhat higher in the females than it is in the males. Whether sexual motivation is involved is not clear but the finding that only small amounts were provoked in females when the mates were isolated from each other indicates that it was the sight (and sound) of the male, when in a re-pairing context, which induced the intolerance seen. Some females, having formed an attachment for a particular male, are willing to maintain that relationship, and maintain it actively, provided that some contact with that male is allowed (i.e., the attachment is reinforced).

Both males and females, in the absence of the mate, are willing to form new bonds and pair formation appears to proceed normally though, on some occasions, possibly reluctantly. Hoffman and Boskoff's (1972) results for imprinted ducklings show interesting similarities to the situation here. They found that the subjects would attack "socialized" ducklings (those imprinted on one another) whenever the imprinted object was shown, but not in its absence. Similarly, Andrew (1972), in a series of experiments on domestic chicks has demonstrated that high levels of male hormones affect the persistence and searching behaviour of males. This suggests that when the level of such hormones is high (e.g., in the breeding season, which for the Zebra Finch could mean throughout the year) the male will be less likely to be distracted in his attempts to gain or regain a female. However, extinction of the response is normal and therefore if the reinforcement is withdrawn (e.g. the pair are separated) then the male, at least, can be expected to quickly loose interest in the former mate and be ready to re-pair. Thus, within the framework of the pair bond there is the possibility that, in the continued absence of reward and reinforcement, a fruitless relationship will be terminated and pair formation begin afresh.

SECTION 10. A GENERAL DISCUSSION

The meaning of pair formation

During the course of this thesis the term "pair formation" has been used on frequent occasions to indicate a period in the breeding cycle of two birds when a pair bond is being first formed. However, it is difficult to provide a precise definition for this descriptive term and the problems that may be inherent in its usage deserve some discussion here. Lack (1940) described pair formation in many bird species and used the term loosely to indicate the early stages of breeding before copulation took place. However, when it is used in reference to a proposed bond between two individuals (i.e., to indicate the period up until the bond has been formed) one has difficulty in deciding when the 'processes' involved are completed or, for that matter, what the bond is. The term appears to become ambiguous, a point which was raised previously in the discussion of results in Section 4.

Lack (l.c.) provided a useful dichotomy of pair formation types one which was echoed by Immelmann (1962). Bird species can be split into those in which the male isolates himself, either on a territory or at a nest site, and species in which pair formation begins in the flock situation. Much of the early work considered birds in the first of these categories in situations in which different individuals could be readily identified and pair formation was marked by a particular display of 'ceremony'. In the estrildids, however, pair formation invariably occurs, or at least begins, in non-breeding flocks (Immelmann, 1962; Güttinger, 1970) and this is certainly the case in the Zebra Finch. In species such as these the flock environment must place different pressures on the pairing birds and Immelmann (l.c.) considered that the 'process' involved a prolonged period of familiarization which was not marked by any particular pair formation ceremony. Hinde described similar situations in the Great Tit (1952) and the cardueline species which form flocks (1955). Thus the confusion probably stems from the use of the term to describe both the initial meeting of a male and female (possibly involving a ceremony) and also the period during which two birds learn to recognise one another and come to behave as a pair. It might be clearer if these two contexts were separated.

Zann (1972) attempted such a separation and proposed that pair formation involved two distinct processes; (i) choice of a certain conspecific, (ii) "manifestations" of this preference and attempts to establish the bond and to make it mutual. These can be shortened to, (i) mate selection, and (ii) bond maintenance. If 'pair formation' is used to include the period up to copulation and ovulation it is clear that it will embrace both of these processes and one is left with the question, when is a pair a pair? In other words, when is pair formation complete?

Mate selection occurs very rapidly in the Zebra Finch and preferences for particular individuals are quickly manifested as the results of Section 4 showed. Immelmann (1962) suggested that females were, though passive during courtship, decisive in terms of mate selection. Zann (l.c.) found, however, that in the Poephila both males and females showed preferences for particular conspecifics and it was clear that a similar situation operated in Zebra Finches in the present study (the "Incompatible" pairs - Section 4). Immediately after this period of choice, behavioural changes are noticeable in the birds concerned. Reactions towards the partner alter within the first few encounters as do reactions towards other conspecifics suggesting that recognition of the partner is quickly established. It could be argued in fact that such birds are 'mates' once they have accepted preferences for one another and that by this stage the bond has been formed. Thus, pair formation would appear to be concluded in a matter of minutes yet changes in the behaviour of the pair continue to occur after this time. These changes, I would argue, are due to pair maintenance activities which as well as prolonging the bond may lead to strengthening of it in the future. Such activities as allopreening, contact behaviour and proximity maintenance appear and are probably involved. Undirected singing may also be implicated. In addition, courtship continues, at a low level, and is largely directed towards the mate. It appears to have two functions (a) it is involved in mate selection, and (b) it may help to re-establish the bond, particularly after the mates become separated (see discussion in Section 5).

It therefore seems likely that the bond between two birds involves the mutual "attractiveness" with which they view one another on first meeting. This is not perhaps the best descriptive term as it implies some sort of quality possessed by an individual which serves to make it attractive. In practice the 'attractiveness' could well involve the way in which the onlooker perceives the individual rather than some attribute he possesses. The term "bond" suggests some tangible force between the male and female which serves to keep them together. It is argued here that the force is the attraction or preference two individuals feel towards one another (probably of a sexual basis) and that this is subsequently reinforced by changes in their behaviour.

Mate selection and imprinting

It has been suggested that imprinting on the parent-type by young birds is an important factor which influences future mate selection and largely ensures that reproductive isolation of the species is maintained (e.g., Immelmann, 1972). Thus preferences for particular individuals may result from juvenile imprinting but before discussing this possibility it must be noted that the learning mechanism involved in the imprinting response bears many similarities with that seen during mate selection. Thorpe (1961) reviewed imprinting and Bateson's (1969) work supported his list of the features of the learning process. In each case similarities with mate selection can be pointed out.

(i) The imprinting response involves a rapid period of learning during which all the features of the stimulus are learned and subsequently a preference is shown towards the imprinted object. Mate selection seems comparable in that preferences are quickly established and a male directs nearly all his subsequent courtship towards the preferred female.

(ii) Imprinting frequently appears to be "unrewarded". A duckling pursuing an object does not need to receive comfort or food from that object for imprinting to take place. A courting male is frequently re-buffed by his preferred female and yet, in both cases, the maintenance of a constant spatial relationship with the moving object appears to be the consummatory factor (i.e., the 'goal').

(iii) The motivational environment of an individual may be altered by imprinting; Thorpe (l.c.) suggested it might "prime the drive". Wiedmann (1956) showed that imprinted ducklings will search for a parent object if they loose contact with it whereas non-imprinted ducklings show no signs of such appetitive behaviour.

Separated mates will call frequently and Butterfield (1970) demonstrated that male Zebra Finches will work in order to gain a sight of their mate.

(iv) Finally, imprinting is said to have a sensitive period during which it is likely to occur and by the end of which the behavioural response does not take place. Immelmann (1972) defined this period as, "the whole space of time in the individuals life during which a particular preference can be determined or altered, whereas outside its limits social experience does not exert a similar influence." In the Bullfinch, he notes, such a period may last for up to two years. If a sensitive period exists for mate selection then it must involve the whole of adult life in the Zebra Finch, whereas with temperate species it may be restricted to the early stages of the breeding cycle each year. In either case, it seems likely that high levels of gonadial hormones will be involved and fluctuations in such levels may influence the readiness of birds to form pairs. Presumably, removal of the mate induces the onset of a further sensitive period, at least in the male, as on reunion preferences are re-established and male courtship occurs. This may explain the occurrence of courtship on reunion of mates as, during the separation, the male's responsiveness to the female has been enhanced.

This is speculation only, but as Hinde (1961) noted, the term imprinting could be used to describe behaviour occurring in contexts other than parent/offspring. It could therefore, presumably, include mate selection. Any differences between imprinting and other forms of learning, he thought, could be attributed to the special situation in which it occurred rather than to a special process. Bateson (1969) came to similar conclusions and proposed that the term imprinting should still be restricted in its usage to descriptions of learning in young animals. It was, he felt, the features of the context in which it occurred which rendered it unique, not the processes involved. It thus is not impossible that male selection and imprinting may involve very similar learning processes. However, to assert that mate selection is a similar process to imprinting does not tell us a great deal more about the actual processes involved, unfortunately; it merely provides us with another label. Whatever the outcome, the result of the operation of the learning process is that preferences for particular conspecifics are quickly learned and the relationship that results between the mates, once established, is resistent to dissolution. It may be that the learning process has a similar basis ta that seen in imprinting.

Discussion of a possible 'sensitive period' for mate selection raised the importance of gonadial hormones to the learning process. Arnold (1975) has recently shown that castrated male Zebra Finches will continue activities such as clumping, allopreening and undirected song in spite of the presumably low levels of gonadial hormones following their operations. It would be interesting to know whether castrated males could form pair bonds, that is, could establish a preference for an individual. Andrew (1964, 1966) showed that administration of testosterone to male chicks induced a change in their reactions to an imprinted object. The chicks attempted to copulate with the object concerned which possibly indicates that with high levels of gonadial hormone a typical imprinting response is modified to include sexual responses. It is not a great step from such a proposal to suggest that adult sexual bonds are similar processes occurring most readily when the gonads are active. If this is the case, then the situation with regard to the female needs clarification. Andrew (l.c.) showed that copulatory responses were seldom given by female chicks treated with testosterone. This raises the possibility that bonding mechanisms may have a different basis in female Zebra Finches.

Returning to the point raised earlier concerning the effect that imprinting on the parent may have on adult preferences, Walter (1973) showed that parental plumage colour affected mate selection. Males showed a preference for parental colour-type whilst females always appeared to choose males with the grey, wild-type, colouration. This again suggests that the establishment of preferences may have a different basis in males compared to females. Immelmann (1972) obtained similar results to Walter (l.c.) and stressed that the effect of imprinting on the males was to establish a type preference. With this the case, one would therefore expect some courtship of individuals other than the imprinted one (i.e., all individuals resembling the parental type). However, Immelmann restricted the learning during imprinting to one involving the recognition of the species. Thus, a Zebra Finch reared by Zebra Finches shows a preference, on becoming mature, for Zebra Finches as courtship objects. Beer (1970c) criticised approaches such as this in that they concentrate too fully on the learning of species differences without taking into account how preferences for individual characteristics may be affected. He proposed that future research should set imprinting in a broader functional perspective than that at present. For the purposes of the present discussion, if imprinting is involved in the determination of preferences then this could help to explain the rapid recognition of the mate after selection.

At present all we can conclude is that mate selection resembles parent/offspring imprinting in a number of ways including that both consist of a rapid period of learning which has long term effects on subsequent behaviour. Preferences for particular individuals at mate selection may be affected by parental imprinting but, as Hinde (1966) has stressed, adolescent and adult experiences are almost certain to affect such preferences. The whole basis of what makes a particular individual attractive as a mate deserves full examination.

Pair maintenance and the strength of pair bonds

The results of experiments described in Section 9 concerning the maintenance of pair bonds suggested that the continuous reinforcement of initial preferences is very important in determining the duration of a relationship. In the absence of the mate the bond weakens and both the male and the female will form a new bond if a suitable partner is provided. This new relationship does not necessarily destroy the earlier alliance, nor does a prolonged period of separation, as when former mates were reunited they invariably chose to return to their 'established' partner rather than remain with a relatively 'new' individual. This demonstrated that birds may possess more than one pair bond at any one time but the results of this investigation suggest that two are never expressed simultaneously. One could envisage a situation in which more than one bond might be in competition and presumably the one which had been most strongly established in the past would be expressed. The results of Section 9 showed that recency of the relationship was not the deciding factor which suggests that the bond between two individuals is not only maintained but enhanced as it becomes stronger with time. The mate will become the releaser for bond maintenance behaviour as the result of the expression of initial preferences and the performance of these activities will, in turn, stimulate the relationship. Without such reinforcement, the response to the mate will wane and may be replaced.

McBride et al (1969) discussed the possible "affiliative mechanisms" that could account for bond maintenance and the waning of aggressive tendencies directed towards the mate. Animals could, they suggested, habituate to the close presence of others merely because of their regular proximity. In addition, fellow animals might become conditioned stimuli due to their consistent presentation with other reinforcing stimuli (e.g., food). Both of these mechanisms could operate in the formation of 'social' bonds between members of the same flock of birds. However, they also suggested the possibility of more active reinforcement, such as copulation, contact behaviour and nesting activities, which would be important in pair bonds as they are usually restricted to behaviour between mates only.

The bond, or "attachment", between two individuals thus emerges as a dynamic relationship and one which is dependent for its duration on continuous visual and auditory contact with the mate. Without the chance of reinforcement, which this contact provides, the bond may be weakened and a new pair formed. There is some evidence from Sections 5 and 9 to suggest that females may be more reluctant to relinquish their old bonds in such situations; they appear to remain aggressive towards a new partner for a longer time than the males in some cases. There appears to be a learning process which is dependent on conditioning to the partner as a feature of the environment which is capable of eliciting both sexual and aggressive tendencies. Whilst the attachment is built up it is essential that constraints are placed on individuals, in particular, the males whose readiness to court strange females is a serious threat to the duration of the relationship. Frickson (1973) stressed the importance of this early stage and concluded that the pair bond was, "more a manifestation of various constraints imposed by the demands of breeding (confinement to the nest, increased aggression) than it was an expression of social attachment between the animals." Such an attachment only came with duration, at least two breeding cycles in the Ring Dove, by which time the rewards of breeding success could be assessed.

This suggests that the nature of the attachment resulting between two individuals fluctuates depending on the sort of reinforcement it has received. The 'constraints' that Erickson (l.c.) spoke of, indicate that a more indirect form of bond maintenance may occur. Fidelity to a nest site, or to the offspring, may serve to maintain the relationship between a pair of birds. It could be that the male and female form a bond with the nest site that serves to keep them together during incubation and rearing of the young at a time when the pair bond may be weakened by the enforced separation of the mates. It has certainly been shown that cases of sexual activity with birds other than the mate often occur at this time (see discussion of Section 5). However, Butterfield (1969) showed that destruction of the nest did not destroy the pair bond between two individuals but it is not known if it may have weakened the relationship. Bonds with the developing young (parent/offspring) may also serve to keep the pair together at this time. Thus, as well as the pair bond there may well be other bonds which could assist in maintaining the attachment between two birds. If these latter should be lacking (e.g., if breeding were to be unsuccessful) then the pair bond might weaken sufficiently to allow re-pairing to occur. This might help to explain Coulson's (1966) findings that unsuccessful pairs of Kittiwakes tend to split up in future years.

Fidelity to the nest and to the young may differ in the sexes. A case was quoted in a previous discussion of a male who was incubating eggs when his female died. He promptly deserted the nest and paired up with a new female. It would be interesting to know whether his behaviour would have been similar had the eggs from the first relationship been hatched at the time of his mates death. In addition, a female's responses to loss of her mate during incubation and rearing is not known. In the Snow Bunting Tinbergen (1939) described cases of males deserting their young and re-pairing with a new female and he proposed that the males became sexually active again before the females. This time in the breeding cycle would seem to be an occasion when the pair bond might be at its weakest. There would be low levels of gonadial hormones which would lead to a reduced expression of the male's preference for his mate. However, in some species the incubation period is a time when copulation occurs quite frequently. Burger (1974) described how in the Franklin's Gull the nest relief ceremony occurring during shared incubation of the eggs involved copulation which would certainly act to reinforce the presumably weaker bond prevalent at this time.

Thus the pair bond may be maintained by a variety of activities other than courtship and contact behaviour and, indeed, may even be affected by the presence of other bond-types or relationships such as with the nest or the young. What seems certain is that during bond establishment a 'central specification' (Andrew, 1972) of the mate is built up in order that recognition in the future is invariably possible. It is unlikely that such a specification will be based on a single parameter nor can it be assumed, with any certainty, that the same parameter will operate throughout the relationship. It may take time, for instance, before vocal characteristics are learned and this could explain why the maintenance of close proximity is at a premium in the early stages of Zebra Finch bonds. Possibly, as time proceeds, greater distances between the mates can be tolerated. The strength of the bond will vary with the time in the breeding cycle and the reinforcement experiences of the birds concerned. Separation may result in less importance being placed on a particular bond but the preference for the former mate is not necessarily lost. In fact it may be enhanced as shown by the high levels of courtship on their reunion. In addition, individual differences in courtship and aggressive tendencies may well influence the success or failure of a particular pair bond as it passes through a period of potential stress.

The individual nature of pair bonds

Bond maintenance involves the cooperation of males and females. In the face of non-mate conspecifics they must act aggressively on occasions and active reinforcement, such as allopreening, clumping or courtship, must be expressed. Yet, in different pairs, males and females are seen to occupy different roles. In some cases the male attacks encroaching non-mates of either sex and the female remains a largely passive bystander. In others, the male may be subordinate to other individuals and the female, becoming aggressive, "defends" him from further attacks (Section 4).

This suggests that different individuals may possess different or fluctuating thresholds for attack and that this may affect the particular form of their relationships. Another variable feature is that of courtship (see Section 5). The amount of courtship shown by males varies and Andrew (1972) has shown that testosterone levels can affect the persistence shown by an individual at any one time. Spencer-Booth and Hinde (1971) and Hinde and Spencer-Booth (1971) noted large differences in the mother/infant bonds of rhesus monkeys and suggested that these affected the relationships such that interactions between mother and infant became complex. They concluded that it was first essential to establish the fundamental characteristics of the mother/infant relationship and then to look at individual differences and the way in which they alter the general form of the attachment.

In this study an attempt has been made to describe the fundamental bonding relationship of the Zebra Finch from its beginning until it becomes functional, in a breeding sense. The individual variation in bonding that was noted might well prove an illuminating topic for study particularly the relationship between bond formation, aggressive tendencies and dominance. In taking an overall view such details may be obscured and written off as irrelevant.

The way ahead

It has been shown that at least two processes are involved in the formation of bonds or pairing relationships. These are mate selection and bond maintenance. In the former preferences, learned or innate, are expressed in the choice of partner to be courted; the latter involves reinforcement of the relationship and the behaviour concerned constitutes the tangible signs of the bond itself. Thorpe (1961) wrote, "there is hardly any aspect of the behaviour of animals which may not have some reference to the problems of human behaviour", and this seems true of bonding. Man is an example of a monogamous species which pairs for prolonged periods, often for life. It would be interesting to discover if similar processes operate as have been located in the Zebra Finch but without a more complete understanding of the latter's situation conclusions would be difficult to draw.

Future research in pair bonding would benefit from a close examination of mate selection and the 'attractiveness' of different individuals. Bond reinforcement warrants attention especially in view of the increasing divorce rates in man. It has been shown here that, in the Zebra Finch, if bond maintenance activities are precluded then new bonds may be formed and the old relationship dissolve. This suggests that a pairing relationship is something that should be worked towards continually by the parties concerned, without the effort on both sides the bond is doomed to failure from the outset. Mother/infant relationships have proved a rewarding study, adult mate and social bonds deserve equal attention. As was noted above, in many cases it may be necessary to observe individual variations in the fundamental relationships before adequate explanations and understanding can be achieved.

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APPENDIX I Measurements of the Calls from Section 6.1.

TABLE 1 Measures of calls of male and female Zebra Finches expressed as mean values with standard errors and coefficients of variation shown. The loud calls

Males	No. of calls	Low frequency (kHz)			High frequency (kHz)			Duration (msec)		
		$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	10	4.8	0.04	2.9	5.3	0.02	1.1	129	1.5	3.9
*2	15	3.0	0.04	5.6	3.5	0.02	2.2	182	1.5	3.9
*3	11	2.7	0.02	2.1	5.1	0.07	4.1	220	3.8	5.5
4	10	3.3	0.05	4.5	4.1	0.06	4.3	174	3.8	6.3
5	14	4.7	0.03	2.9	5.6	0.02	1.4	121	1.5	5.0
6	19	3.7	0.03	2.7	4.4	0.03	2.6	144	1.5	4.2
7	15	4.7	0.02	1.6	5.7	0.03	1.8	159	2.3	5.0
8	10	4.1	0.03	1.6	4.9	0.03	1.7	151	2.3	5.3
9	12	4.3	0.13	9.8	5.3	0.20	13.1	167	3.0	6.6
10	12	4.7	0.03	2.1	5.6	0.03	1.8	121	1.5	5.0
*$\bar{X}$	102	4.3	0.20	13.1	5.1	0.21	11.0	157	10.9	19.7
Females										
1	12	2.9	0.03	3.4	3.4	0.02	1.5	265	11.4	14.7
2	10	3.5	0.04	3.8	4.0	0.04	3.5	227	8.3	11.9
3	12	3.1	0.02	2.2	3.9	0.05	4.5	265	6.8	8.7
4	10	2.7	0.02	2.1	3.2	0.03	3.7	242	13.6	17.8
5	11	2.9	0.04	4.3	3.5	0.02	1.9	242	9.1	12.0
6	12	2.6	0.02	2.6	3.4	0.08	8.1	204	4.5	8.3
7	11	3.1	0.03	3.5	3.8	0.04	3.7	250	7.6	9.6
8	11	4.2	0.04	3.4	4.7	0.02	1.2	189	3.8	6.4
9	10	2.8	0.03	2.4	3.4	0.06	6.4	197	7.6	12.2
10	13	2.9	0.03	4.0	3.2	0.03	4.1	356	11.4	11.8
$\bar{X}$	112	3.1	0.14	14.2	3.7	0.15	12.5	244	15.1	19.6

* These males had no measurable harmonics and are excluded from the calculation of mean scores for their sex (*$\bar{X}$)

TABLE II Measures of Loud/Soft calls

		Low frequency (kHz)			High frequency (kHz)			Duration (msec)		
Males	No. of Calls	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	II	4.7	0.03	1.6	5.2	0.03	1.4	121	4.5	12.4
*2	10	2.6	0.05	5.8	4.3	0.03	1.9	144	10.6	22.9
**3	0	-	-	-	-	-	-	-	-	-
4	10	3.2	0.07	6.4	4.1	0.07	5.1	159	6.8	13.2
5	10	4.2	0.11	8.0	5.1	0.16	9.2	114	2.3	6.1
6	10	3.6	0.03	2.1	4.3	0.13	8.8	144	3.8	7.6
7	14	4.7	0.04	3.6	5.4	0.05	3.2	121	4.5	14.1
8	10	3.9	0.05	4.1	4.7	0.05	3.2	129	5.3	13.2
9	11	3.8	0.07	5.9	4.3	0.05	3.9	167	5.3	10.8
10	10	4.3	0.06	4.4	5.0	0.04	2.5	98	3.0	9.2
$\bar{X}$	96	4.1	0.18	12.5	4.8	0.17	10.2	133	7.9	16.7
Females										
1	15	2.7	0.02	2.7	3.2	0.03	4.1	144	4.5	11.8
2	12	3.2	0.06	6.1	3.7	0.03	2.7	121	6.8	19.8
3	10	3.0	0.03	2.6	3.7	0.06	4.8	197	7.6	12.7
4	10	2.6	0.03	3.5	3.1	0.04	4.3	189	12.1	20.6
5	9	2.8	0.03	3.2	3.2	0.03	2.3	151	7.6	15.9
6	11	2.6	0.02	2.6	2.9	0.13	3.4	136	8.3	19.9
7	3	3.1	-	-	3.6	-	-	182	-	-
8	12	3.7	0.03	2.7	4.0	0.04	3.5	136	6.1	16.2
9	10	2.7	0.03	2.4	3.2	0.02	1.8	144	6.8	15.3
10	13	2.7	0.01	1.2	3.2	0.03	2.4	212	12.1	22.2
$\bar{X}$	115	2.9	0.10	11.3	3.4	0.11	10.0	161	9.8	19.2

* This male had no measurable harmonic and his scores are excluded from mean male values ($\bar{X}$)

** This male gave no L/S calls.

TABLE III **Measures of Soft calls**

		Low frequency (kHz)			High frequency (kHz)			Duration (msec)		
Males	No. of calls	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	15	2.9	0.03	3.1	3.2	0.03	3.2	91	3.0	12.1
2	24	2.7	0.01	1.6	2.9	0.01	1.4	91	1.5	6.6
3	18	3.0	0.02	2.5	3.4	0.02	2.2	88	1.5	11.8
4	11	2.7	0.03	2.7	3.1	0.02	1.6	68	2.3	11.8
5	10	3.0	0.03	2.5	3.7	0.02	1.2	91	2.3	7.8
6	9	2.7	0.02	2.2	2.9	0.03	2.9	83	5.3	19.3
7	19	3.3	0.02	2.3	3.5	0.01	1.4	61	1.5	13.1
8	13	2.7	0.02	1.9	2.9	0.02	2.3	83	2.3	9.6
9	14	2.7	0.03	3.0	3.1	0.03	3.8	76	3.8	17.1
10	10	2.8	0.01	1.2	3.0	0.02	1.9	68	5.0	16.2
$\bar{X}$	143	2.9	0.07	7.3	3.2	0.09	8.5	78	3.6	14.5
Females										
1	12	2.7	0.03	2.7	3.1	0.02	1.9	114	5.3	15.8
2	10	3.0	0.03	3.9	3.4	0.08	6.6	83	6.1	22.9
3	10	2.9	0.03	3.7	3.4	0.03	2.2	121	3.0	7.4
4	11	2.7	0.02	2.1	3.0	0.02	1.4	121	7.6	19.8
5	12	2.8	0.02	2.4	3.1	0.02	1.4	83	2.3	9.6
6	20	2.6	0.02	2.6	2.7	0.02	2.7	98	2.3	11.2
7	11	3.0	0.03	2.5	3.4	0.06	3.4	91	4.5	16.5
8	13	3.5	0.01	1.2	3.8	0.03	2.0	98	3.0	11.2
9	26	2.7	0.02	3.1	3.1	0.01	1.9	98	3.0	14.3
10	13	2.8	0.03	2.7	3.1	0.02	1.6	114	5.3	15.8
$\bar{X}$	138	2.9	0.08	8.9	3.2	0.10	9.5	102	4.6	14.2

TABLE IV <u>Measures of Tet calls</u>

		Low frequency (kHz)			High frequency (kHz)			Duration (msec)		
Males	No. of calls	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	10	2.8	0.03	2.9	3.0	0.03	2.8	61	2.3	9.8
2	15	2.7	0.03	3.1	3.1	0.03	3.5	61	1.5	8.2
3	26	3.2	0.02	2.1	3.6	0.02	2.6	61	2.3	16.4
4	10	2.7	0.02	2.2	3.2	0.03	3.4	68	2.3	11.8
5	10	3.0	0.03	2.8	3.5	0.03	2.6	68	2.3	10.3
6	10	2.6	0.03	3.9	2.9	0.03	3.7	61	3.0	14.8
7	10	3.1	0.03	3.0	3.6	0.03	1.9	53	3.0	18.9
8	10	2.6	0.03	3.2	2.9	0.05	5.1	61	1.5	8.2
9	9	2.8	0.05	5.6	3.3	0.07	6.0	76	3.8	14.5
10	15	2.7	0.03	3.1	3.0	0.02	1.9	68	2.3	13.4
$\bar{X}$	125	2.8	0.07	7.5	3.2	0.08	8.2	64	2.0	9.9
<u>Females</u>										
1	15	2.7	0.03	3.0	3.1	0.03	4.1	76	3.0	17.1
2	11	2.9	0.03	3.1	3.6	0.05	4.4	68	3.0	13.2
3	16	2.8	0.03	2.9	3.5	0.03	3.6	83	3.0	14.5
4	10	2.7	0.02	2.2	3.1	0.03	3.3	61	1.5	8.2
5	11	2.9	0.04	4.6	3.4	0.03	3.2	61	2.3	11.5
6	11	2.5	0.02	2.7	3.1	0.04	15.4	83	4.5	19.3
7	12	2.6	0.03	3.9	3.0	0.02	1.9	68	2.3	11.8
8	10	3.1	0.03	2.7	3.6	0.05	4.2	68	1.5	7.4
9	9	2.7	0.02	1.9	3.0	0.03	3.3	83	2.3	8.4
10	15	2.8	0.02	2.4	3.3	0.03	1.1	68	2.3	13.4
$\bar{X}$	120	2.8	0.06	6.3	3.3	0.08	7.4	72	2.8	12.1

APPENDIX II Measures of the courtship and undirected song of male Zebra Finches (from Section 6.2)

MALE 1

(a) Courtship Song (N = 9) * After Marler and Isaac (1960)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			*Accurate measure of duration (msec)		
Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	3.2	0.03	2.9	3.5	0.03	2.6	91	3	8.8	121	0.7	1.7
2	2.8	0.04	4.9	3.6	0.04	3.3	144	6	13.2	174	0.7	1.3
	4.5	0.03	2.0	5.7	0.03	1.6	129	4	9.3			
3	2.7	0.02	1.9	3.6	0.03	2.3	121	2	4.1	167	0.0	0
	4.0	0.04	2.9	4.5	0.05	3.2	106	1	29.2			
4	3.1	0.04	3.5	3.4	0.03	2.2	129	4	10.1	167	0.7	1.4
	5.3	1.05	2.8	6.0	0.04	2.1	159	2	2.5			
5	2.9	0.08	7.7	3.2	0.11	10.3	23	2	17.4	129	1.2	3.0
	4.1	0.04	3.1	5.7	0.02	1.0	121	4	9.1			
6	3.9	0.01	1.1	4.2	0.01	1.0	38	2	13.2			
								Total		802	3.0	1.2

(b) Undirected Song (N = 11)

1	3.1	0.01	1.4	3.4	0.03	2.7	91	2	8.8	121	0	0
2	2.8	0.05	6.1	3.6	0.03	2.3	144	5	11.1	174	0.7	1.3
	4.7	0.04	2.5	5.7	0.06	2.2	144	4	9.7			
3	2.7	0.03	3.1	3.4	0.04	3.4	129	2	3.9	167	1.4	2.7
	3.8	0.05	4.4	4.3	0.06	4.2	136	13	30.9			
4	3.0	0.03	2.8	3.4	0.03	2.7	135	3	7.4	174	1.2	2.2
	5.3	0.03	2.1	6.0	0.03	1.5	159	4	7.6			
5	2.8	0.05	6.4	3.2	0.05	4.7	30	2	16.7	136	1.2	2.8
	3.9	0.03	2.8	5.8	0.02	1.3	144	3	7.6			
6	3.9	0.02	1.6	4.1	0.12	2.1	45	1	8.9			
								Total		810	3	1.4

SE = Standard Error

CV = Coefficient of Variation (%)

Total = The total duration of the call (Overlapping of elements means that the sum of element durations does not necessarily equal the total duration).

MALE 2 - Phrase 1

(a) Courtship Song (N = 13)

	Low frequency (kHz)			High Frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV	$\overline{X}$	SE	CE	$\overline{X}$	SE	CV
1	3.5	0.03	3.6	3.8	0.01	0.9	91	1	5.5	129	1.1	3.0
2	3.6	0.05	5.4	4.3	0.03	2.4	68	3	14.7	91	0.7	2.5
3	3.8	0.03	2.9	4.0	0.01	1.1	68	4	20.6	76	0.9	4.0
4	3.5	0.02	1.9	4.3	0.04	3.1	61	2	13.1	76	0.7	3.0
5	4.3	0.02	1.4	4.4	0.01	0.9	63	3	13.3	114	2.2	6.7
6	3.6			4.3			164					
								Total		477	6	4.8

(b) Undirected Song (N = 1)

2	3.5			4.2			75					
3	3.8			4.0			76					
4	3.6			4.5			83					
5	4.3			4.4			98					
									Total	485		

Song Phrase 2

(a) Courtship Song (N = 23)

1	3.4	0.02	3.4	3.8	0.01	1.6	83	1	9.6	151	1.0	3.0
7	4.3	0.02	1.9	4.7	0.02	2.0	129	2	8.5	182	1.0	3.4

(b) Undirected Song (N = 14)

1	3.3	0.03	3.7	3.8	0.01	1.8	91	1	6.6	151	1.2	3.0
7	4.3	0.01	1.2	4.7	0.02	1.3	129	3	8.5	182	0.8	1.7

MALE 3

(a) Courtship song (N = 9)

	Low Frequency (kHz)			High Frequency (kHz)			Duration (msec)			Accurate measure of Duration		
Element	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV
1	4.4	0.02	1.5	5.8	0.02	0.9	76	1	5.3	91	1	4.4
2	4.8	0.05	3.2	6.3	0.03	1.2	53	2	9.4	53	0	0
3	4.2	0.01	1.0	5.6	0.03	1.8	121	9	22.3	167	1	2.4
4	2.8	0.03	2.7	6.2	0.07	3.5	227	2	2.7	212	2	2.4
								Total		530	2	0.9
(b) Undirected song (N = 13)												
1	4.3	0.02	1.8	5.6	0.02	1.2	83	2	8.4	91	1	3.3
2	4.9	0.04	3.1	6.3	0.03	1.6	61	2	8.2	53	1	5.7
3	4.1	0.02	1.4	5.5	0.02	1.1	144	11	26.4	166	1	1.8
4	2.8	0.05	6.8	6.1	0.05	2.9	265	8	10.2	219	3	4.1
								Total		575	7	4.2

MALE 4

(a) Courtship song (N = 11)												
1	2.8	0.04	5.0	7.2	0.10	4.7	68	2	8.8	129	1	1.6
2	2.8	0.06	7.3	6.7	0.12	5.9	71	2	6.6	76	0	0
3	2.4	0.09	11.4	7.2	0.08	3.8	91	2	6.6	121	1	1.7
4	3.6	0.02	1.4	3.8	0.02	1.3	204	3	4.9	197	1	2.0
								Total		545	3	1.9
(b) Undirected Song (N = 11)												
1	3.0	0.01	1.5	7.0	0.05	2.5	83	3	9.6	136	1	2.9
2	2.9	0.04	4.3	6.8	0.09	4.3	76	2	7.9	76	1	3.9
3	2.3	0.08	10.7	7.2	0.10	4.9	91	1	5.5	129	1	1.6
4	3.5	0.02	1.4	3.7	0.01	1.2	219	3	5.0	204	1	2.0
								Total		575	3	1.9

MALE 5

(a) Courtship Song (N = 13)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV	$\overline{X}$	SE	CV
1	3.3	0.02	2.1	3.6	0.02	2.1	83	1	6.0	114	1	2.6
2	3.0	0.04	4.7	3.5	0.04	3.8	114	2	5.3	159	1	1.3
	4.7	0.03	2.5	5.8	0.04	2.6	121	2	5.0			
3	3.1	0.03	3.8	3.4	0.02	1.7	121	2	6.6	159	1	2.5
	4.0	0.02	1.7	4.4	0.03	2.5	106	5	17.0			
5	3.0	0.05	6.1	3.3	0.04	4.1	23	1	21.7	129	1	3.1
	3.9	0.08	7.2	5.8	0.03	1.7	144	6	13.9			
6	3.8	0.03	3.2	4.1	0.02	1.7	45	1	11.1			
								Total		606	3	1.5
(b) Undirected Song (N = 10)												
1	3.3	0.02	2.0	3.6	0.03	3.0	106	5	16.0	114	0	0
2	2.9	0.05	4.9	3.5	0.02	1.9	136	4	8.8	159	1	2.5
	4.8	0.02	1.6	5.4	0.03	1.7	121	7	19.0			
3	3.0	0.02	2.0	3.3	0.03	2.8	136	6	14.0	159	1	2.5
	4.0	0.03	2.3	4.4	0.03	2.3	174	2	4.6			
5	2.9	0.03	3.7	3.3	0.03	2.8	32	2	18.8	136	1	2.9
	4.0	0.03	2.7	5.7	0.05	2.5	204	8	13.2			
6	3.9	0.04	4.2	4.3	0.02	1.8	38	2	13.2			
								Total		613	2	1.3

MALE 6

(a) Courtship Song (N = 10)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	2.8	0.05	5.0	5.9	0.11	5.8	61	1	8.2	91	1	4.4
2	3.7	0.07	6.4	4.9	0.05	3.0	91	2	6.7	121	1	3.3
	4.7	0.05	3.0	5.2	0.05	3.2						
3	4.6	0.03	2.2	5.1	0.05	3.0	83	2	7.2	129	2	3.9
4	3.1	0.07	6.8	5.9	0.08	4.2	61	2	9.8	83	2	6.0
5	3.0	0.08	8.6	3.3	0.02	1.5	61	1	6.6	91	0	0
6	4.0	0.03	2.7	4.7	0.02	1.3	144	2	3.5	144	0	0
								Total		651	3	1.5
(b) Undirected Song (N = 10)												
1	2.9	0.06	6.6	6.1	0.03	1.5	61	2	8.2	91	0	0
2	3.6	0.02	1.9	4.9	0.05	3.1	98	2	6.1	121	2	4.1
	4.8	0.04	2.6	5.3	0.02	1.3						
3	4.6	0.06	3.8	5.1	0.02	1.5	76	2	10.5	121	2	4.1
4	3.2	0.03	2.9	6.1	0.03	1.8	61	3	16.4	83	1	4.8
5	5.0	0.02	2.2	3.3	0.02	1.8	68	2	8.8	91	0	0
6	4.1	0.04	3.3	4.8	0.02	1.4	151	1	3.3	151	2	3.3
								Total		666	2	1.2

MALE 7

(a) Courtship Song (N = 13)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	1.8	0.09	12.4	5.4	0.11	5.2	76	3	10.5	114	0	0
1	1.8	0.11	16.2	5.5	0.12	5.6	83	3	8.4	114	0	0
2	2.0	0.05	8.3	5.7	0.07	4.1	114	1	2.6	136	1	2.9
1	1.8	0.02	4.3	5.8	0.16	10.1	83	2	9.6	98	5	11.2
2	1.9	0.02	2.2	5.5	0.09	4.1	114	1	2.6	136	3	3.7
1	1.8	0.05	7.1	5.4	0.07	3.4	83	3	10.8			

(b) Undirected Song (N = 11)

1	1.8	0.06	9.1	5.3	0.03	4.3	76	3	11.8	114	0	0
1	1.8	0.06	8.6	5.6	0.21	9.7	83	4	13.3	114	0	0
2	2.0	0.05	7.5	5.8	0.17	9.9	114	1	3.5	136	1	2.9
1	1.8	0.05	8.6	6.2	0.30	15.1	83	2	9.6	98	4	13.3
2	1.9	0.04	6.7	5.8	0.15	8.7	114	1	3.5	136	1	3.7
1	1.8	0.05	9.6	6.0	0.25	13.6	91	2	8.8			

MALE 8

(a) Courtship Song (N = 10)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	2.8	0.02	1.8	2.8	0.01	1.5	30	1	13.3	53	1	3.8
2	3.6	0.13	12.3	6.0	0.05	3.3	91	2	5.5	129	1	1.6
	4.8	0.04	2.5	5.2	0.02	1.0						
3	4.7	0.04	2.9	5.1	0.02	1.0	91	1	4.4	136	2	3.7
4	3.0	0.04	4.5	5.8	0.06	3.3	61	2	8.2	76	1	2.6
5	3.0	0.02	1.7	3.2	0.02	1.6	68	1	5.9	91	1	2.2
6	4.2	0.04	3.0	4.7	0.02	1.4	151	2	3.3	151	2	3.3
								Total		636	2	1.3

(b) Undirected Song (N = 11)

Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	2.8	0.02	1.8	2.8	0.02	1.8	30	1	13.3	53	1	3.8
2	3.5	0.01	10.0	4.8	0.04	2.8	91	1	2.2	129	1	3.1
	4.8	0.03	2.1	5.1	0.02	1.2						
3	4.6	0.03	2.2	5.1	0.01	0.8	83	2	8.4	136	1	2.9
4	3.0	0.02	2.0	5.7	0.03	1.5	61	2	11.5	76	2	6.6
5	2.9	0.01	1.4	3.1	0.01	1.4	68	2	8.8	98	0	0
6	4.1	0.02	1.8	4.6	0.02	1.3	159	2	3.2	151	1	1.3
								Total		659	2	0.9

MALE 9

(a) Courtship Song (N = 36)

	Low frequency (kHz)			High frequency (kHz)			Duration (msec)			Accurate measure of duration		
Element	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV
1	2.4	0.03	6.5	6.8	0.11	9.6	83	1	6.0	114	1	4.4

(b) Undirected Song (N = 37)

1	2.1	0.03	9.4	6.6	0.07	6.7	83	1	7.2	114	1	4.4

MALE 10

(a) Courtship Song (N = 42)

1	2.3	0.04	11.1	6.0	0.07	7.4	83	1	7.2	116	1	4.0

(b) Undirected Song (N = 45)

1	2.0	0.08	25.0	6.2	0.04	4.2	76	1	6.6	116	1	4.0

APPENDIX III The Spearman Rank Correlation coefficients for calling by mates and non-mates during separation and again after introduction (from Section 7.3)

TABLE I <u>Total Number of calls given</u>

(a) During Separation

Pair No.	Between established mates	Between male and a female non-mate	Between female and a male non-mate
1	0.792*	0.544*	0.844*
2	-0.138	0.486*	0.776*
3	0.975*	0.918*	0.147
4	0.695*	0.904*	0.827*
5	0.158	0.294	0.855*
6	0.075	0.832*	0.677*
7	0.868*	0.675*	0.888*
8	0.731*	0.601*	0.787*
9	0.746*	0.638*	0.870*
10	0.888*	0.864*	0.322*
$\overline{X}$	0.514*	0.676*	0.699
(b) After introduction			
1	0.664*	0.672*	0.113
2	0.726*	0.174	-0.182
3	0.728*	0.429*	-0.224
4	0.929*	0.376*	0.723*
5	0.628*	0.236	0.087
6	0.600*	-0.671*	0.360*
7	0.791*	0.793*	0.477*
8	0.638*	0.468*	0.050
9	-0.055	0.571	0.025
10	0.482*	-0.187	0.768*
$\overline{X}$	0.614*	0.286	0.220

* = $p < 0.05$

TABLE II <u>Number of Loud calls given</u>

(a) During Separation

Pair No.	Between established mates	Between male and a female non-mate	Between female and a male non-mate
1	0.747*	1.000*	0.746*
2	0.121	0.446*	0.672*
3	0.928*	0.000	0.150
4	0.757*	0.745*	0.870*
5	0.504*	0.148	0.854*
6	-0.164	0.677*	0.683*
7	0.316*	0.888*	0.999*
8	0.626*	0.633*	0.329*
9	0.517*	0.766*	0.470*
10	0.442*	0.281	0.588*
$\bar{X}$	0.512*	0.558*	0.636*
(b) After introduction			
1	No calls	0.172	-0.360*
2	-0.131	-0.453*	-0.180
3	0.000	-0.013	-0.010
4	0.607*	0.471*	0.515*
5	0.000	-0.071	0.000
6	1.000*	-0.002	0.052
7	No calls	0.777*	No calls
8	0.065	0.119	1.000*
9	1.000*	0.799*	0.236
10	0.004	0.216	0.000
$\bar{X}$	0.456*	0.202	0.225

* = $p < 0.05$

TABLE III <u>Number of Soft calls given</u>

(a) During Separation

Pair No.	Between established mates	Between male and a female non-mate	Between female and a male non-mate
1	0.135	0.544*	0.306*
2	0.725*	0.380*	0.171
3	0.924*	-0.104	0.080
4	0.313*	-0.071	0.412*
5	-0.013	-0.696*	0.759*
6	0.907*	0.687*	-0.111
7	0.901*	0.635*	0.698*
8	-0.087	-0.662*	0.020
9	0.713*	0.269	0.639*
10	0.613*	0.309*	-0.077
$\bar{X}$	0.513*	0.129	0.290
(b) After introduction			
1	0.664*	0.637*	0.125
2	0.702*	-0.214	-0.225
3	0.726*	0.662*	-0.190
4	0.945*	-0.102	0.673*
5	0.503*	-0.166	0.196
6	0.649*	0.090	0.706*
7	0.791*	0.718*	0.477*
8	0.638*	0.195	0.042
9	-0.083	0.459*	0.104
10	0.532*	-0.211	0.753*
$\bar{X}$	0.607*	0.207	0.266

* = $p < 0.05$