THE IMPORTANCE OF VISUAL, VOCAL AND BEHAVIOURAL CUES FOR SONG TUTOR CHOICE IN ZEBRA FINCHES

N. S. Clayton

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THE IMPORTANCE OF VISUAL, VOCAL AND BEHAVIOURAL CUES FOR SONG TUTOR CHOICE IN ZEBRA FINCHES.

N. S. CLAYTON.

Submitted in fulfilment of the Ph. D. thesis at the University of St. Andrews.

CONTENTS.

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DECLARATION.

I, Nicola Clayton, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

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ABSTRACT.

This thesis examines the importance of visual, vocal and behavioural cues for song tutor choice in zebra finches, Taeniopygia guttata.

Zebra finch males normally copy song at 35 to 65 days of age. In the wild the young become independent at about 35 days of age and form small flocks in the area of the colony where they will be exposed to a variety of song tutors. In Chapter 3 captive zebra finches are provided with the opportunity to learn from two conspecifics at 35 days of age. Female-raised males which are housed with two unrelated tutors prefer to learn from the one who is most aggressive towards them. Normally-raised males which are housed with an unrelated tutor and one whose song is similar to the father's tend to copy the tutor with the similar song: this relies on the young bird learning some characteristics of his father's song before independence. Chapter 4 shows that males and females can discriminate between their father's song and those of other males.

Visual, vocal and behavioural cues are all important for species-specificity. Cross-fostering using Bengalese finches, Lonchura striata, as foster-parents is an important tool for studying this. Chapter 5 looks at Bengalese finch song development; Chapter 6 compares song development in cross-fostered zebra finches and Bengalese finches.

Visual cues are important for tutor choice and young males of both species which are provided with a zebra finch singing Bengalese song and a Bengalese finch singing zebra finch song prefer the conspecific tutor (Chapter 7). Chapter 8 suggests that conspecific song elements are not important for zebra finches: there is no tendency to prefer a tutor with normal song over one singing Bengalese song.

Cross-fostering can also influence the timing of song learning. Males which are housed successively (Chapter 9) or simultaneously (Chapter 10) with both species tend to reproduce song which they heard before independence in addition to learning from the tutor which they heard after independence at 35 to 65 days of age: this indicates that the timing of the sensitive phase is flexible and mediated by both experience and age.

There are a number of similarities between song learning and sexual imprinting which are discussed in Chapter 11.

Crucial to these studies is a knowledge of the two species' behaviours. Chapter 2 compares parental behaviour in captivity. Chapter 12 concludes with a plea for more research in the wild.

Chapter 1.

INTRODUCTION.

This thesis examines the importance of visual, vocal and behavioural cues in song tutor choice in zebra finches, *Taeniopygia guttata*.

The zebra finch is one of several species of grassfinch, family Estrildidae, whose song development has been extensively studied (Immelmann 1967, 1969; Hall 1962; Price 1979; Böhner 1983; Eales 1985a). Only the male sings (Nottebohm and Arnold 1977). The soft, sometimes toneless, song has been likened by Morris (1954) to a squeaking wheel. Each short song phrase consists of a series of notes or elements which are repeated several times during a song bout.

For Estrildid finch males the main function is in mate attraction. Courtship or directed song, so called because the bird directs his head towards the female while singing (Morris 1954; Immelmann 1962), forms part of a highly elaborate male courtship display. Outside courtship undirected song is performed, by males in mixed or monosexual groups, by males which have been separated briefly from their mates, and even sporadically by courting males between series of courtship songs and dances (Sossinka and Böhner 1980). The function of this is less clear. It may strengthen the pairbond (Zann 1984) and keep the ovaries in a permanent state of semiactivity (Farner and Serventy 1960). Song, together with call notes, may facilitate individual recognition. Zebra finches are not territorial (Hall 1962; Kunkel 1959), so there is probably little selection for male-male recognition, but the young of both sexes can recognise their father's song and that of any other male with whom they can visually and vocally interact (Miller 1979a; Eales 1987a).

Undirected and courtship song are virtually identical in all physical characteristics (Immelmann 1969; Butterfield 1970) but the intensity of courtship may increase the volume and rate of singing. Some males incorporate loud call notes into their song when highly sexually motivated (Sossinka and Böhner 1980). Since males tend to vary greatly in their degree of sexual motivation it is best to consider only undirected song in studies of song learning.

Zebra finch sexual activity and song begin very early in life. Song develops continuously from the young birds' begging calls. Initially it is very quiet and sporadic, lacking the adult song structure. It contains a great range of notes many of which are never found in the adult repertoire. The onset of subsong varies, but usually occurs at about 27 to 35 days. By 60 to 70 days the juvenile's song clearly resembles that of the tutor from whom it was learnt and full song is acquired by 9 to 11 weeks of age (Immelmann 1962).

In common with all oscines studied to date the zebra finch has to learn its song. A young male deprived of the opportunity to listen to adult song during ontogeny will not develop normal song. The Kaspar Hauser songs of birds of various species reared in isolation may possess species-specific characteristics but they are usually slower and more variable with fewer song elements (see review by Slater 1983). Immelmann (1969) and Price (1979) found that male zebra finches which were hand-raised or raised by the mother alone produced songs with only half as many song elements as normally-raised males. The songs were of a simple uniform structure, with an abnormally slow tempo and lacking any of the complicated elements found in normal song. Many of these songs contained an infusion of female call notes but there was considerable variation between isolates and even among sibs reared together.

Song acquisition occurs by two processes. There is a phase when song is memorized. At this stage the bird cannot convert the learnt information into the correct vocal output. During motor development vocalizations are developed, from the initial sqeaks of subsong to fully crystallized adult song. Both processes may be affected by the social experiences a young bird receives during ontogeny but they need not be affected in the same way. A bird may learn certain song elements during the memorization phase but this does not necessarily mean that it will develop and include these elements in its full song. Indeed many of the song elements present in subsong are never produced by the adult bird. Although female zebra finches do not normally sing they are capable of discriminating between the song of their father or mate versus another male (Miller 1979a, Chapter 4). The distinction between discrimination learning and song performance learning is discussed in Chapter 4.

In many species the two stages are separated by several months eg. in the whitecrowned sparrow, Zonotrichia leucophrys, and the swamp sparrow, Zonotrichia georgiana (Marler 1970; Marler and Peters 1977). For zebra finches there is temporal overlap: young males normally memorize and develop their songs at the same time. The timing of the memorization phase depends on social experiences the juvenile gains early in life but motor development proceeds irrespective of whether memorization has occurred (Eales 1985b).

Nonetheless development is affected by the behaviour of other birds. The vocalizations of other young males can stimulate a bird to practice so that song elements are acquired more quickly (Eales 1985a).

In some species there may be more than one period of song learning. In territorial species such as the great tit, Parus major, there may be two such periods, one in the nest at about the time of fledging and one at the time of territory establishment in the following Spring. These may represent two periods of exposure during a single sensitive phase for song learning or two separate periods of sensitivity. Some birds eg. canary, Serinus canaria, appear to be capable of learning throughout life (Nottebohm and Nottebohm 1978). In the village indigobird, Vidua chalybeata, all the males in a display area have similar songs but if a male moves to a new area he changes his song appropriately (Payne 1981, 1986).

Zebra finches have only one sensitive phase. In captive, normally-raised zebra finches this occurs at about 35 to 65 days of age (Eales 1985b). "The most striking feature is the fairly early sensitive period for song acquisition and the especially early end of that period." (Immelmann 1969). The biological significance of this is best explained in terms of the breeding biology of the species. Most species living in temperate zones undergo a complete regression of the gonads outside the breeding season (Farner and Follett 1966). All sexual activities including song are arrested until the next breeding season. In zebra finches, however, there is no regression of the gonads due to tonic gonadotrophic activity of the hypothalamo-hypophysial system (Farner and Serventy 1960). The zebra finch sings and courts throughout the year and this is a great advantage where breeding seasons are irregular: the birds are "always ready for action" and can begin breeding as soon as conditions become favourable. When they are not breeding zebra finches live in mixed flocks (Immelmann 1962). As a consequence of their frequent and close contact with other species it may be important for the young to acquire species-specific song immediately after fledging.

The function of song may also influence the timing of the sensitive phase and choice of song tutor. In some species it may be beneficial for a territorial male to learn from his neighbours at the time of territory establishment (eg. Payne 1982 for Indigo buntings, *Passerina cyanea*; McGregor and Krebs 1982 for Great tits). For song to be used in kin recognition amongst males a bird would need to learn his father's song and use this as a standard for assessing song elements in common with other males. In zebra finches the function of song is primarily sexual and it might be important for both sexes to learn song from the father early in life to ensure optimal outbreeding (Bateson 1982, Miller 1979b, Chapter 3).

The timing of the sensitive phase is not always simply age dependent. In the wild, environmental factors such as daylength (Kroodsma and Pickert 1980 for marsh wrens, *Cistothorax palustris*) and the sound of other singing birds in the neighbourhood (Baptista 1972 for the wild house finch, *Carpodacus mexicanus*) can play an important role. For zebra finches suitable experience, rather than age, is the most important factor determining the timing of the sensitive phase: birds exposed to poor song, or deprived of any song, can learn later in life should a suitable opportunity arise (Eales 1985b, Chapter 9).

This flexibility in song learning provides a safeguard for birds who fail to experience normal conspecific song during the juvenile period, the young remaining open to learning until appropriate experience has been acquired.

In most species constraints on learning ensure that in nature only the correct species song is produced. There appear to be two mechanisms by which this can be achieved: a tendency to acquire vocalizations of a certain tonal structure and quality eg. chaffinch, *Fringilla coelebs* (Thorpe 1958) and white-crowned sparrow (Marler 1970); and a tendency to learn from the male by whom the youngster was reared eg. Bullfinch, *Pyrrhula pyrrhula* (Nicolai 1959), Bengalese finch, *Lonchura striata var. domestica* (Dietrich 1980) and zebra finch (Immelmann 1969).

A young zebra finch will learn the father's song provided he can interact closely with his father throughout development (Immelmann 1969). In his absence the young bird will learn just as readily from another male he can see and hear. Eales (1985b) removed young males from their father at various stages during the sensitive phase (35-65 days of age). Those isolated at 50 days learnt more song elements during the first half of their sensitive phase but those given a new model at 50 days learnt more from the tutor presented in the second half. The young bird may learn the general form of song to copy from the male who reared him, but this may be modified by song heard in the second half of the sensitive phase when the young male is most rapidly developing his song output.

Parental influences appear to be important in governing the young male's appropriate choice of song model. If the father is still present a youngster will not learn from another male, irrespective of song output (Böhner 1983). Female-raised zebra finches which can interact with their father and another male from thirty-five days of age reproduce their father's song elements if their mother is still present which suggests that the mother may direct the young bird's choice of tutor (Eales 1987b).

In the wild young zebra finches become independent at about 5 weeks old. From then on, during the sensitive phase for song learning, they associate predominantly with other juveniles within the flock (Immelmann 1962). Nonetheless, experience before independence may affect tutor choice. Chapter 3 considers the question of song tutor choice by providing young males with the opportunity to learn from two conspecific song tutors at independence. Female-raised zebra finches are given the choice of two unrelated tutors and normally-raised males are housed with an unrelated male and one whose song is similar to that of the father. The tendency to copy from a tutor with a similar song to the father depends on the young bird being able to recognise his father's song before independence. In Chapter 4 male and female zebra finches are tested for their ability to learn some characteristics of their father's song at various stages prior to independence.

It is becoming increasingly apparent that visual and behavioural factors can be very important and the method of song model presentation plays a critical role in determining what is learnt and from whom (e.g. Kroodsma and Pickert 1984; Payne 1981; Todt et al

1979). In zebra finches, physical contact with the song tutor is not required for song learning to proceed normally but vocal, and particularly visual, interactions are very important in determining what a young zebra finch male will learn and from whom (Eales 1985a; Price 1979). Chapters 7 and 8 investigate the role of visual and vocal cues in selecting which species to learn from. Chapter 7 examines the relative inportance of visual and vocal cues by giving young males the choice of two cross-fostered song tutors at independence, a zebra finch singing Bengalese finch song and a Bengalese finch singing zebra finch song. In Chapter 8 newly independent zebra finches are housed with two zebra finch song tutors, one who sings with a normal song and one who sings Bengalese finch song elements to see whether they specifically prefer a male with normal song.

Chapter 9 considers the influence of cross-fostering experience on the timing of song learning, by asking at what stage in development these experiences are most influential. Can zebra finches which have been housed with Bengalese finches during the time when normally-raised birds would learn their song, secondarily imprint on a conspecific song tutor? What is the effect of the experience prior to independence?

In Chapter 10 these questions are tackled from a different viewpoint by raising zebra finches and Bengalese finches with both species simultaneously. Who do these males copy song from? How important are the mother and father for subsequent song learning?

Imprinting is a phenomenon common to both song learning and the development of sexual preference. To what extent are the two processes similar? Chapter 11 considers the effects of cross-fostering experience on the development of sexual preference and examines the relationship between song learning and sexual imprinting by comparing the song learning data from Chapters 7, 9 and 10 with the mate preference results of these birds.

While there are a number of studies on zebra finch song learning, virtually nothing is known of Bengalese finch song development. For valid comparisons between the two species in the various cross-fostering regimes a knowledge of the similarities between the two species' song development is essential: this is discussed in Chapter 5, which looks at selective aspects of Bengalese finch development; and in Chapter 6 song learning in cross-fostered zebra finches and Bengalese finches are compared.

Crucial to all these studies is an understanding of the behaviour of the two species. The following chapter discusses the similarities and differences in parental behaviour and the effect that raising zebra finch chicks by the mother alone might have on subsequent song learning.

Chapter 2.

THE PARENTAL BEHAVIOUR OF ZEBRA FINCHES AND BENGALESE FINCHES.

ABSTRACT.

In this chapter the parental behaviour of zebra finches and Bengalese finches is compared. Bengalese finch chicks develop at a slower rate than zebra finch chicks: this includes subsong and may also include the onset of the sensitive period. However, both species produce full song at three months and learn from tutors presented at 35 to 70 days. The slower development of Bengalese finches is correlated with a lower percentage time parents spend feeding chicks and with less parental aggression (i.e. less encouragement to leave the nest).

Normal and paternally-deprived zebra finch chicks are also compared. When the male is removed the female attempts to compensate, especially for brooding, but the chicks receive considerably less food. Development is slower although the onset of subsong occurs at about the same time. In both groups birds learnt song from tutors presented at 35 to 70 days. Paternal deprivation appears to have little affect on song development but visual, vocal and behavioral stimuli from either or both parents may be important in tutor choice.

INTRODUCTION.

The Zebra Finch and its Breeding Biology.

The zebra finch is a very sociable species and large flocks can be seen throughout Australia (T.g. castonosis) and the Lesser Sundra Islands (T.g. guttata) where the birds breed colonially in response to rainfall (Bourke 1941). The flocks coalesce during the drier seasons at available water sites. In some parts of the range rain is unpredictable but zebra finches pair for life and are ready to breed all year round: this helps them exploit the ephemeral rainfalls (Immelmann 1962, 1965).

In the aviary, if given appropriate food and nest sites, they will breed every month and often a second clutch is laid as soon as the first nestlings have fledged. Young captive birds may begin breeding as early as eight weeks of age and yet many five year old birds will still breed regularly. This, coupled with their early song development, makes them the ideal subject for study.

The Bengalese Finch and its Breeding Biology.

The Bengalese finch is also an excellent subject for research, it is one of the hardiest and easiest to breed in the grassfinch family. It does not exist in the wild but is thought to be a domesticated form of the Striated finch, Lonchura striata, which has been kept in captivity for the last two hundred years (Eisner 1957).

METHODS.

Five pairs of Bengalese finches and five pairs of zebra finches were observed throughout the reproductive period. In addition four pairs of zebra finches were observed both during normal rearing and with the male removed when the chicks hatch.

Housing Conditions.

All the breeding birds were housed in the same room, so the chicks could hear many adults' songs, but each pair was housed in a separate cage (measuring 60cm x 45cm x 30cm). Each cage had 3 perches and a nest box measuring 11cm x 11cm x 11cm, partially filled with hay. Fresh nesting material was given daily during the egg laying period. After egg laying the amount of fresh hay was limited to avoid "egg layering", common in captive birds.

Daylight hours were extended by artificial lighting from 05.00-20.30 hours and a temperature of 20-25° C was maintained. The birds were given bathing water, cuttlebone, grit, fresh drinking water, Haith's Foreign Finch seed, egg biscuit mix and lettuce. As parental feeding often does not begin until the second or third day posthatch the chicks were hand-fed with egg biscuit mix until parental feeding started. Removal of the male often resulted in delayed or arrested feeding and in these cases hand-feeding continued until the female resumed feeding.

Observations.

Two half hourly periods of observations were made at the same time each day, at least one hour after the nests had been examined and food and water had been refreshed.

The behaviour of each pair was recorded with "on the dot sampling" every 30 seconds to reveal changes in parental behaviour on a day to day basis throughout the cycle. This method of sampling gives a good measure of time spent in different activities (Altmann 1974).

RESULTS.

(A). A Comparative Study of the Breeding biology of Zebra Finches+Bengalese finches.

Figs. 2.1-2.6 summarize the main results. The mean period of Egg-laying, Incubation, Fledging, and onset of parental aggression and subsong are shown for each pair in table 2.I.

Courtship.

In the initial phase of zebra finch courtship the male and female fly rapidly from perch to perch, frequently beak-wiping and orienting their tail plumage towards each other. After several jumps the female stops and the male advances towards her in a rhythmic pivoting dance. The male adopts a fluffed out posture: the crown feathers are depressed and head feathers raised to display the black and white face markings and chestnut ear patches to the female (fig. 2.7). A receptive female assumes a horizontal position and begins tail quivering. Copulation then occurs. The whole sequence, including copulation may be repeated several times. After dismounting rapid preening is usually seen (Morris 1954).

Courtship in the Bengalese finch is similar but the male's tail is raised slightly. A further difference is the carrying of nest material during courtship (fig. 2.8). The male performs a pivoting dance, singing continuously but unlike the zebra finch courtseys are added to the dance in high intensity displays.

Nesting.

In Bengalese finches both male and female carry nest material to the nest but in zebra finches the male does most of the carrying. One male may carry as many as 630 pieces of grass in one hour (Immelmann 1983). Usually a nest requires about 400 pieces of grass. The nest chamber is often lined with feathers. In both species the male and female participate in nest construction (fig. 2.9).

Egg-laying.

Nestbuilding increases throughout the periods of Egg-laying and incubation. In zebra finches 4 to 6 eggs are usually laid, glazed white with a blueish tinge. Clutch size is more variable in Bengalese finches: 2 to 9 glazed white eggs may be laid.

Incubation.

Fertile zebra finch eggs hatch in 12 to 14 days, incubation beginning when the third or fourth egg has been laid (Immelmann 1965). The incubation period for Bengalese finches is slightly longer (mean = 16.4 days). Females spend more time incubating than males ($U=0$, $n_1=5$, $n_2=5$, $P<0.01$ for zebra finches; $U=3$, $n_1=5$, $n_2=5$, $P<0.05$ for Bengalese finches) and Bengalese finches spend more time sitting in the nest than zebra finches, particularly the male ($U=1$, $n_1=5$, $n_2=5$, $P<0.01$ for males; $U=2$, $n_1=5$, $n_2=5$, $P<0.05$).

Hatching - Prefledge.

Singing and nestbuilding rapidly decrease once the eggs hatch. Both sexes help rear the young. Zebra finches usually start feeding the chicks when the first chick begins to make begging calls, at 2 or 3 days old. In Bengalese finches it usually occurs a day later. Zebra finches spend a higher percentage of the time feeding chicks in the first 20 days posthatch (Ten Cate 1982; pers. obs.).

Conspicuous mouth markings guide the parents in feeding the brood (fig 2.10). Initially the chicks orient their open gapes upward, but at about 8 days of age their eyes open and nestlings beg at their parents (Muller and Smith 1978). In zebra finches this is accompanied by a lateral wagging of the tongue. Bengalese finch chicks are much less active and do not beg as frequently.

Begging calls become increasingly louder. Initially only the nestling who is being fed vocalizes and only while being fed. From day 4 to 12 all nestlings vocalise during feeding bouts and after 10 days they may continue calling after the feeding has finished. At about 14 days, the nestlings also vocalise prior to feeding when a parent comes into the nest (Eisner 1960; Muller and Smith 1978).

In the first week the nest site is rarely left unattended. In zebra finches there is a sudden decrease in the time spent in the nest after 7 to 10 days. In Bengalese finches the change is more gradual, taking place at about 11 to 14 days posthatch. One possible reason for this difference is that Bengalese finch chicks have less down and would therefore lose heat more quickly.

The chicks' food consumption increases, reaching a maximum at 14 days in zebra finches and 16 days in Bengalese finches, and then decreases with the rate of chick growth.

Fledging - Independence.

Zebra finch chicks fledge at about 19 days of age: parental care (i.e. brooding and feeding the chicks) becomes more intense at this time (see Ten Cate 1982) and the young continue to depend on their parents for at least another 10 days.

Bengalese finches fledge around day 24. Unlike zebra finches, they spend only short periods outside the nest at first. By day 27 in zebra finches, and day 34 in Bengalese finches, the chicks are capable of feeding themselves. At this stage they are still vulnerable to predation and attack by conspecific adults so their parents sit close to them. Zebra finch chicks stop clumping with their parents by 30 days of age (Ten Cate 1982). Clumping behaviour is much more prevalent in Bengalese finches and the chicks clump with their parents for much longer (Ten Cate 1982).

Zebra finches are more aggressive both to other adults and towards their young (Ten Cate 1982, pers.obs.). Parental aggression coincides with the start of incubation of the next clutch, at about day 27 in zebra finches and seven to ten days later in Bengalese finches. There is a conflict between allocating time to feeding the older clutch and incubating the new eggs. Often the male continues feeding the chicks while the female spends a greater proportion of her time incubating the new clutch. In addition there is a parent-infant conflict in which parents attempt to maximise their parental investment in each successive clutch whilst the young persistently beg for food, sometimes several days after the parents have ceased responding (Muller and Smith 1978).

The amount of father's song the chicks hear varies from clutch to clutch. In some zebra finch pairs the male's maximum song output occurred before the clutch had fledged; in all the Bengalese finch pairs the male did not begin to court and mate until after fledging.

In zebra finches subsong usually begins at about 27 days of age and full song is complete by three months but there is considerable variation both in the timing and the song output and some males have been observed subsinging at 19 days of age (Böhner, pers. comm.). Bengalese finch subsong is also variable, beginning when the bird is about 32 days old. It starts as a very quiet whisper (Eisner 1960) but gradually the song becomes louder, with a fuller tone. Initially the bird adopts a stretched, upright position without the ruffled abdominal feathers and raised tail but by three months full song development is complete and the bird adopts the adult posture.

(B). The Effect of Paternal Deprivation on Zebra Finch Development.

A comparison is made of the behaviour of four pairs of zebra finches under two conditions: group A chicks remained with both parents until independence; in group B the father was removed on the fourth day, before the fourth chick hatched.

Hatching to Pre-fledging.

In group B the female spends twice as much time sitting in the nest. Group B females also spend more time feeding their chicks, and as a consequence, feeding themselves, but the increase is less marked and the chicks may receive as little as half the food (in terms of percentage time parents spend feeding their chicks) of normally-raised chicks (figs. 2.11 and 2.12).

After seven to ten days the time spent in the nest decreases markedly for all pairs in group A. Group B females also spend less time in the nest once the chicks are over a week old but the decline is much more gradual.

Chicks raised by their mother alone develop more slowly, presumably as a consequence of receiving less food and warmth. The mean fledging age is 20.4 days in group A and 23.6 days in group B.

Fledging - Independence.

Once the chicks have fledged all pairs in group A spend an increasing proportion of their time in the nest preparing for their second clutch. Rebuilding of the nest may also occur at this stage. Egg-laying is resumed on day 22 or 23 posthatch and incubation usually begins about 24 hours later. The onset of parental aggression occurs later (mean onset for pecking by the mother is day 25 for group A and day 30 for group B; mean onset for the female driving away the chicks is day 28 for group A and day 33 for group B) and the mother shows less aggression.

In group A the amount of time the father spends singing increases at about the time of fledging although there is considerable variation between pairs. Since the male is removed in group B these chicks are not presented with the opportunity to hear their father's song. In both cases the chicks began subsong at 27 to 35 days of age and all learnt song elements from male tutors presented at 35 to 70 days posthatch, the parent(s) having been removed (see Chapter 3).

DISCUSSION.

(A). A Comparison of the Parental Behaviour of Bengalese Finches and Zebra Finches: Its Effects on Song Development.

The results of this study show that the two species have similar breeding patterns but Bengalese finches tend to develop more slowly and receive less parental care during the first 20 days of life than zebra finches. Bengalese finch parents are less aggressive to their chicks, particularly in the period between fledging and independence.

As a result, Bengalese finch song development may also occur slightly later. The onset of subsong is variable in both species but seems to start about three days later in Bengalese finches. The sensitive period for song learning might also be delayed although the results in chapter 5 suggest that song learning is complete by 70 days in both species.

Inter-specific behavioural differences may also affect tutor choice. Ten Cate, Los and Schilperoord (1984) found that parental aggression played an important role in governing a young bird's choice of mate. The results of zebra finch tutor choice in Chapter 3 support this. In Bengalese finches, where less aggression is seen, the relative weights for tutor choice criteria may be different.

Nonetheless both species have similar patterns of development in which parental influence is likely to be very important in song development. In both species, if the father is present a youngster will not learn song from another male (Böhner 1983; Dietrich 1980). It seems very probable that maternal influence is also important in both species (see Eales 1987a for zebra finches).

(B). Paternal Deprivation: Its Effects on Song Development.

Removal of the father has a significant effect on the behaviour of both the mother and the chicks: this may affect song development. The female spends almost twice as much time in the nest. She also spends more time feeding the chicks but the increase is less marked and varies greatly between females. Chick development is slower and the chicks fledge about two days later.

Group B chicks are not exposed to any adult song until 35 days but subsong occurs at about the same time, and since the sensitive period does not occur until then, paternal deprivation is unlikely to affect song development. Nonetheless the visual, vocal and behavioural stimuli to which the chicks are exposed prior to independence may influence a young male's choice of song tutor. Both the amount and onset of parental aggression is markedly less in chicks raised by their mother alone: this might affect tutor choice.

(C). Relevance to the Behaviour of Wild Zebra Finches: a Cautionary Note.

Zebra finches have been bred in captivity for nearly 200 years. This has led to changes in their behaviour and physiology, with important consequences for song learning (Sossinka 1970). Although there are no significant differences in clutch size, incubation or feeding chicks, in domesticated birds gonad development is considerably slower, the male shows less sexual activity and there is a delay in the female's response to breeding when conditions become favourable. In captivity selection to be "ready for action" is reduced because reproduction can occur at any time.

In addition to changes in sexual development laboratory birds show increased contact behaviour as a result of confined space. This may also affect song learning, particularly tutor choice. In the wild chicks experience parental contact prior to independence because separate nests are available for parents to sleep in (Immelmann 1962) and adults can avoid contact so the amount of aggression and preening is lower (Eales 1985a).

As a result of these differences caution is required in relating the behaviour of laboratory stocks to wild birds. Nonetheless, song learning studies of both wild and captive birds should consider parental behaviour because differences in rearing are likely to have a substantial effect on what a young male will learn, when and from whom.

TABLE 2.I: Results of the parental behaviour study for five pairs of zebra finches and five pairs of Bengalese finches.

Z pair	Egg laying period (days)	Incubation period (days)	No. chicks hatched	Age at fledging (days)	Onset of parental aggression		Start of subsong (days)
					pecks	chases	
R+M	6	14	6	20	25 27	25 27	25
T+J	3	12	3	21	23 27	27 27	30
Z+Z	6	12	6	20	25 25	25 26	22
P+P	3	13	1	19	25 24	25 31	29
M+M	4	13	4	18	25 26	26 26	27
B pair							
WBD	6	14	5	26	36 37	36 37	31
DD	6	16	5	25	30 31	32 35	32
BB	4	16	1	24	32 30	- -	35
TT	4	18	1	25	34 33	37 37	34
QKY	7	18	6	23	33 32	36 34	30

Figure 2.1:

The percentage time the male and female spend in the nest and the total time the nest is occupied throughout the breeding period for two typical pairs of zebra finches, P + P and T + J.

Key:-

EL Period of egg-laying.

I Incubarion period.

H Hatching period.

F Fledging period.

FIG 2·I

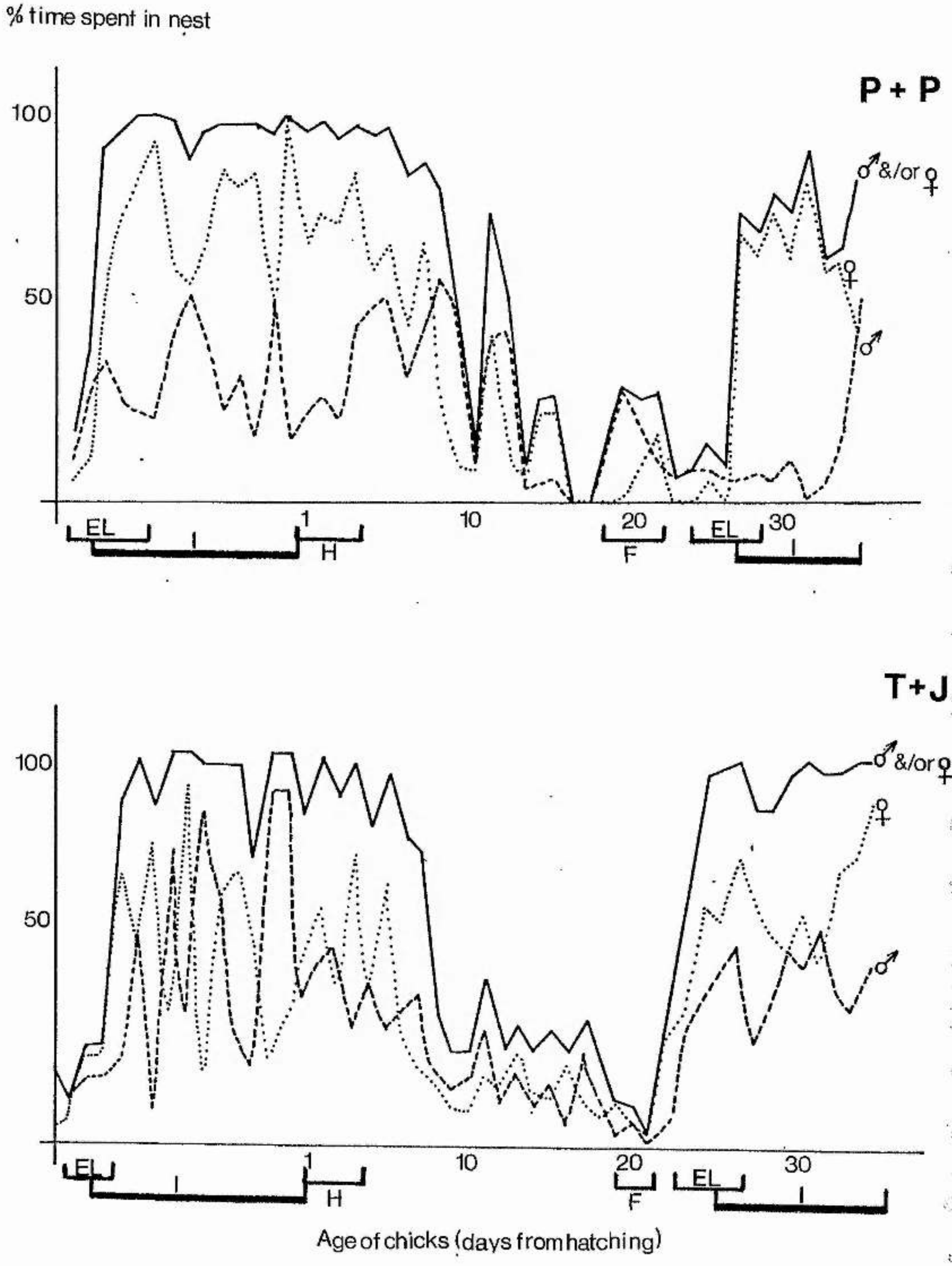

% time spent in nest
P + P
100
50
♂&/or ♀
♀
♂
EL
I
1
H
10
20
F
EL
30
I
T+J
100
50
♂&/or ♀
♀
♂
EL
I
1
H
10
20
F
EL
30
I
Age of chicks (days from hatching)

Figure 2.2:

The percentage time the male and female spend in the nest and the total time the nest is occupied throughout the breeding period for two typical pairs of Bengalese finches, QKY and DD.

FIG 2·2

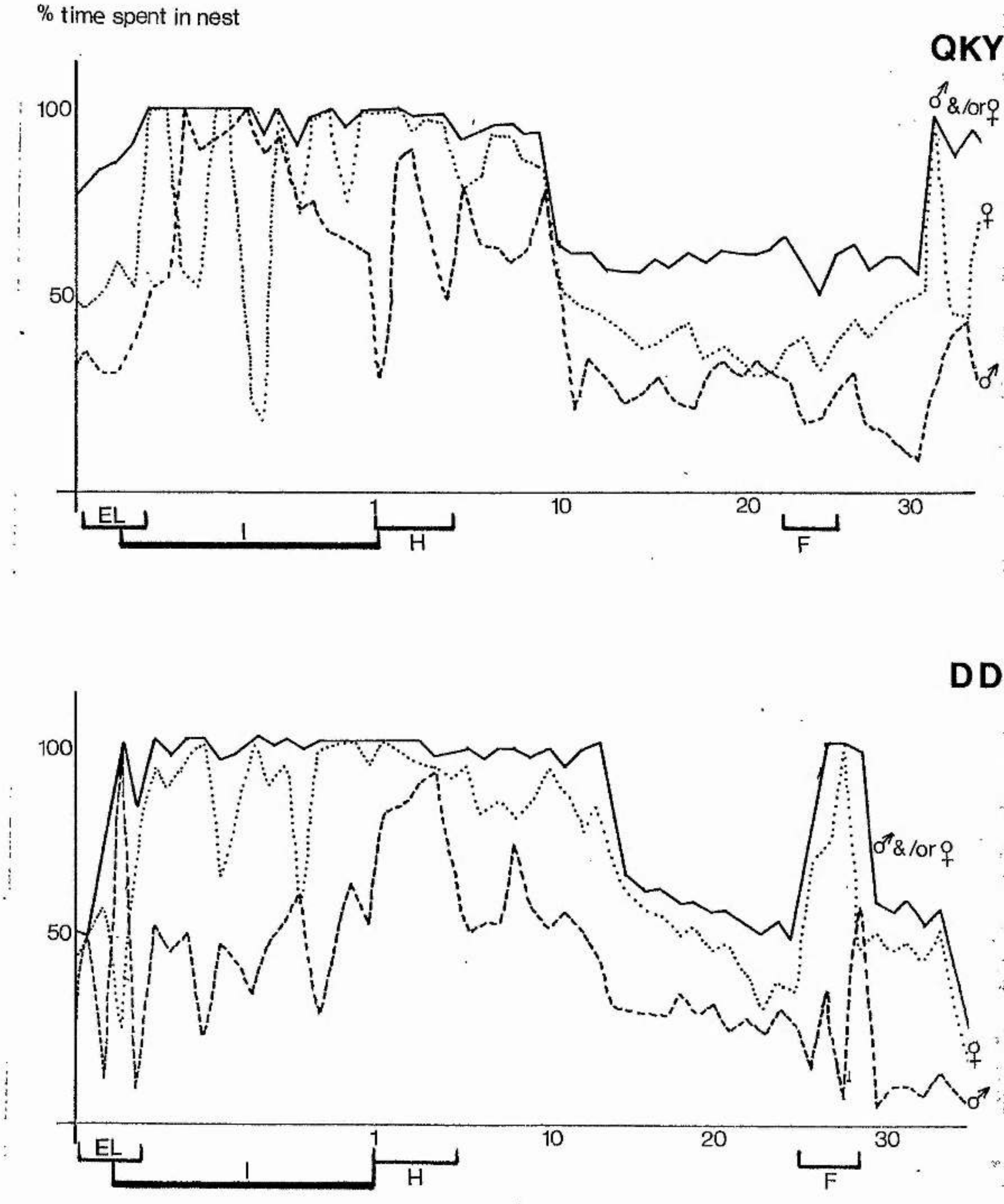

% time spent in nest
QKY
100
50
♂&/or♀
♀
♂
1
10
20
30
EL
I
H
F
DD
100
50
♂&/or♀
♀
♂
1
10
20
30
EL
I
H
F
Age of chicks (days from hatching)

Figure 2.3:

The percentage time two zebra finch males spend singing, Z + Z and T + J.

FIG 2·3

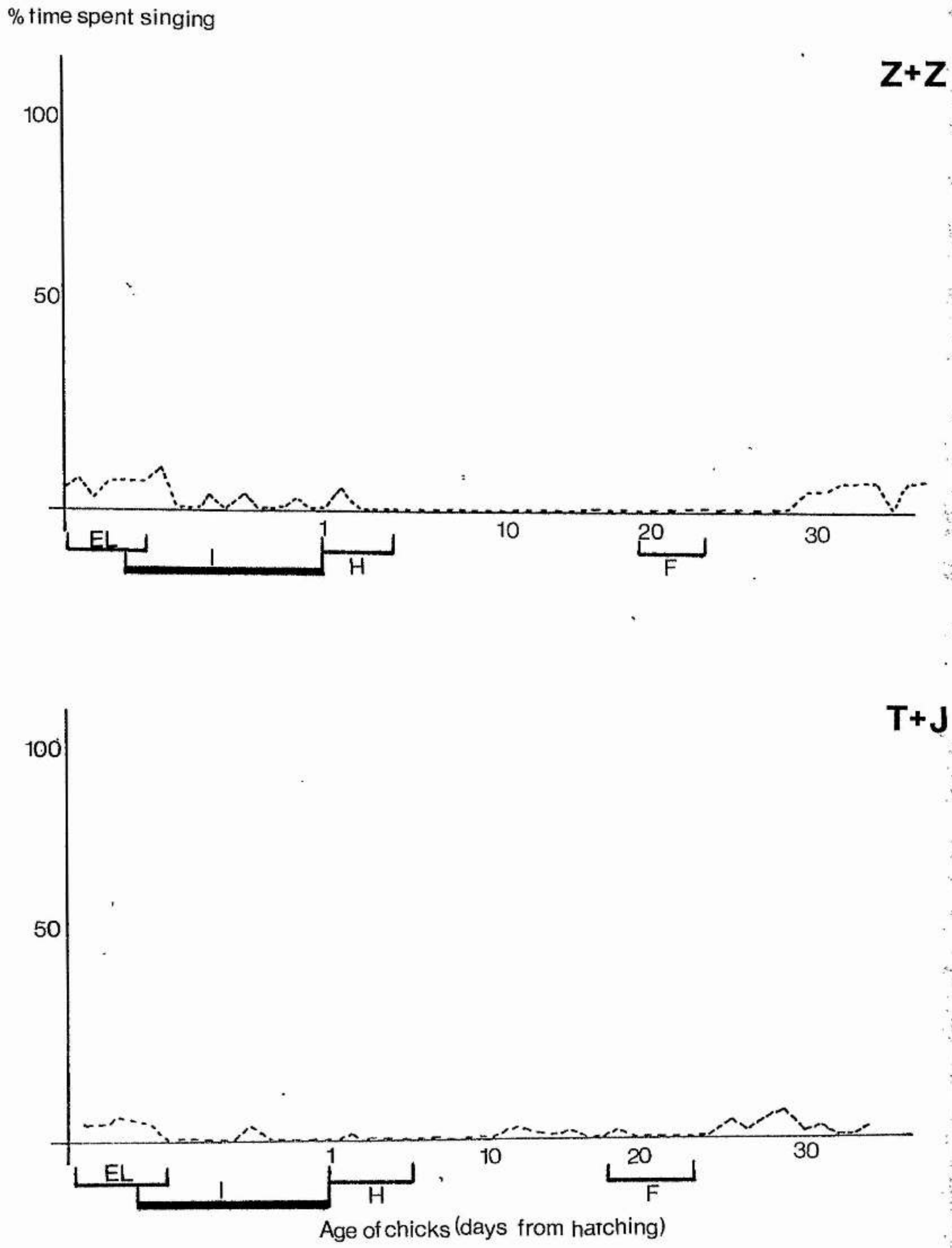

% time spent singing
Z+Z
100
50
1
10
20
30
EL
I
H
F
T+J
100
50
1
10
20
30
EL
I
H
F
Age of chicks (days from hatching)

Figure 2.4:

The percentage time two typical Bengalese finch males spend singing, TT and BB.

FIG 2·4

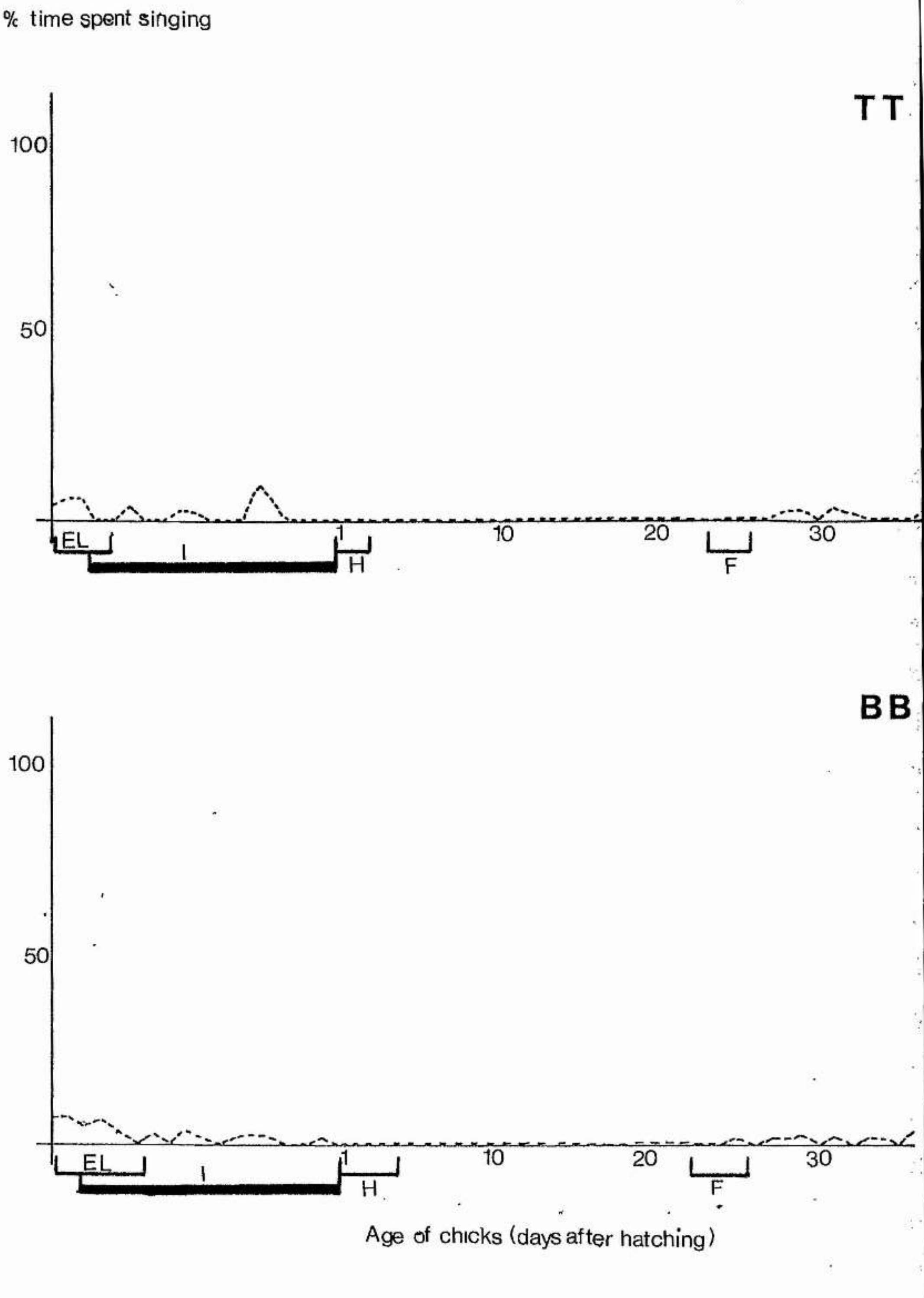
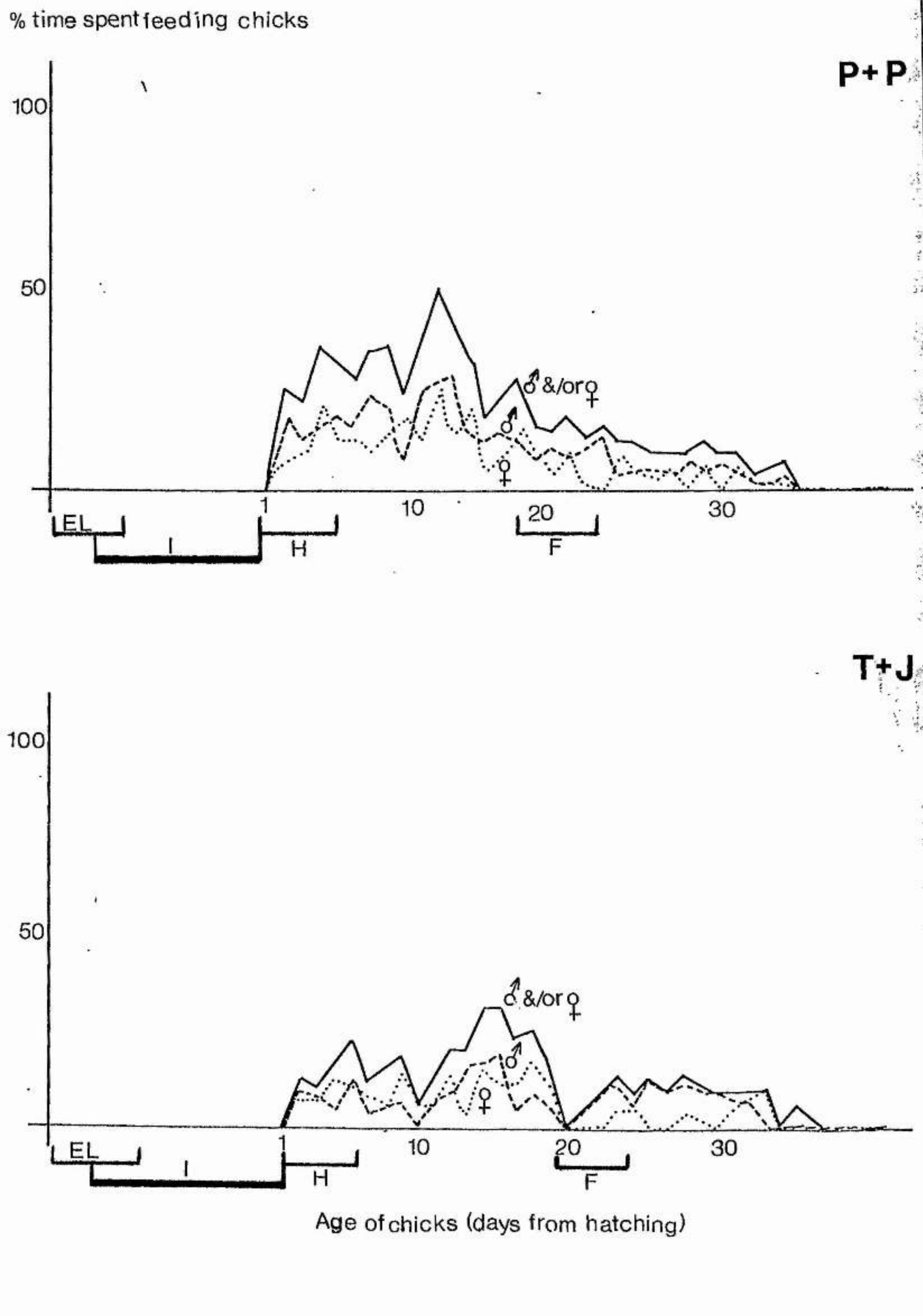

% time spent singing
TT
100
50
EL
I
1
H
10
20
F
30
BB
100
50
EL
I
1
H
10
20
F
30
Age of chicks (days after hatching)

Figure 2.5:

The percentage time two typical pairs of zebra finches spend feeding their chicks, P + P and T + J.

FIG 2·5


% time spent feeding chicks
100
50
♂&/or♀
♂
♀
1
10
20
30
EL
I
H
F
100
50
♂&/or♀
♂
♀
1
10
20
30
EL
I
H
F
Age of chicks (days from hatching)

P+P

T+J

FIG 2·6

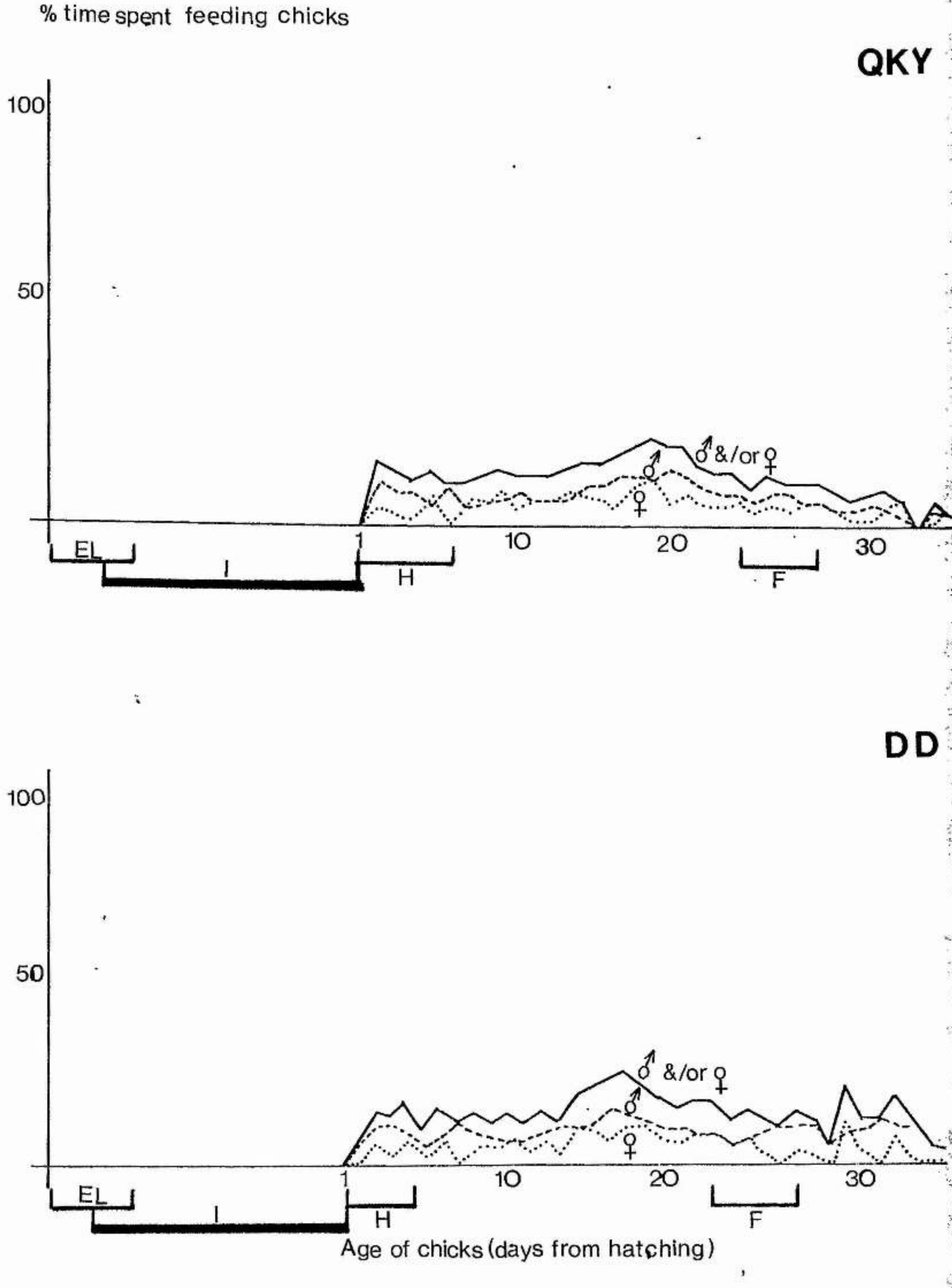

% time spent feeding chicks
QKY
100
50
♂ &/or ♀
♂
♀
1
10
20
30
EL
I
H
F
DD
100
50
♂ &/or ♀
♂
♀
1
10
20
30
EL
I
H
F
Age of chicks (days from hatching)

Figure 2.6:

The percentage time two pairs of typical Bengalese finches spend feeding their chicks, QKY and DD.

Figure 2.7:

During the courtship dance the male zebra finch sings almost continuously to the female. If the female is receptive she solicits to her mate.

FIG 2·7

ZEBRA FINCH COURTSHIP

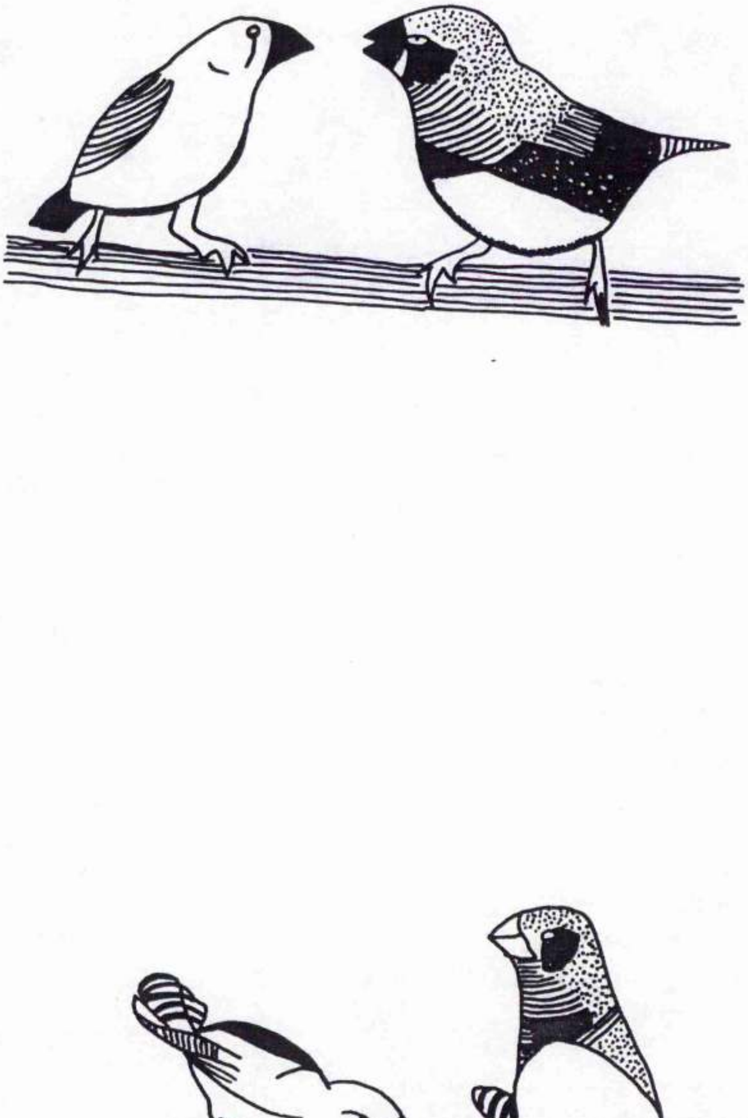
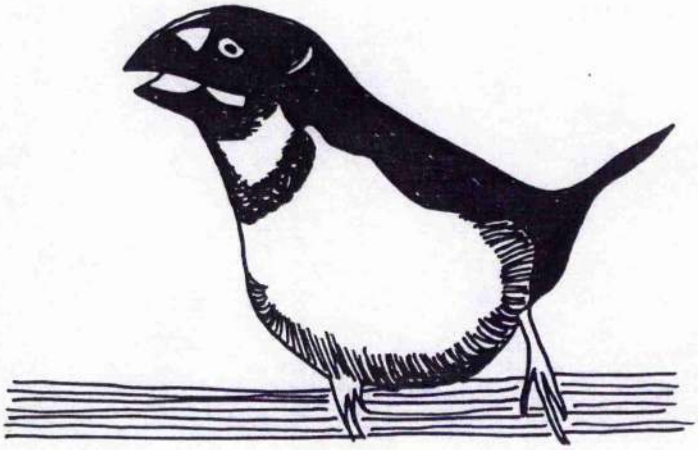


Figure 2.8:

The Bengalese finch male during courtship. As part of the courtship ceremony the Bengalese finch male carries a blade of grass. His mate sits on the perch below.

FIG 2·8

BENGALESE FINCH COURTSHIP



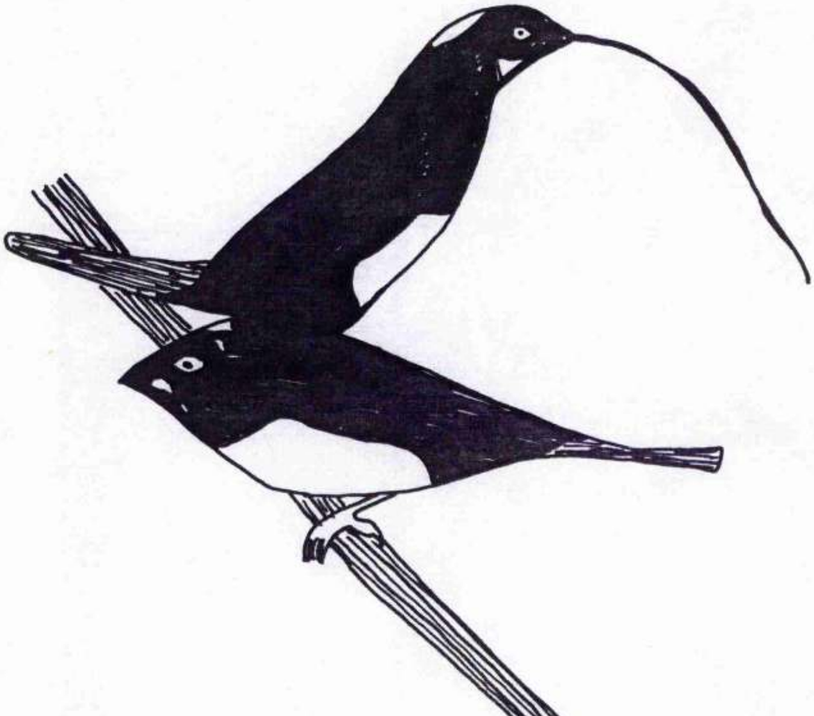
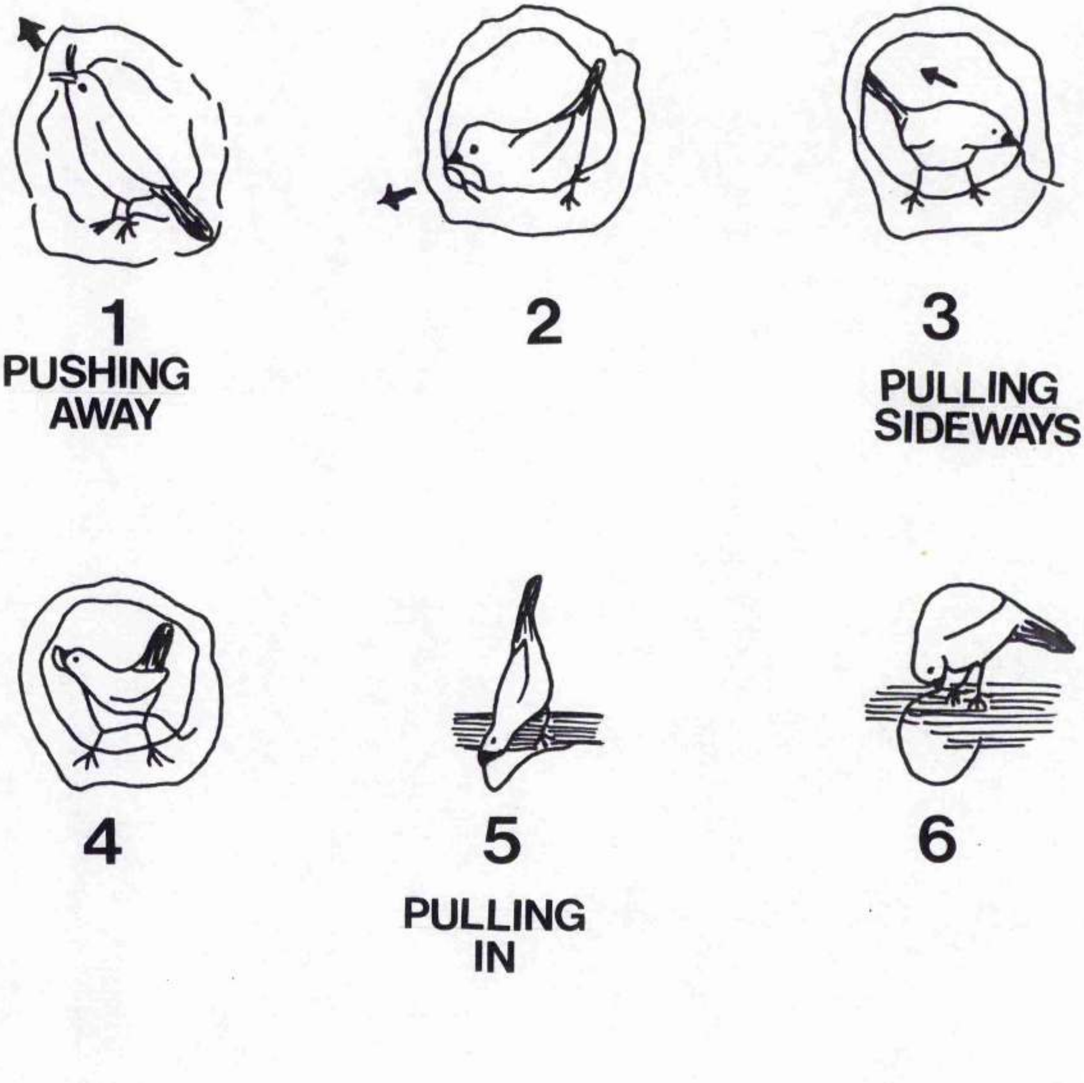


Figure 2.9:

The sequence of nest building behaviour in Estrildid finches.

FIG 2·9

NEST-BUILDING



1 PUSHING AWAY

2

3 PULLING SIDEWAYS

4

5 PULLING IN

6

(AFTER KUNKEL).

Figure 2.10:

Mouth markings in zebra finch chicks consist of a domino pattern of black dots on the palate.

In Bengalese finches the yellow palate has a black horse shoe mark and a pair of smaller black dots below. The pattern is quite variable: the darker the plumage the more complete the markings (Eisner 1960; pers. obs.).

FIG 2·10

MOUTH MARKINGS

ZEBRA FINCH

VARIATION IN BENGALESE FINCHES

DARK PLUMAGE - HORSESHOE
COMPLETE

INTERMEDIATE - INCOMPLETE
HORSESHOE

PALE PLUMAGE - MARKS
ABSENT

Figure 2.11:

Graphs of the percentage time zebra finches (Z + Z) from group A and B spend in the nest throughout the breeding cycle.

FIG 2·II

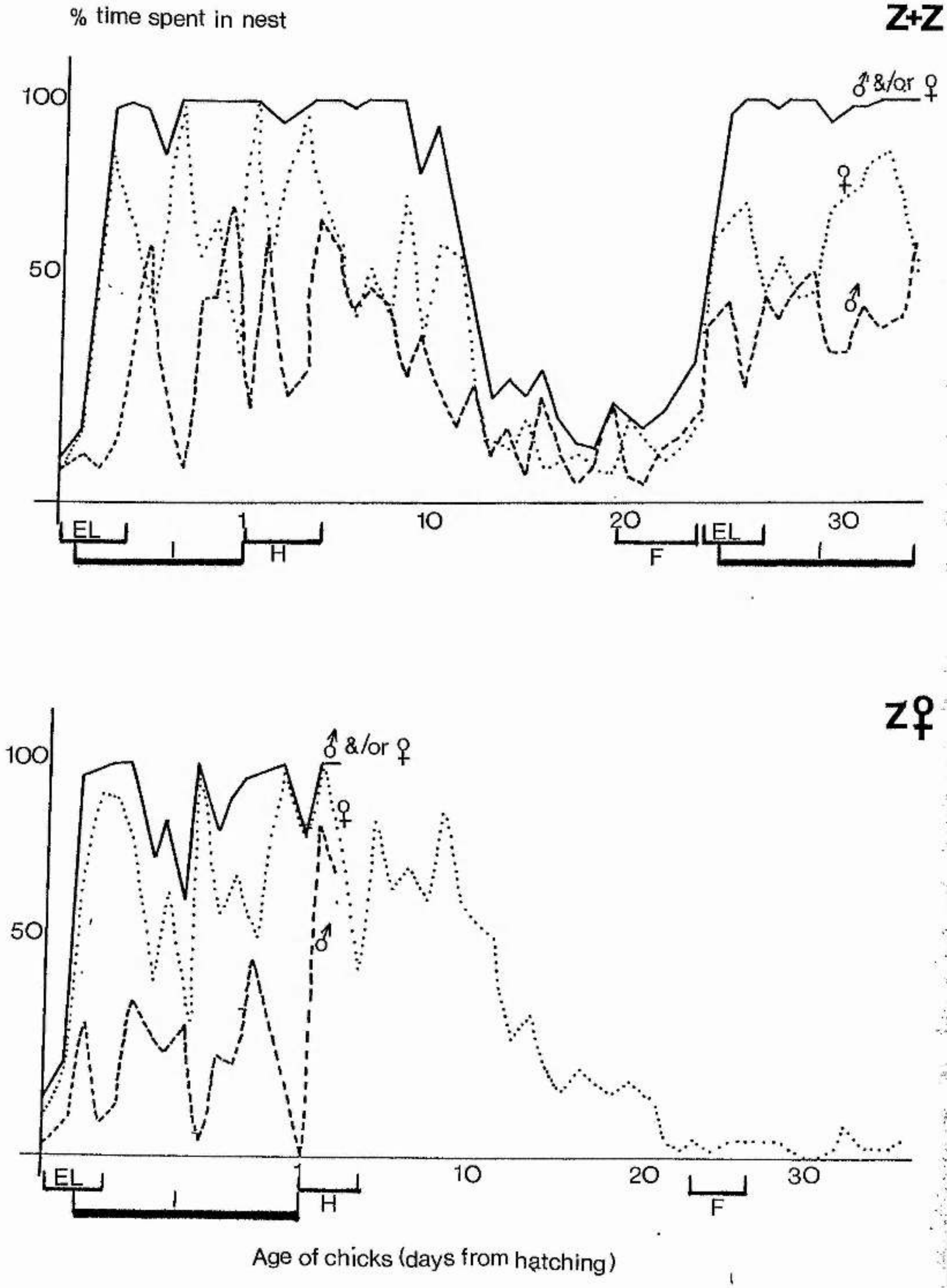
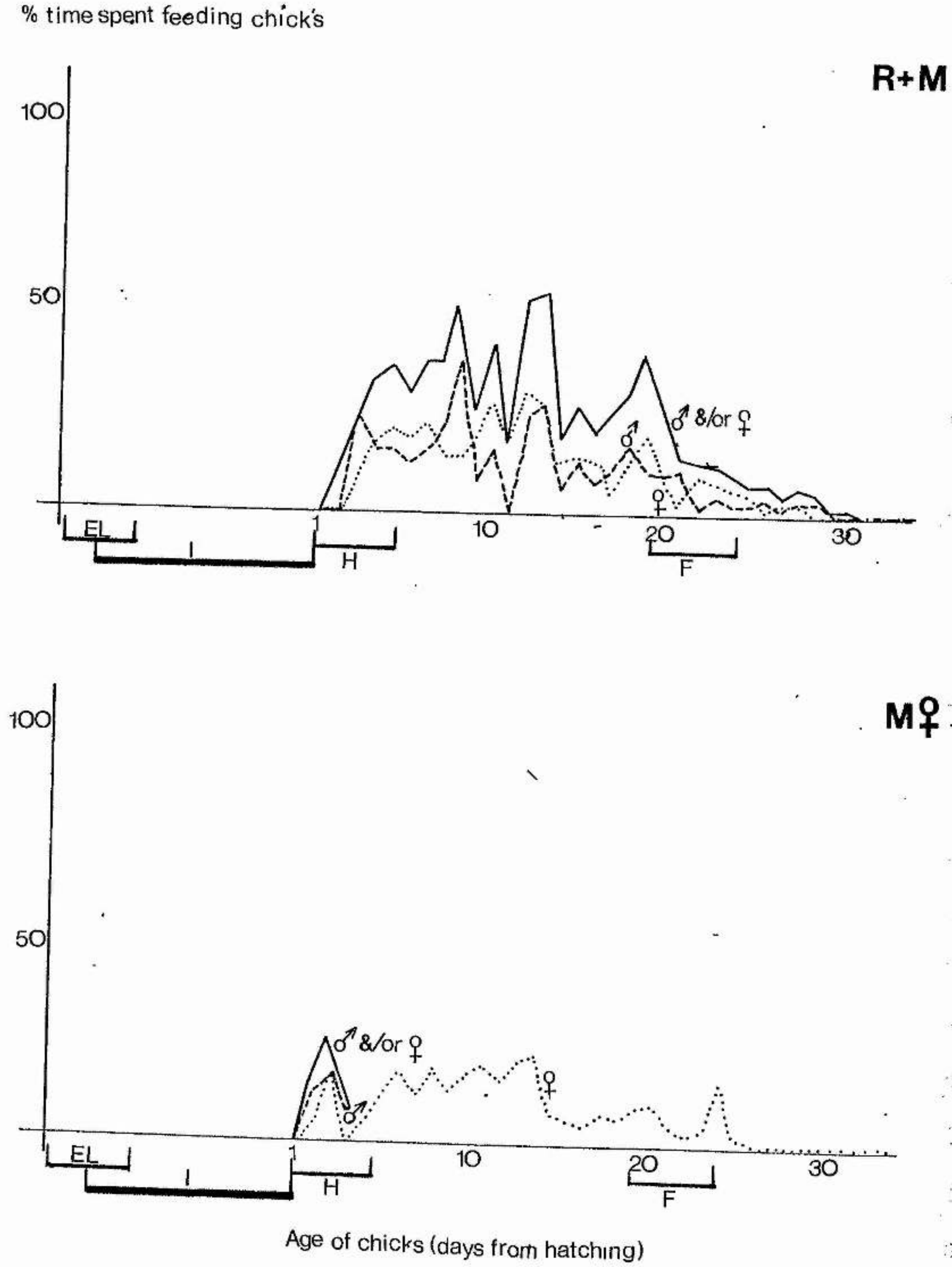

% time spent in nest
Z+Z
100
50
♂ &/or ♀
♀
♂
EL
I
1
H
10
20
F
EL
30
I
Z♀
100
50
♂ &/or ♀
♀
♂
EL
I
1
H
10
20
F
30
Age of chicks (days from hatching)

Figure 2.12:

The percentage time typical group A and B zebra finches (R + M) spend feeding their chicks.

FIG 2·12


% time spent feeding chick's
R+M
100
50
♂ &/or ♀
♂
♀
EL
I
1
H
10
20
F
30
M♀
100
50
♂ &/or ♀
♂
♀
EL
I
1
H
10
20
F
30
Age of chicks (days from hatching)

Chapter 3.

HOW DO ZEBRA FINCHES CHOOSE THEIR SONG TUTORS?

ABSTRACT.

This chapter considers the question of song tutor choice in zebra finches. Males selectively learn song elements from one tutor when given a choice of two. In zebra finches raised by their mother alone behavioural differences between song tutors appear to be important in tutor choice: young males prefer to learn from the tutor who is most aggressive towards them. Paternal influence is also extremely important and normally-raised males selectively learn from tutors with similar songs to their father. This could provide a cue for optimal outbreeding if females were to select mates on the basis of song similarity to their father.

Based on a paper in Anim. Behav., 35, 714-721.

INTRODUCTION.

In most species of songbird, including the zebra finch constraints on song learning guarantee that, in the wild, only the song of conspecifics is chosen as a model from which to learn. The specificity of these constraints varies considerably between species and the criteria employed presumably depend on how likely a bird is to be misled in its natural environment.

Selectivity may operate on the structural and temporal organization of song. Swamp sparrows, Melospiza georgiana, will only learn the syllables of their own species but learn these even if they are presented in song sparrow patterns whereas song sparrows, M. melodia, will learn either species' song syllables provided they are organized in the species-specific pattern (Marler and Peters 1977, 1981).

In other species it seems to be the social context which ensures that only the species-specific pattern is learnt. Whether a young male learns from neighbours or from his father is likely to depend on the main function the song performs and on the opportunities the bird has for learning. In some territorial species young males may copy their neighbours' songs at the time of territory establishment e.g. saddlebacks, Philesturnus carunculatus (Jenkins 1978). The adaptive significance of this is probably in song matching, enabling the bird to produce distinctive cues which would enable neighbours to distinguish it from intruders and so defend the territory accordingly (Payne 1981; Falls et al 1982). In non-territorial species the young male may learn from his father or from other conspecific males with whom he associates after independence. In species such as the zebra finch, with early sexual maturity, it is advantageous for young birds to acquire species-specific song immediately after fledging, before they begin to breed. Young zebra finch males will learn from their father if he is present throughout their development (Immelmann 1967, 1969). Females can also discriminate between their father and another male on the basis of song (Miller 1979a) and it is possible that variation in song could be used as a cue to ensure optimal outbreeding (Bateson 1983).

Captive zebra finches presented with two song tutors at independence, the father and another male, only learn their father's song irrespective of song output (Böhner 1983). In the wild, however, zebra finches gain independence after five weeks and from then on associate mainly with other juveniles and non-breeding adults in the flock (Immelmann 1962). This coincides with the sensitive phase for song learning and, since the father usually sings very little until this time (Chapter 2), it seems unlikely that a young male would have the opportunity to learn his father's song. Eales (1985b) has shown that if the father is removed at thirty-five days the young bird will copy the song of another male he can see and hear. This resurrects the question of from whom a young zebra finch would learn in the wild.

It seems possible that parents might direct a bird's choice of song tutor. In choice tests female-raised zebra finches selectively chose to learn song from the male who courted their mother, either because of his greater attractiveness to their mother, or because he was aggressive to them when they approached her (Eales 1987b). The father's vocalizations might also be important. If song acts as a marker for individual recognition and closely related males have a high proportion of song elements in common, then a young male might learn song from a male whose song is similar to his father's. For this to occur a young male would need to learn sufficient features of his father's song to enable him to discriminate between the father' song and that of another male, and, during the sensitive phase, learn from a song tutor accordingly. This study examines whether captive zebra finch males selectively learn song from the male with a similar song to their father, when given the choice of two song tutors.

Experiences which a young male encounters immediately after independence are also likely to be influential. Behavioural differences between two possible tutors, particularly dominance rank and aggression towards the chicks, may have an important role. To investigate this possibility zebra finches were given the choice of two song tutors at independence, having been raised with their mother only, so that there was no opportunity to learn song before independence or to be influenced by the father.The aim of this study was to determine which criteria a young male uses to select a suitable song tutor to learn from.

METHODS.

Birds and Housing Conditions.

Five broods of zebra finches were normally-raised by both parents until independence (NR group) and five broods were reared with their mother only, their father being removed before the fourth chick hatched (FR group). Some females were reluctant to stop brooding their chicks once the male had been removed so their chicks were hand fed until feeding was resumed. For the first ten days all the chicks were handled to control for human contact.

At independence (mean age of the young birds = 35 days) the males were removed and housed with two normally-raised zebra finch song tutors, one with fawn plumage and one with wild type (grey). All the song tutors had been used in previous studies of parental behaviour and were known to have normal song outputs. Each pair of song tutors was selected on the basis of song structure, i.e. with songs as different as possible, yet still representative of normal zebra finch song (see Sossinka and Böhner 1980). In the NR group one tutor (ts) had a high proportion of song elements in common with the young birds' father whereas the other tutor (TD) did not share any song elements with the father (see Table 3.I).

All the birds were housed in wooden, wire-fronted cages but after independence the tutors in the NR group were separated from each other and from the young males by wire mesh screens which divided the cages into three identical portions. Wire mesh prevents physical encounters but visual and vocal interaction is maintained, thereby permitting normal song learning to occur (see Eales 1987b).

Song Terminology and Method of Song Analysis.

Zebra finch males normally sing only one song phrase, which is usually repeated several times during a bout of singing. Within each phrase there are a number of different elements (4 - 11 in this study, mean = 8), usually sung in a fixed sequence. An element is the smallest continuous trace on a sonagram which is temporally distinct from neighbouring song elements. Occasionally two different elements were combined and learnt as one. These fused elements were scored as two separate elements since each occurred individually in the songs of other males with common song learning history.

The songs of both tutors and the young males were recorded with a Uher 4000 tape recorder at 4 months of age. At least ten song bouts per bird were analysed on a sound-spectrograph (Kay Digital Sonagraph 7800). The song structure of each pupil and his tutors were compared by making traces of typical song phrases and assessing the similarities in frequency pattern, modulation and length of song elements. This assessment was done blind: tutors' and pupils' songs were compared before the behavioural observations had been analysed.

Elements were classified as either common to both tutor and pupil or as unrelated in structure. In most cases the classification was not difficult. However, elements were not always copied accurately and males varied considerably in this respect. In Fig. 3.1 for example, element "d" in B258's song was copied more accurately by P3 than by P5. Nonetheless, the context in which these occur and their similarity in a number of respects suggests they are based upon the tutor element concerned, rather than improvised or based on other elements. Other zebra finch workers independently made the assessment and a high degree of inter-observer reliabilty was reach (90%). The amount of song a pupil learnt from his tutors was calculated in two ways: the proportion of song elements a bird learnt from each tutor and the proportion of each tutor's song the bird learnt. The first value was calculated as the number of different elements learnt from a tutor divided by the number of different elements in the young male's song. The second measure was the number of elements in the tutor's song that was learnt as a proportion of the number of elements each tutor sang in a typical song phrase.

Behavioural Observations.

Behavioural observations were made for two 30-minute periods each day to monitor interactions between the two tutors and their pupils for all ten clutches since behavioural differences between tutors might govern the pupil's selection of song elements to learn. The birds were colour-ringed to facilitate individual recognition, and the plumage type noted.

Physical encounters with all other birds in the cage were recorded continuously throughout each thirty-minute period. Clumping, preening, tutor aggression towards the young males (measured as the number of pecks and chases to each individual) were monitored. Dominance rank between tutors was determined by the number of aggressive attacks directed towards the other tutor. The song output for each tutor was calculated as the total number of song phrases recorded during the periods of observation.

RESULTS.

Tutor Choice.

The results in Tables 3.II and 3.III show that nine out of ten males in the NR group and all eleven young males in the FR group learnt song elements from only one of the song tutors but there was considerable variation in the proportion of elements copied. Fig. 3.1 shows the sonagrams of pupils P3 and P5 and their two song tutors in the FR group. Both of these pupils learnt song elements from B258 but none from B259. Fig. 3.2 shows the sonagrams of pupils P50 and P52 in the NR group. Both pupils learnt only from the tutor whose song was similar to their father's.

Choice Criteria.

To determine the criteria which a young male zebra finch uses in selecting a song tutor I examined three possible cues: visual imprinting on the mother, siblings or self; vocal differences between the two tutors and differences in the degree of physical interaction the two tutors had with their pupils.

(1). Visual imprinting:- Immelmann et al (1978) found that differences in plumage colour between wild type and white birds were important in zebra finch mate choice. Males visually imprint on the plumage of their parents and select a mate of the same type. Visual imprinting might also occur between fawn and wild type individuals.

For song learning, however, I found no evidence of visual imprinting to the mother (χ^2 test, ns). Similarly, sibling plumage colouration had no significant effect on tutor choice (χ^2 test, ns) and there was no evidence of auto-imprinting to plumage type (χ^2 test, ns).

(2). Vocal differences between tutors:- Differences between the two tutors in the number of different elements in a song phrase and song output, measured in terms of the number of singing bouts recorded in one hour's observations per day during the period of observations, were examined. Given that only tutors with normal song outputs were used in the experiments, variation within these limits did not affect a pupil's choice of song tutor (Wilcoxon test, ns); this confirms the results of Böhner (1983).

The number of song elements in the two tutor's song phrases does not appear to be important in tutor choice for either group or for both groups combined (Wilcoxon, ns).

For the normally-raised young males, however, element-type is important (χ^2=6.400, df=1, $P<0.05$). Nine out of ten males chose song elements common to TS and F; the other male sang a hybrid song composed of two original elements, two TD elements and two elements present in the songs of both TS and F. Only one bird sang an element peculiar to the father's song whereas five birds sang one or more elements which were specific to TS (see Table 3.III). This suggests that most of the elements common to TS and F were learnt from ts after independence; this agrees with Eales (1985b).

(3). Physical interactions:- Ten Cate et al (1984) found that zebra finches crossfostered by Bengalese finches were more likely to prefer a Bengalese finch mate if the foster-parents had been aggressive towards them. The results presented here for the FR group show that aggression is also important in song learning. All eleven pupils chose to learn from the tutor which was most aggressive towards them (χ^2=11.0, df=1, $P<0.001$), irrespective of the overall difference in amount of aggression displayed by the two tutors (χ^2 test, ns) or in their dominance ranking (χ^2 test, ns). In the NR group aggression was prevented by the wire partition.

Other physical interactions, i.e. preening and clumping, were examined but there was no evidence that they are important in tutor choice.

Although the amount of aggression directed towards the pupil is important in tutor choice there is no significant correlation between the level of tutor aggression and the amount of song learnt (Wilcoxon, ns). The latter may be a consequence of individual differences in learning capacity.

DISCUSSION.

The results of this experiment agree with those of Böhner (1983), that young zebra finch males tend to select one song tutor to learn from. In a large flock it may be easier for a young male to learn all his song from one male rather than producing a blend of elements from several males and, for species such as the zebrafinch, with an early sensitive phase, learning from a conspecific with whom the young male can visually and vocally interact may be the most economical way of achieving species-specific song.

Not all passerines select only one tutor for song learning. Territorial males may learn from several neighbours enabling a territory owner to match song types, distinguish neighbours from rivals and defend the territory accordingly (Lemon 1968). Neighbours often learn from each other and, when countersinging on territorial boundaries, they tend to match the song types they sing (e.g. Krebs, Ashcroft and van Orsdol 1981). In social species such as the zebra finch, where song matching is not important, there is unlikely to be selection for learning from a variety of song tutors.

Learning from only one song tutor might be a consequence of captivity. Confinement to cages results in increased contact between individuals. In addition to this caged zebra finches are denied the opportunity to mix with many different individuals. Immelmann (1962) found no evidence for zebra finch dialects in the wild and suggested this was due to extensive intermingling of flocks.

For captive zebra finches the behaviour of the tutors seems to be influential in guiding a young male's choice of song tutor. In the FR group where individuals could physically interact freely with each other young males appear to select a song tutor on the basis of aggression: the more aggressive a tutor is to his pupil the more likely the pupil is to learn from him. This is also true for indigo buntings where young males copy song from the tutor from whom they receive the greatest number of supplanting attacks (Payne 1981).

The use of aggression as a criterion for tutor choice might be an artefact of confined space in the laboratory. Levels of aggression are much lower in wild zebra finches, although the parents will drive their young away if they attempt to approach the new nest site once breeding has been resumed. Nonetheless for captive birds the results reported here indicate that it is not physical interactions in general but aggression specifically directed to the pupil that is important.

Correlation need not imply causation: pupil-directed aggression may be a consequence of tutor choice. A young male might choose a song tutor and interact more closely with him. As a consequence of the increased contact the tutor might direct more aggression towards the young male. Ten Cate (1986a) has observed "listening behaviour" in cross-fostered zebra finches: the birds follow the song tutor and turn their heads towards him. In normally-raised zebra finches, however, there is, as yet, no evidence of listening behaviour (ten Cate 1986a, pers. obs.), but further studies will be required to investigate this more fully.

However, aggression is not always a consequence of the young bird approaching the tutor: often the tutor will fly up to the pupil and peck him or drive him off the perch. So the most likely possibility is that the more aggressive a male is to the young male the more attention he will pay to him and as a consequence, the young male is likely to learn his song. A similar mechanism might also explain the results of Ten Cate et al (1984) on mate choice. Baptista and Petrinovich (1984) have also found that white-crowned sparrows learnt song from a strawberry finch, Amandava amandava, even if they could hear conspecific song, provided they could experience aggressive interactions with the strawberry finch song tutor.

In addition to behavioural interactions vocal cues are also important: young males prefer to learn from the tutor whose song is most similar to their father's. For zebra finches living in mixed species flocks this may be a way of ensuring species-specificity.

If closely-related males have similar songs then song could be used as a cue for mate choice to ensure assortative mating (see Bateson 1983). Young males need not learn song directly from their father provided they learn from a tutor whose song is similar. If this applies to zebra finches then, during the sensitive phase for song learning, a young bird should choose, from the other males in the flock, a tutor who shares a large proportion of song elements with the father. For optimal outbreeding a female should choose as her mate a male who sings a song slightly different from her father's. There is evidence (Miller 1979a) that female zebra finches can discriminate between their fathers' songs and those of other males. A young male would also need to learn some features of his father's song prior to independence.

An important point is that discriminating between a song that has been heard previously and one that has not might not require the same extent of learning as song copying. A bird might not even have to learn the entire song phase but might only select specific elements as markers for kin recognition. Zebra finches may learn to recognise a number of songs which they never normally sing. Indeed, the two types of learning may be quite different: this is the topic of the following chapter.

TABLE 3.I: No. elements in songs of tutors used for normally-raised zebra finches and the no shared between them.

Brood	No elements in song phrase			No shared elements in song phrase		
	F	TS	TD	F+TS	F+TD	TS+TD
1	11	11	11	7	0	0
2	11	11	4	7	0	0
3	8	8	6	6	0	0
4	10	10	11	9	0	0
5	10	9	13	9	0	0

Key:-

F = Father

TS = Tutor with similar song to the father

TD = Tutor with dissimilar song to the father

TABLE 3.II: Results of song tutoring in female-raised zebra finches.

Brood	Bird	%song learnt from tutors		% tutors' songs learnt	
		(fawn)	(wild type)	(fawn)	(wild type)
1	P 3 (f)	92	0	92	0
	P 5 (f)	100	0	92	0
2	Y10 (f)	57	0	40	0
3	O 9 (f)	0	44	0	46
	R 9 (f)	0	87.5	0	54
4	Y 8 (wt)	83	0	63	0
	B 8 (f)	100	0	75	0
	R 8 (f)	0	64	0	58
	Bk8 (wt)	0	67	0	42
5	O 7 (f)	0	80	0	73
	R 7 (f)	0	85	0	82

TABLE 3.III: Results of song tutoring in the normally-raised group.

Brood	Bird	% song learnt from tutors		% tutors' songs learnt	
		TS	TD	TS	TD
1	P46	67	0	54	0
	P47	83	0	45	0
2	P49	100	0	72	0
3	P50	100	0	62.5	0
	P52	100	0	75	0
4	P62	80	0	40	0
	P63	80	0	40	0
5	P67	67	0	67	0
	P68	33	33	22	40
	P69	55	0	55	0

TABLE 3.IV: Origin of pupil's song elements in the normally-raised group.

Brood	Bird	No elements learnt from				No elements in bird's song
		TS + F	F	TS	TD	
1	P46	4	1	2	0	9
	P47	3	0	2	0	6
2	P49	7	0	1	0	8
3	P50	4	0	1	0	5
	P52	6	0	0	0	6
4	P62	3	0	1	0	5
	P63	4	0	0	0	4
5	P67	6	0	0	0	9
	P68	2	0	0	2	6
	P69	5	0	0	0	9

Figure 3.1:

Sonagrams of pupils P3 and P5 in the female-reared (FR) group with their song tutors B258 and B259. B258 has 13 elements in his song phrase; B259 has 4 elements. Pupil P3 has 13 song elements in his song phrase: 12 were learnt from B258 and 1 was improvised.

Pupil P5 also has 13 song elements, all of which were learnt from B258. 12 of B258's elements were learnt, one of these was repeated. Neither pupil learnt from B259.

Letters represent sections of song common to two or more individuals.

FIG 3·1

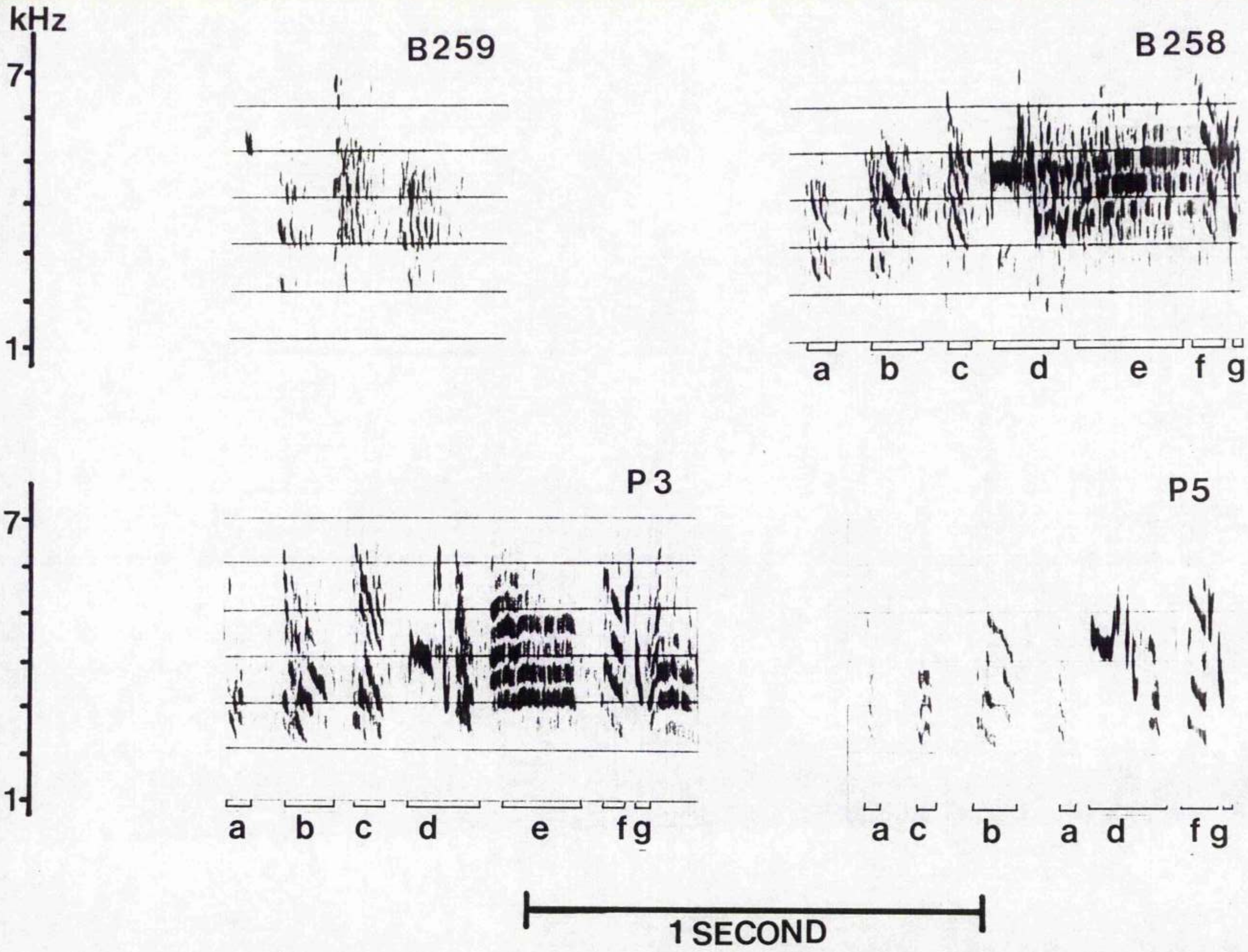
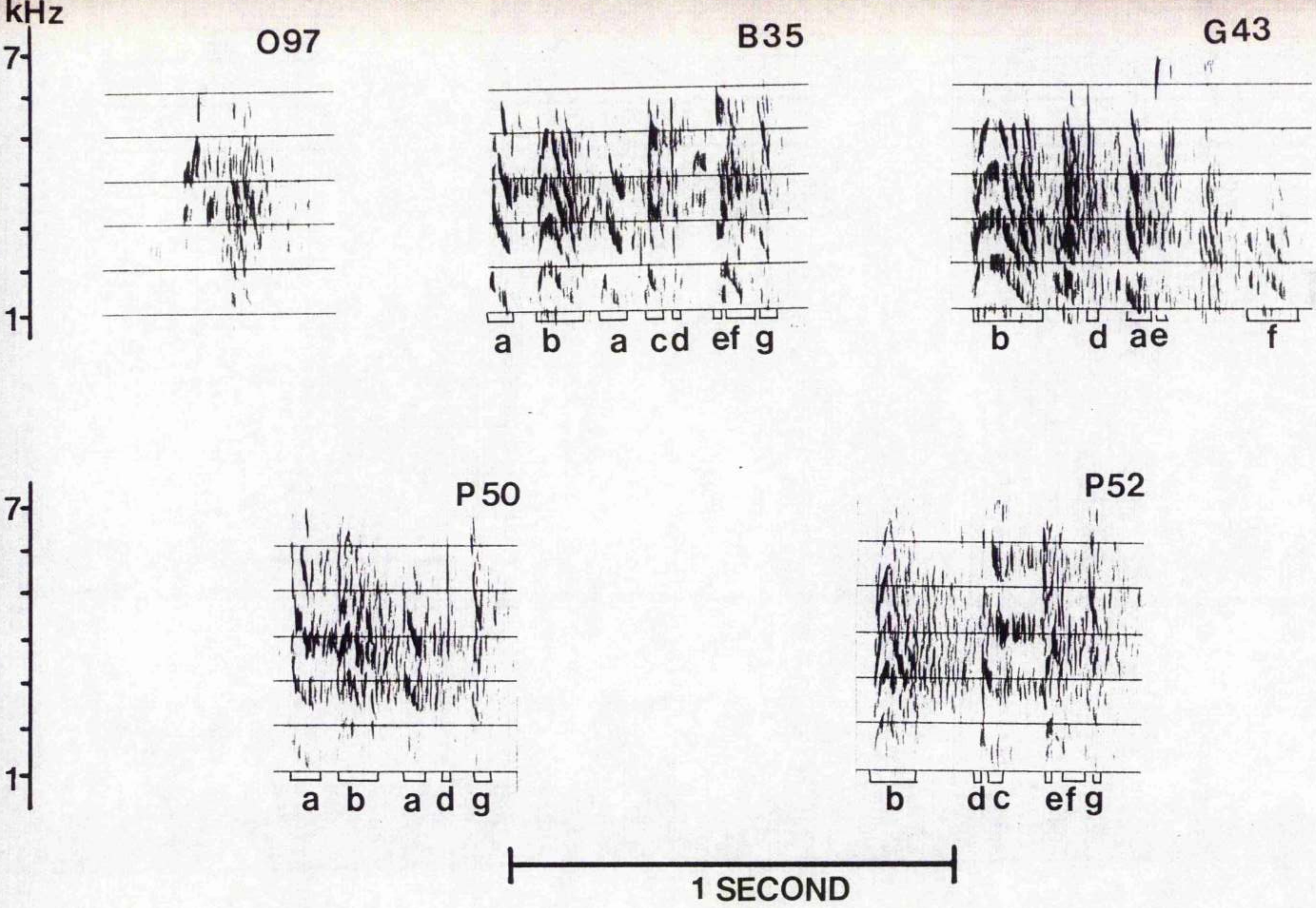


Figure 3.2:

Sonograms of pupils P50 and P52 in the normally-reared (NR) group with their father G43 and the song tutors B35 and 097. G43 has 8 elements in his song phrase. B35 also has 8 elements, 6 of these are shared with G43. 097 has 6 elements, none of these are common to either the father or tutor B35.

Pupil P50 sings a song phrase made up of 5 elements, 4 from B35 and/or G43 and 1 from B35.

Letters represent sections of song common to two or more individuals.


kHz
7
1
O97
B35
a b a cd ef g
G43
b d ae f
7
1
P50
a b a d g
P52
b dc ef g
1 SECOND

Chapter 4.

SONG DISCRIMINATION LEARNING IN ZEBRA FINCHES.

ABSTRACT.

Young zebra finches were tested for their ability to discriminate between the song of their father or tutor versus another male on the basis of two types of preference test, one with a male whose song was dissimilar to that of the father or tutor and one with a male who sang a similar song. Two groups were raised by their parents and then housed with the mother alone so that they could not hear any adult song. These birds were tested on removal from their father at 25 (group A) or 35 days (group B) and again at 4 months. Group C were raised by their parents until 35 days, transferred to a second pair of conspecifics until 70 days, isolated until 4 months and then transferred to a third pair of conspecifics. These birds were tested at 35 days, at 4 months and at 6 months of age. In addition, the mother birds were tested with their mates' songs.

The results suggest that birds learn to prefer their father's song by the time they are 35 days old but can continue to learn after this time. Possible reasons for this are discussed and the results are compared with those for song performance learning.

Based on a paper submitted to Anim. Behav.

INTRODUCTION.

In spite of the extensive research into song learning in birds the vast majority of studies have considered only one type of song learning, performance learning: a song element is said to be learnt if the young male incorporates it into his vocal repertoire. It is becoming increasingly apparent, however, that birds learn at least some features of many more songs than they sing (McGregor and Avery 1986, Shy et al 1986), and that a second type of learning, that of discriminating between a song that has been heard previously and one that has not, is also important in the process of song acquisition.

Discrimination learning is important for both males and females. Territorial males can discriminate between neighbours and strangers on the basis of familiarity with their songs (e.g. Brooks and Falls 1975 for white-throated sparrows, Zonotrichia albicollis, Falls and D'Agincourt 1982 for eastern and western meadowlarks, Sturnella neglecta, and Payne 1981 for indigo buntings). Males of some species tend to match song types when countersinging on territorial boundaries and they can estimate their distance from each other by comparing the extent of sound degradation between the matched versions (Falls et al 1982). Great tits can discriminate between degraded and undegraded songs only if the song type is familiar, i.e. if it is in their own repertoire or that of a neighbour (McGregor and Krebs 1984). This lends further support to the suggestion that territorial males can memorise their neighbours' songs.

Song discrimination learning is also important for females. Miller's results (1979a) suggest that, although female zebra finches do not normally learn to sing their fathers' songs, they can nonetheless recognise them: they consistently show a preference for their father's song, even when discriminating between males with similar songs. They can also distinguish between the songs of their mates and those of other males: this might provide an acoustic basis for mate recognition (Miller 1979b).

Captive male zebra finches which are housed with two song tutors during the sensitive phase for song performance learning prefer to copy from the tutor whose song is similar to their father's (Chapter 3). Where closely related males tend to have a large proportion of song elements in common, song could be used as a cue for optimal outbreeding, if females select mates on the basis of song similarity to their father (McGregor and Krebs 1982, Bateson 1983, Grant 1984, Chapter 3).

In the wild zebra finches gain independence at about 35 days of age and from then on associate primarily with other juveniles and nonbreeding adults in the flock (Immelmann 1962). In captive males the sensitive phase for song copying does not usually begin until after 35 days (Eales 1985). This means that young zebra finches would need to have learnt some characteristics of their father's song prior to independence, before the sensitive phase for song performance learning.

The aim of this study is to determine the age at which a preference for the father7s song is established in zebra finches, whether there are differences between the two sexes, and the extent of the similarity with song performance learning.

The two types of learning might be quite different. Song discrimination might not require the same extent of learning as song copying and a young bird need not memorise the entire song phrase, merely a few specific elements which act as markers for recognition. In great tits discrimination learning occurs over a longer time period than song copying (McGregor and Avery 1986). This study tests whether this is also true of zebra finches by giving males and females, which have been housed with a song tutor during the sensitive phase for song copying (35 - 70 days), the opportunity to learn from another song tutor after 4 months of age, 6 weeks after song performance learning has normally been completed.

METHODS.

Birds and Housing Conditions.

Ten pairs of domesticated zebra finches were housed in wooden, wire-fronted breeding cages, 60 cm x 45 cm x 30cm. Each pair had been observed daily for three months in a previous investigation of parental behaviour and had successfully reared at least one brood of young. All the males sang typical zebra finch song phrases and had normal song outputs.

Two groups of young birds remained with their parents until they were 25 or 35 days old and were then housed with the mother alone so that they could not hear any adult song (groups A and B respectively).

A third group (group C) were raised by their parents until 35 days of age and then transferred to a pair of non-breeding, adult conspecifics. These conditions were maintained until the young birds were 4 months old. Group C were then housed with a third pair of zebra finches for a further 8 weeks (Fig. 4.1).

Song discrimination was measured indirectly: young males and females were tested for their song preferences in tests with their father's song and that of another male. The birds in each group were tested both on the day that they were separated from the father and at 4 months of age and the birds in group C were also tested tutor 1's song at 4 months of age, and with both tutors and the father at 6 months of age. In addition, the mothers were tested with mates' songs.

Apparatus.

The test apparatus consisted of a double choice cage measuring 150 cm x 45 cm x 30cm, divided into two approach zones, each 30 cm long, and a central, neutral zone 90 cm in length (Fig. 4.2). In the central zone there were two high perches (30cm); each approach zone had a low perch (10 cm) at the far end. Adjacent to the approach zones, at each end, were two loudspeakers (RS twin cones) connected to two Uher 4000 tape recorders.

Song Stimuli.

The songs of the ten adult male zebra finches were individually recorded in an anechoic, sound-proof box using a Uher 4000 tape recorder and Marantz Electret microphone. Only undirected songs were recorded to reduce the possibility of measuring sexual response, rather than recognition, in the preference tests.

Songs were re-recorded onto 1-minute tape loops (TDK EC-1) using the Uher in conjunction with a Marantz superscope C180 tape recorder. There was considerable variation in the duration of songs (mean = 5.22s, SD = 2.45s, n = 50 songs) but songs of similar length were selected for the tests so that each tape-loop contained five song phrases, all from only one male, and each separated by approximately 5.0s of silence.

Preference tests.

Individual birds were tested at least one hour after transfer from the breeding room into the quiet testing room. For the mate preference tests, the female was isolated from her mate for two to three days under a 14/10 light/dark cycle: this matches the maximum time for which a female might be separated from her mate in the wild (see Miller 1979b).

Each test began with the bird in the central portion of the cage. When the two tape recorders were first switched on the songs of the two males were broadcast synchronously but this was altered slightly due to the varying song durations. Each bird was given two 30-minute tests, with each song broadcast from different speakers in the two tests to control for possible side preferences.

All the young birds were given two types of test: the song of the father (F) versus an unrelated male with a different song (D) and the father's song versus the song of a male with at least 75% of song elements common to father (S). Group C were also tested with tutor 1's song versus that of a dissimilar male (D) and versus a male (S) whose song is similar to that of tutor 1, and with tutor 2's song versus that of a dissimilar (D) and similar (S) male. For each of the ten breeding pairs the mother was also given both types of test, using song from her mate (M) tested against ones similar and dissimilar to it. For each bird only the songs of the father, tutor 1, tutor 2 or the mate were used in all the tests, the other songs were only used once for any one bird.

During each test three measures were taken:-

(i). Number of calls a bird gave in response to the two songs. Only calls which were given while the bird was facing the speaker broadcasting song were recorded as a measure of response.

(ii). Latency of response (initial time spent in the neutral zone before hopping to either approach zone).

(iii). Total time spent in each approach zone.

A bird was scored as having discriminated between two songs if it spent at least twice as much time in one approach zone as in the other for a total of at least three minutes in each test (10% of the trial). By taking a more stringent criteria than the majority of overall time spent in either approach zone the possibility that emphasis might be put on chance differences was minimised. Where the criteria was reached a bird was said to have a preference for the song which it approached.

RESULTS.

Fig. 4.3 shows the number of birds in groups A, B and C which preferred the father's song, and the number of birds in group C which preferred tutor 1's song, as a proportion of the number of birds which responded in the preference tests at 4 months of age. In groups B and C 15 out of 17 birds preferred their father's song in tests with another male whose song was dissimilar to the father's. This gave a significant difference from group A where none of the birds preferred their father's song (χ^2=32.68, df=2, $P<0.001$ for A vs B vs C; χ^2=25.57, df=1, $P<0.001$ for A vs B; χ^2=25.57, df=1, $P<0.001$ for A vs C; ns for B vs C). Group A also differed significantly from the other two groups in tests with the father versus a male who sang a similar song to the father's (χ^2=14.22, df=1, $P<0.001$ for A vs B; χ^2=13.85, df=1, $P<0.001$ for A vs C; ns for B vs C).

In the first set of trials none of the birds in group A responded at 25 days of age. Of the nine birds in group B (3♂♂, 4♀♀ which responded at 35 days of age seven preferred the father and all six in group C (3♂♂, 3♀♀) which responded preferred the father: these results did not differ significantly from the results at four and six months of age (χ^2 tests, ns). For group C a comparison of the results at four and six months gives no significant differences (χ^2 tests, ns). The birds in group C discriminated between the songs of tutor 2 and the other male and preferred tutor 2: this shows that birds can continue to learn until they are at least four months old (Fig. 4.4). Fig. 4.5 shows that there is no significant difference between the number of mothers which discriminated between the two songs in the tests with the mate versus a dissimilar male and the mate versus a similar male (

χ^2 tests, ns); in both types of test mothers preferred their mates' songs.

For each group, birds tended to have shorter latencies of approach to the father's or tutor's song but this was not significant (Wilcoxon tests, ns). Tables 4.I and 4.II show that groups B and C spent significantly more time in the father's or tutor's approach zone than in the other male's approach zone ($T=0$, $P<0.001$ for all tests) and these birds also called more frequently to the father or tutor ($T=0$, $P<0.001$ for all tests). This is also reflected in Table 4.III which shows the mean number of calls and the mean amount of time spent in each approach zone for females in the mate preference tests.

The number of calls each bird made to the father or tutor was calculated as a proportion of the total number of calls made to either male for males and females at four months of age with the two types of test (F vs D, F vs S for groups A, B, C; T vs D, T vs S for group C). The results of a multivariate Anova gave significant differences between the groups ($F=15.8$, $P<0.001$, $df=3$) and between the two types of test ($F=22.0$, $P<0.001$, $df=1$) but there was no interaction between the two or with sex. A Newman Keuls test comparing groups showed that group A differed significantly from the other groups and group B differed significantly from group C in tests with the father and another male ($P<0.05$ for all tests). For each bird the proportion of time spent in one approach zone was calculated in terms of the total time spent in either approach zone. A multivariate Anova indicated that differences were due to the groups alone ($F=21.3$, $P<0.001$, $df=3$) and that there was no interaction with sex or the type of test. The results of a Newman Keuls test showed that group A differed significantly from the other groups at P<0.05 but the other groups were not significantly different from each other.

Although there was no significant effect of interaction between group and the type of preference test, Figs. 4.6 and 4.7 show that the groups differed in their response to the father and the other male in the two tests on the basis of calls and time spent in each approach zone. Group A failed to show a preference for the father or the other male whereas group C discriminated equally well between the song of the father and and that of the other male and preferred the father, irrespective of whether the other male had a similar or dissimilar song to the father. However, group B males showed a stronger preference for the father in the tests with dissimilar males. The same is true of group C males tested with songs of tutor 1 and another male. At six months of age group C can discriminate between the father and another male and show an equally strong preference for the father in either test (T=39.5, ns for calls; T=37, ns for time spent). This is also true for tests with tutor 2 and another male (T=38.5, ns for calls; T=37, ns for time spent). However, they show a show a stronger preference for tutor 1 in tests with a dissimilar male (T=17.5, P<0.001 for calls; T=27, P<0.02 for time spent).

DISCUSSION.

The results of this chapter show that male and female zebra finches can learn to discriminate between the songs of their father and other males and prefer their father's song. Birds raised by their father until day 25 and then isolated with their siblings until sexual maturity do not show a preference for their father's song which suggests that they have not learnt sufficient to discriminate between the songs of their fathers' and those of other males. Although it seems unlikely, the possibility cannot be ruled out that they are capable of discriminating even though they do not show a preference. The results of group B show that by 35 days, however, the newly independents have had sufficient experience to discriminate quite accurately: these males spent significantly more time in the approach zone of the speaker broadcasting their father's song and called more in response to his song. Dietrich (1981) also found call rate to be a good indicator of recognition. She found that female Bengalese finches call three times as frequently to songs of males they had heard previously than to songs of strange males.

The results for group C, where birds were housed successively with two other males (tutor 1 and tutor 2) after 35 days, indicate that discrimination learning can occur over a longer period of time, from before day 35 until after 4 months of age. These birds preferred their father's song and those of their two tutors. Group C had an equal preference for the father in both types of test whereas group B spent more time in the approach zone broadcasting the father's song and gave more calls to the father in tests with a dissimilar male. Since both groups heard their father for equal periods of time (0-35 days) and were tested at the same age this difference cannot be the result of memory decay. One possible explanation is that hearing song after independence stimulated the birds in group C to remember their father's song. There might simply be a "practice effect" so that the greater the number of different songs a bird hears the better it becomes at discriminating between songs.

What is surprising is that group C had a weker preference for the tutor 1 in tests with the tutor 1's song and that of a male with a similar song. At 4 months group C spent more time in the approach zone broadcasting the first tutor's song and gave more calls to tutor 1 in tests with a dissimilar male than in tests with the similar male. The results also show that the birds spend a greater proportion of their time responding to the similar male than the dissimilar male. These birds were housed with tutor 1 during the normal sensitive phase for song production learning and, since the birds were housed with their siblings throughout the study, a likely explanation is that the birds discriminate between the two males and prefer the similar male's song because it sounds like their own or that of one of their brothers. Group C might have discriminated between these songs but have preferred both tutor 1's song and that of another male, if his song was sufficiently similar to the siblings' songs. This explanation might also account for the results in group B where birds showed a weaker preference for the father tests with the father's song versus that of a male with a similar song. Group B males, which were denied a song tutor during the normal sensitive phase for song learning, sang poor copies of their father's song (Clayton in prep.). Bohner (1986) has found that zebra finches will copy their father's song if they are housed with him until 35 days and then isolated from all adult song.

Alternatively, these results might be the result of proactive memory interference where learning features of the father's song interferes with learning tutor 1's song.

These two hypotheses can be tested post-hoc using the results of group C at six months. If the first explanation (preference for siblings' songs) is correct then the birds should prefer the father, and tutor 2 in either type of test but they should show a weaker preference in tests with tutor 1 and a similar male. However, if the second explanation (proactive interference) is correct then the birds should show an equally strong preference for the father and tutor 1 in both types of test but should discriminate between the songs of tutor 2 and another male less well in tests with a similar male. The results agree with the first hypothesis.

This raises a number of points. Firstly, it illustrates the more subtle effects which social interactions with siblings might have. Clearly, the study needs repeating with males housed individually during the "isolation" periods. Equally important is the difficulty in measuring discrimination. A female might, for example, discriminate between the two and prefer either male or demonstrate no preference for either. In this respect call notes might be a better indicator of discrimination than time spent in the approach zone; the latter might reflect a preference for one of the males. Nonetheless since there were no significant differences between the sexes, the results are suggestive of discrimination learning rather than sexual preference.

The most important result is that song discrimination learning, measured in terms of song preference, occurs over a longer time period than song production learning in zebra finches. By the time of independence at 35 days young males and females can learn sufficient about their father's song to discriminate between the father and other males and prefer their father's song: this is before the time when males would normally learn to copy song. Learning at least some features of other males' songs continues until after four months of age and probably throughout life. This would explain why the mothers could discriminate between the songs of their mates and other males.

For zebra finch females the significance of learning to discriminate between males on the basis of their songs probably lies in mate recognition. The results in the previous chapter suggest that discrimination learning is also important for song tutor choice, with males preferring to learn from the tutor whose song is most similar to the father. If closely related males have similar songs then song could be used as a cue for female choice.

One must always be cautious when relating the results of captive studies to the wild. Nonetheless, it is worth speculating why zebra finches might show a preference for their fathers' and brothers' songs. It might be that they simply prefer a familiar song to a novel one. Little is known about what happens in the natural situation, whether they associate with their siblings when they first leave their parents to join the flock and if so, whether this is a consequence of preferring to learn song from the same tutor (presumably one whose song is similar to the father's), yet such details are vital for interpreting the functional significance of results for captive zebra finches.

Table 4.I: The mean results of the preference tests with the father (F) or tutor (T) and another male whose song was dissimilar to the father's (D) for each group at 4 months of age. Standard deviations are given in brackets. Wilcoxon tests were done on each group.

Group	No calls to			Time spent in the approach zone (s)		
	F		D	F		D
A	18.5	T=34.5	17.6	322	T=35	295
(n=14)	(10.8)	ns	(10.4)	(190)	ns	(134)
B	31.2	T=0	17.0	791	T=0	308
(n=17)	(9.7)	P<0.001	(6.1)	(174)	P<0.001	(88)
C	26.6	T=0	12.2	759	T=0	312
(n=17)	(8.7)	P<0.001	(6.6)	(205)	P<0.001	(129)
	T		D	T		D
C	29.5	T=0	10.2	876	T=0	297
	(12.1)	P<0.001	(5.9)	(304)	P<0.001	(127)

Table 4.II: Mean results for the preference tests with the father (F) or tutor (T) and a male with a similar song (S). Standard deviations are shown in brackets. Wilcoxon tests were done on each group.

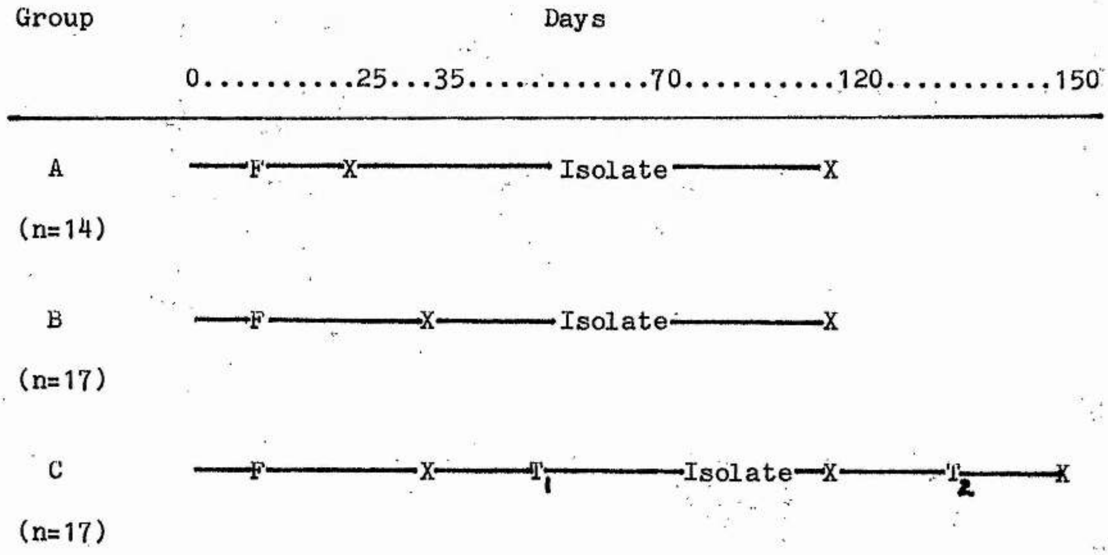
Group.	No. calls to			Time spent near approach zone (s)		
	F		S	F		S
A	18.2	T=23.5	18.2	284	T=30.5	281
(n=14)	(10.1)	ns	(12.1)	(138)	ns	(183)
B	30.1	T=0	20.3	709	T=1	400
(n=17)	(8.3)	P<0.001	(6.3)	(170)	P<0.001	(98)
C	26.6	T=0	18.2	645	T=0	391
(n=17)	(18.2)	P<0.001	(6.6)	(241)	P<0.001	(165)
	T		S	T		S
C	28.8	T=0	13.9	868	T=0	332
	(14.2)	P<0.001	(10.7)	(239)	P<0.001	(185)

Table 4.III: Results of preference tests for mothers with mate (M) versus another male (S or D). Standard deviations are shown in brackets. Wilcoxon tests were done on each group.

Group	No. calls to			Time spent in approach zone (s)		
	M		D	M		D
	27.6	T=0	8.4	1024	T=3	317
	(10.9)	P<0.001	(8.7)	(317)	P<0.02	(309)
	M		S	M		S
	33	T=0	13	908	T=5	427
	(10.1)	P<0.001	(8.9)	(421)	P<0.05	(368)

Fig. 4.1 shows the housing conditions for the three groups of zebra finches.

Housing conditions for the three groups of zebra finches.



Key:-

X	Preference Tests.
F	Father
T	1st Tutor
T	2nd Tutor

Fig. 4.2 shows the apparatus used in the preference tests.

Key:-

LS loudspeaker

A approach zone

N neutral zone

F food

W water

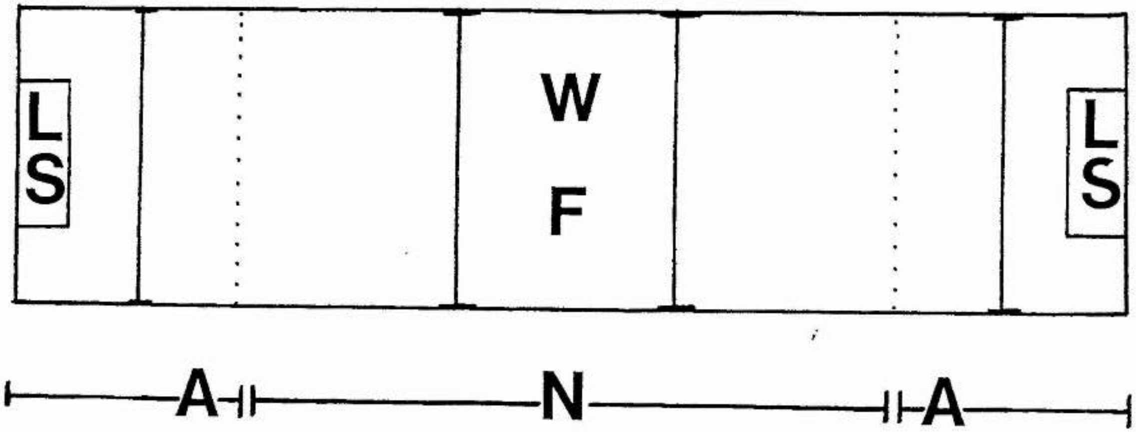


FIG 4-2

Fig. 4.3 shows a histogram of the proportion of birds in each group which preferred the father (F) or tutor (T) on the basis of his song in tests with a male whose song was dissimilar (D) or a male whose song was similar (S) at four months of age.

Key:-

□ F/T vs D

▒ F/T vs S

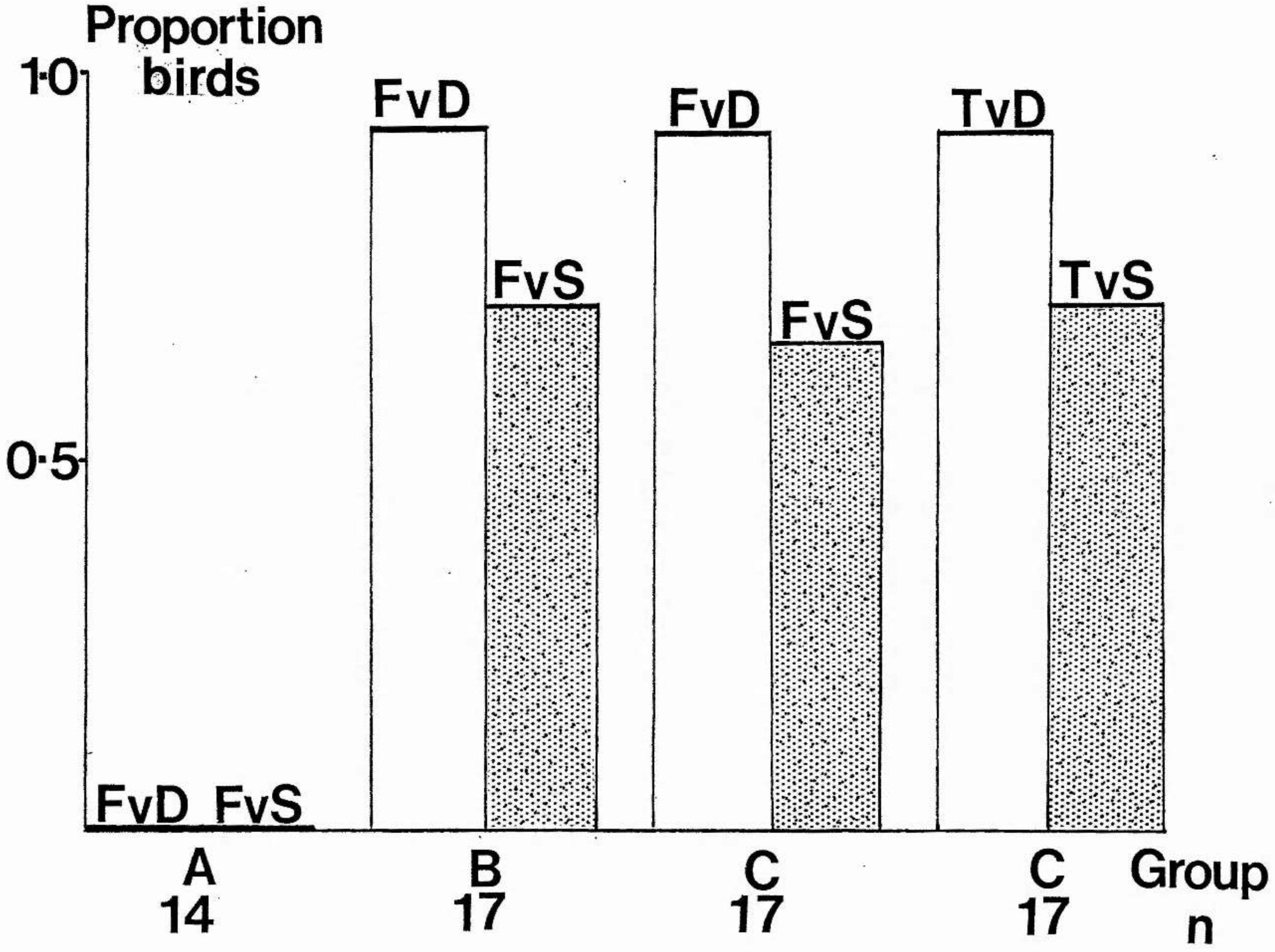

Proportion birds
1·0
0·5
FvD
FvS
FvD
FvS
FvD
FvS
TvD
TvS
A
14
B
17
C
17
C
17
Group
n

FIG 4·3

Fig. 4.4 shows a histogram of the proportion of birds in group C which preferred the song of the father, tutor 1 or tutor 2 in tests with a male whose song was dissimilar (D) or a male whose song was similar (S) at six months of age.

Key:-

□ F/T_1/T_2 vs D

░ F/T_1/T_2 vs S

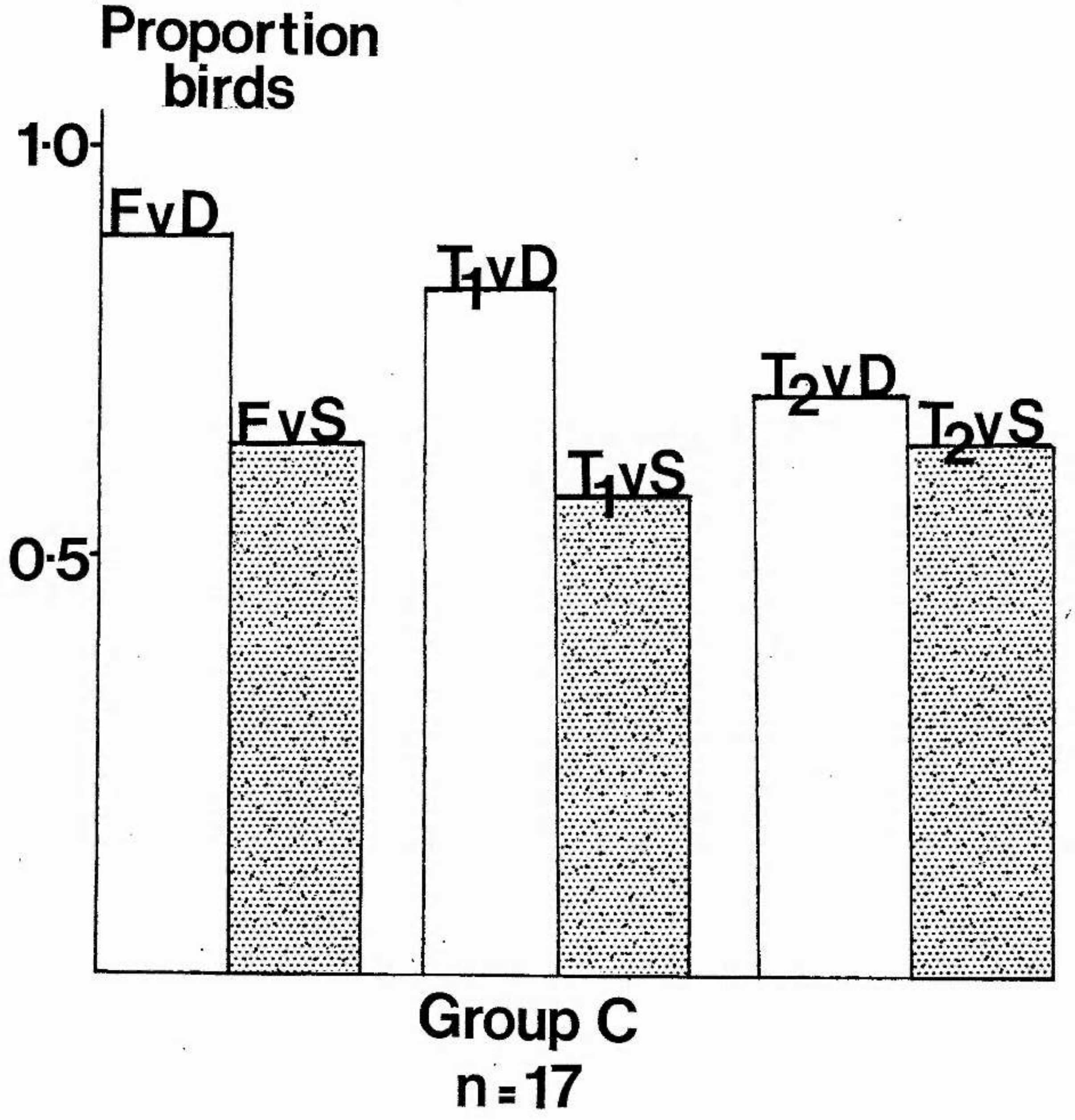

Proportion birds
1·0
0·5
FvD
FvS
T_1vD
T_1vS
T_2vD
T_2vS
Group C
n = 17

FIG 4-

Fig. 4.5 shows a histogram of the proportion of mothers which preferred the song of their mates (M) in tests with males whose songs were dissimilar (D) and those whose songs were similar (S).

Key:-

☐ M vs D
▨ M vs S

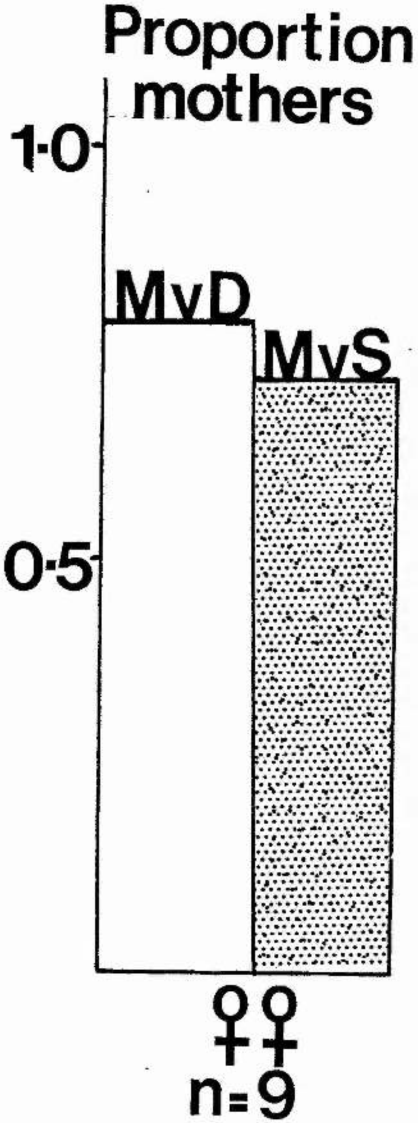


FIG 4·

Fig. 4.6 shows a histogram of the mean proportion of calls made to the father or tutor in tests with the song of father (F) or tutor 1 (T1) versus that of a male whose song was dissimilar (D) or similar (S) for each group at four months of age. The results of Wilcoxon tests are shown for each group.

<u>Key:-</u>

□ F/T1 vs D

▒ F/T1 vs S

FIG 4·6

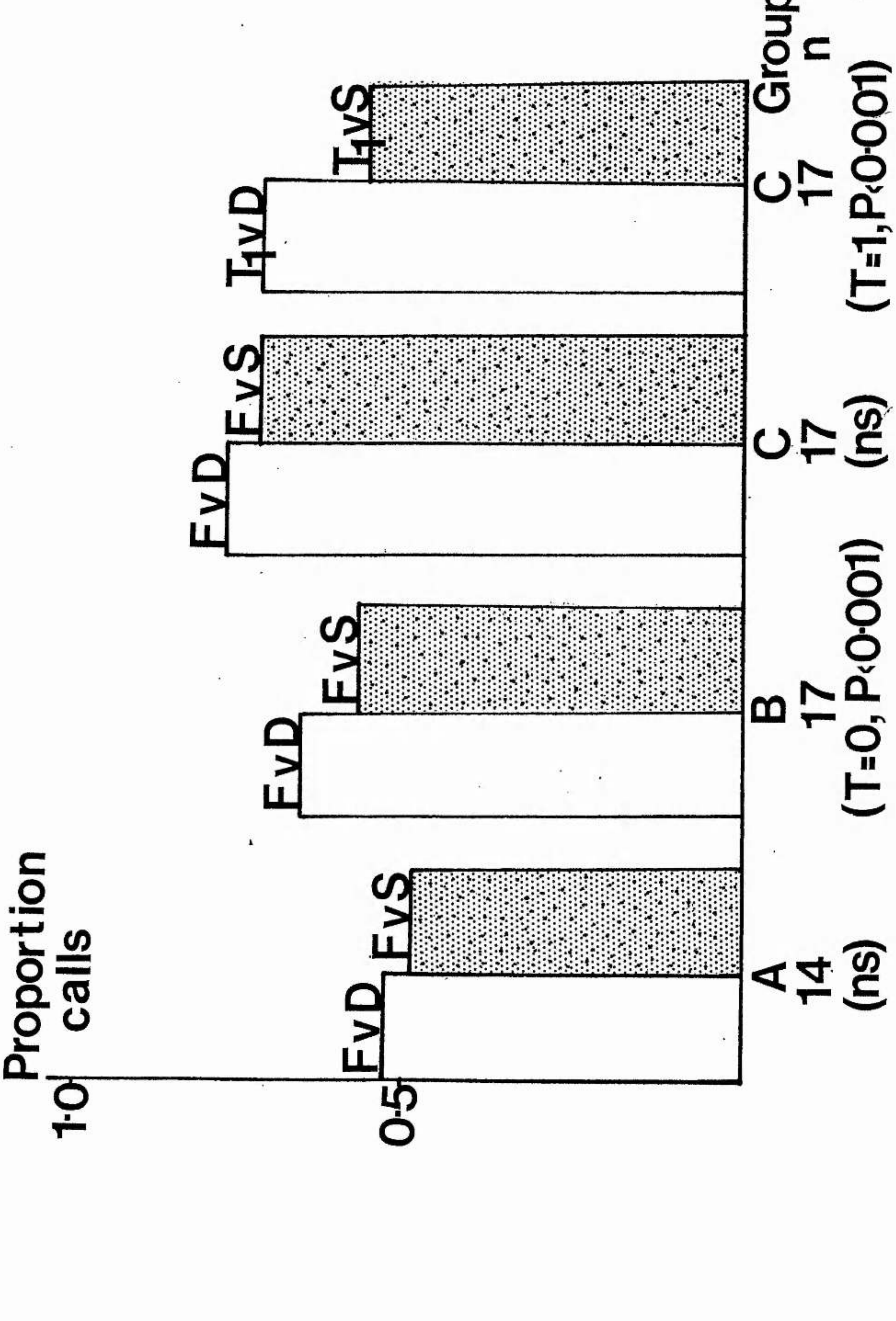

Proportion calls
1·0
0·5
FvD
FvS
A
14
(ns)
FvD
FvS
B
17
(T=0, P<0·001)
FvD
FvS
C
17
(ns)
T1vD
T1vS
C
17
(T=1, P<0·001)
Group
n

Fig. 4.7 shows a histogram of the mean proportion of time spent in the father's or tutor 1's approach zone in tests with the song of the father (F) or tutor 1 (T_1) versus that of a male whose song is dissimilar (D) or similar (S) for each group at four months of age. The results of Wilcoxon tests are shown for each group.

Key:-

☐ F/T_1 vs D

▨ F/T_1 vs D

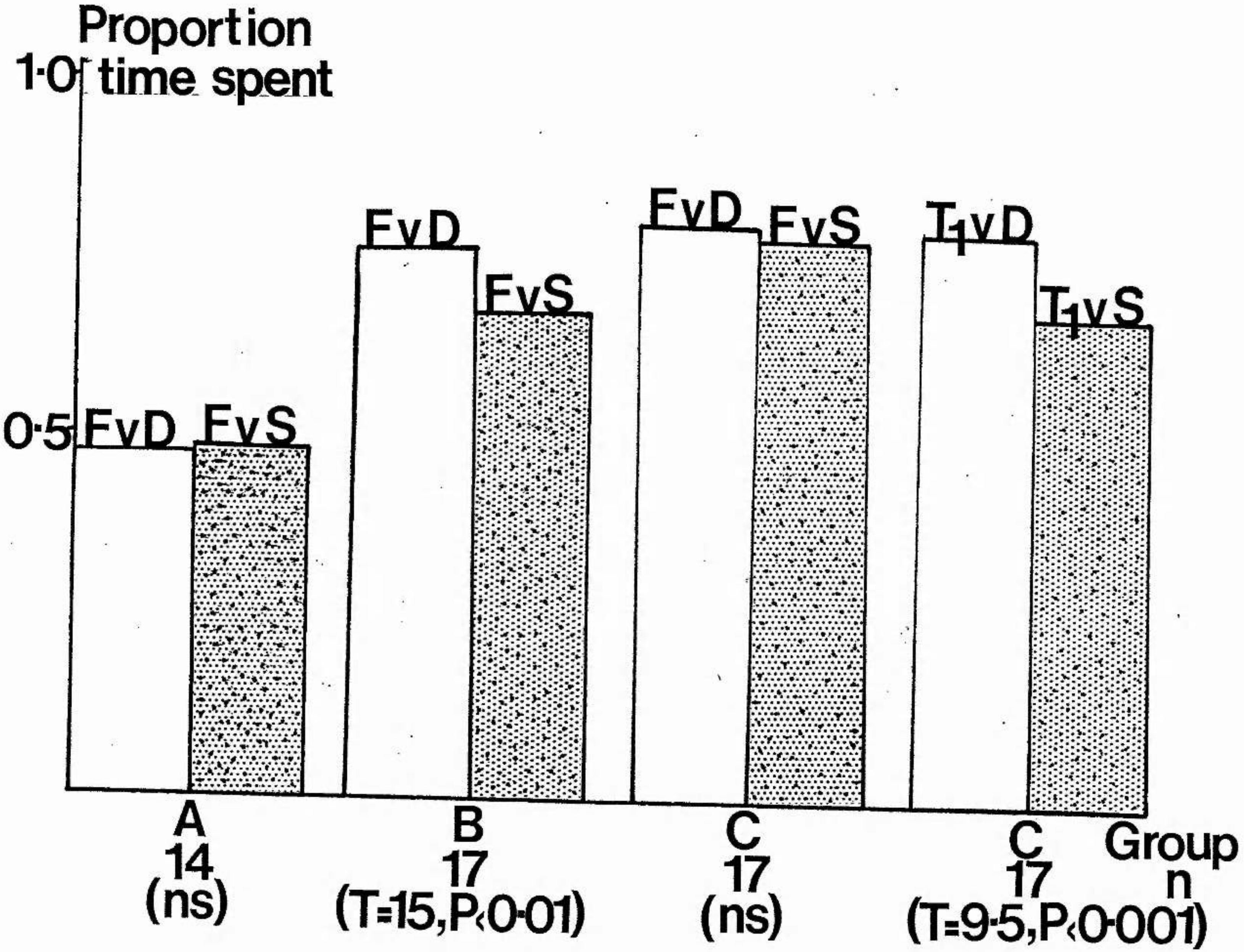

Proportion
time spent
1·0
0·5
FvD
FvS
FvD
FvS
FvD
FvS
T_1vD
T_1vS
Group
n
A
14
(ns)
B
17
(T=15,P‹0·01)
C
17
(ns)
C
17
(T=9·5,P‹0·001)

FIG 4·

Chapter 5.

SONG LEARNING IN BENGALESE FINCHES: A COMPARISON WITH ZEBRA FINCHES.

ABSTRACT.

Male Bengalese finches learn their song from an adult male conspecific with whom they can interact at 35 to 70 days of age and normally-raised males fail to reproduce song which they have only heard before or after this time. Birds which have been raised by their mother alone and those which have been deprived of a song tutor during the learning phase produce abnormal songs with indistinct elements and little or no phrase structure; this is typical of males which fail to hear adult song during their development. These songs are unstable and are replaced by normal songs, if there is an opportunity to learn from an adult male conspecific. Presumably, this flexibility in the time when young males learn acts as a safeguard to ensure that normal conspecific song is produced.

These results bear striking similarity to those on zebra finch song development. Differences between the two species, especially in the learning of call notes by female zebra finches, are discussed.

Based on a paper to appear in Ethology (in press).

INTRODUCTION.

The previous two chapters considered how zebra finches choose their song tutors when they are presented with two conspecific tutors. In the remainder of this thesis these questions are examined at the species level: which cues are important for ensuring that species-typical song is learnt and to what extent does early social experiences influence song acquisition? Such questions are best examined using cross-fostering techniques: for zebra finches the young have often been transferred as eggs to incubating pairs of Bengalese finch foster-parents whose own eggs are removed. At sexual maturity the songs of cross-fostered individuals are then recorded and compared from sonagrams with those of normally-raised birds. To assess the effects of cross-fostering a knowledge of both species' song development is required. Although song learning has been studied extensively in zebra finches (e.g. Immelmann 1969; Bohner 1983; Eales 1985a), comparatively little work has been done on Bengalese finches.

Male Bengalese finches have only one song phrase which is learnt early in life, around the time of independence at about 40 days of age (Dietrich 1980). A male denied the opportunity to copy other adult males during the sensitive phase will fail to develop normal song when adult (Immelmann 1969). This isolate song resembles subsong, which is produced by juveniles before the song is fully developed; it is slower and consists of a few, long elements which are simple and uniform in structure. This is also true of zebra finches. In both species, isolate song contains species-specific elements which appear to be arranged in species-typical song phrases (Immelmann 1969; Price 1979).

Social factors are extremely important in governing what is learnt and when, to the extent that even species-specificity can be overridden: young Bengalese finches will learn song from a zebra finch foster-father and vice-versa (Immelmann 1969).

Zebra finches copy song from a tutor with whom they can visually and vocally interact during the sensitive phase; usually this starts immediately after independence, at about 35 days of age (Eales 1985b). Given the choice of several song tutors after reaching independence they will preferentially learn from their father (Bohner 1980), but if he is removed at independence, so that only unfamiliar males are available as song tutors, they tend to copy song from tutors whose songs are similar to their father (Chapter 3). Bengalese finches also exhibit this pattern of song learning (Dietrich 1980). Before independence, at the start of the sensitive phase for song learning, Bengalese finch young are capable of learning from several song tutors; learning exclusively from one tutor, preferably the father, does not occur until later in development. This allows a substitute song tutor to be accepted, should the father be lost.

The limited data available suggest that song learning in Bengalese finches bears is similar to that of zebra finches. Nonetheless caution is required because subtle differences in experimental design can play a crucial part in the development of species' preferences (Chapter 9). The aim of this study is to provide a direct comparison of song learning in the two species by rearing Bengalese finches under the same conditions as Eales (1985a) has done for zebra finches.

METHODS.

Birds and Housing Conditions.

Twenty clutches of Bengalese finches were divided into four groups:-

The birds in group A were raised in sound proof boxes by their mother alone, the father being removed on the fourth day after the first chick hatched. Some females were reluctant to leave the nest to feed and so their chicks had to be hand-fed. To control for the effects of human contact the chicks in all four groups were handled daily for the first ten days of life. At 70 days the mother was removed; the chicks remained in the sound proof boxes until 4 months of age.

Group B were raised by their parents until 35 days of age. They were then separated from all adult birds and housed together in the acoustically-stimulating environment of the birdroom until they were four months old.

Group C were also raised normally until 35 days. For the following five weeks they were housed with a pair of non-breeding Bengalese finches (tutor 1) and then housed together, in the absence of adults, until 4 months of age.

The control birds in group D were raised by their parents until 70 days and then isolated from all adults until they were 4 months old.

Songs were recorded when the birds were 4 months old. Subsequently all the birds were housed with an unfamiliar pair of non-breeding adults (tutor 2) and their songs were re-recorded at 6 months of age.

Songs and Sonagrams.

Bengalese finch song occurs in bouts during which a stereotyped song phrase is repeated several times. Each male has an individually distinct song phrase, consisting of a number of discrete notes or elements which are usually sung in a fixed sequence (6-14 different song elements in this study, mean = 11.25).

The song structure of each young male was compared with that of his father and tutors by making tracings of sonagrams of typical song phrases (see Chapter 3 for further details).

Two measures of song learning were used; the proportion of song learnt from a particular tutor (either the father or another tutor) was calculated as the number of different song elements a young male learnt from that tutor as a proportion of the number of different elements in the young male's song phrase. A second measure examined the proportion a tutor's song which a young male learnt, in terms of the number of different elements in the tutor's song which the young male learnt as a proportion of the number of different elements that tutor sang in a typical song phrase.

RESULTS.

Figure 5.1 shows the results of song learning in the four groups, illustrated as the mean proportion of song which had been learnt from the father, tutor 1 and tutor 2 at 6 months of age. There was no significant difference between the four groups in the proportion of song which had been learnt, relative to the proportion of improvised song elements, or in the proportion of the father's or tutor's song which was learnt (Kruskal Wallis tests). However, the four groups differed significantly in the time at which they learnt, with all the males in groups A and B learning after 4 months of age while those in groups C and D learnt exclusively from a tutor present before this time (χ^2=20, df=3, P<0.001).

An example of song learning in each of the four groups is shown in Figs. 5.2-5.5. Further details are given in Appendix c5a.

All 10 males in group D learnt from their father and all 9 males in group C learnt from tutor 1 after 35 days of age. None of the males in either group learnt song after 4 months of age.

The 11 males in group A and 9 males in group B showed a different pattern of song learning, however. At four months of age the birds in both groups sang highly abnormal songs. These consisted of a series of quiet, indistinct elements which resembled those normally produced during subsong and lacked the stereotyped phrasing typical of normally-raised males.

All the males in groups A and B learnt some of the tutor's song after 4 months of age. These males tended to learn less accurately, although differences between the four groups in the proportion of their song which was learnt did not reach statistical significance (Kruskal Wallis test). Males varied considerably in the extent of their song learning, with those in group B learning a little less than those in group A. In both groups some males still had abnormal songs at 6 months of age: these were often very quiet (2 in group A and 2 in group B), had variable sequencing (1 in group A and 2 in group B) or the elements were widely spaced (1 in group A and 1 in group B). None of these features were found in the songs of group C and D males.

DISCUSSION.

The results of this study show that Bengalese finches have a very similar pattern of song development to zebra finches; in both species young males base their song on that of the tutor with whom they can interact at 35 to 70 days of age and normally-raised males fail to reproduce song elements which they have heard before or after this time. For those raised by the mother alone (group A), and those raised normally by both parents until independence but then deprived of song during the learning phase (group B), abnormal songs are produced, with features typical of isolate birds. A further similarity with zebra finches (Eales 1895a) is that these songs are unstable and are replaced by normal songs, should the opportunity to learn from an appropriate song tutor arise. Presumably, this flexibility in the time at which young males learn acts as a safeguard to ensure that normal conspecific song is produced despite variations in experience.

In contrast to zebra finches, Bengalese finch males which have been raised by their mother alone do not incorporate her call notes into their songs; instead they produce songs typical of groups of males which have been isolated from their parents. The zebra finch song phrase typically includes several call notes, often with a distance call in the middle or at the end of the phrase (Price 1979); these are not present in Bengalese finch song phrases. For zebra finches, inclusion of the distance call may be particularly important in that the call is sexually dimorphic (Zann 1984) and, unlike most calls (Guttinger and Nicolai 1973), a young male must hear the distance call of conspecific males during the first 40 days of life in order to develop the terminal noise element, the most sexually dimorphic feature of the call (Zann 1985). The zebra finch distance call might provide one means of recognising adult male conspecifics; this would allow a young female-raised male to adjust his choice of song tutor accordingly. However, visual and behavioural differences between the two sexes are also likely to be important for song tutor recognition.

Bengalese finches are not sexually dimorphic and so, presumably, the birds must rely on vocal and behavioural cues to indicate the appropriate song tutors to learn from. In this respect, it would be interesting to consider whether the young female-raised males would learn solely from a conspecific male later in life or whether the general stimulus of any song would be sufficient for further learning. Are young males capable of recognising a male conspecific, never having been exposed to him before?

A further difference between Eales' results for zebra finches and the ones presented here for Bengalese finches concerns the copying accuracy of the birds in groups A and B: in this study the two groups did not differ significantly whereas Eales (1985a) suggested that zebra finches raised in a socially-stimulating environment learnt more than those housed in sound-proof boxes once a suitable tutor was available. However, this difference might be a consequence of sample size. Eales' work was based on the results of 4 and 5 males respectively; this study involved 9 and 11 males. This explanation seems likely in view of the large amount of variation between males in the accuracy with which they copy their tutor's song. Alternatively, the difference might relate to differences in song structure: for female-raised zebra finches, which base their song on female call notes which they have heard during the song learning phase, subsequent learning might be reduced because the memory has been partially filled.

The important point for both species is that extension of the learning phase is not the result of a lack of stimulation from adult conspecifics since later learning is not exclusive to those birds raised in sound-proof boxes. For both, it seems that experience, in combination with age, determines when a young male learns his song.

It is also interesting to compare the results presented here with those obtained by Dietrich (1980). In her study of Bengalese finch song development young males were raised with their parents and other conspecifics in flight cages until 40 days of age. They were then isolated (group 1), housed in groups with new song tutors (group 2), or remained in the flight cage with the father and other conspecifics (group 3). The birds in groups 1 and 3 copied their father's song, although those in group 3 also learnt from neighbouring males with whom they had been housed in the first 40 days of life. Group 2 males learnt from new tutors with whom they interacted after independence; of these, they tended to learn from tutors who sang a similar song to that of the father. From these results Dietrich concluded that Bengalese finches can learn from their father before 40 days of age. However, copying song exclusively from the father, rather than other males with whom they can interact, does not occur until later and is complete by about 70 days.

There are a number of methodological differences between this study and Dietrich's which might account for the difference in timing of song learning. It is becoming increasingly apparent that subtle differences in experimental desigh can yield quite different results (e.g. Chapter 9). For example, in Dietrich's study the young males were exposed to the father for an extra 5 days. According to the results presented here some learning could have occured by the 40th day since the males in group C learnt between 35 and 70 days of age but not before day 35 (group B). Another essential difference between the two studies concerns the housing conditions. The birds in this study were only exposed to one song tutor at any one time whereas Dietrich's birds were housed with several tutors with whom they could freely interact before and during the learning phase. The difference is thus one of successive versus simultaneous choice of a song tutor. Behavioural interactions between tutors might be influential in guiding a young male's choice: in zebra finches it is the relative amount of aggression which tutors direct to the young birds which appears to be important, the young males learning from the tutor who is most aggressive towards them (Chapter 3). This might also be important in Bengalese finches. In this respect, housing birds in breeding cages rather than flight cages might have a significant effect on tutor choice and crowding conditions might be crucial, particularly if differences in circulating levels of androgens are also influential (see Prove 1981).

From a comparative point of view this study shows that song acquisition in Bengalese finches and zebra finches is remarkably similar. The next chapter examines the effects of cross-fostering on what the two species will learn and the extent to which the two species use similar structural rules for song selectivity.

Figure 5.1:

The results of song learning at six months of age for the four groups of Bengalese finches (A - D), showing the proportion of improvised elements and the proportion of song learnt from the father and two tutors.

Key:-

■ Proportion of song improvised.

□ Proportion of song learnt from the father.

▥ Proportion of song learnt from tutor 1.

░ Proportion of learnt from tutor 2.

FIG 5

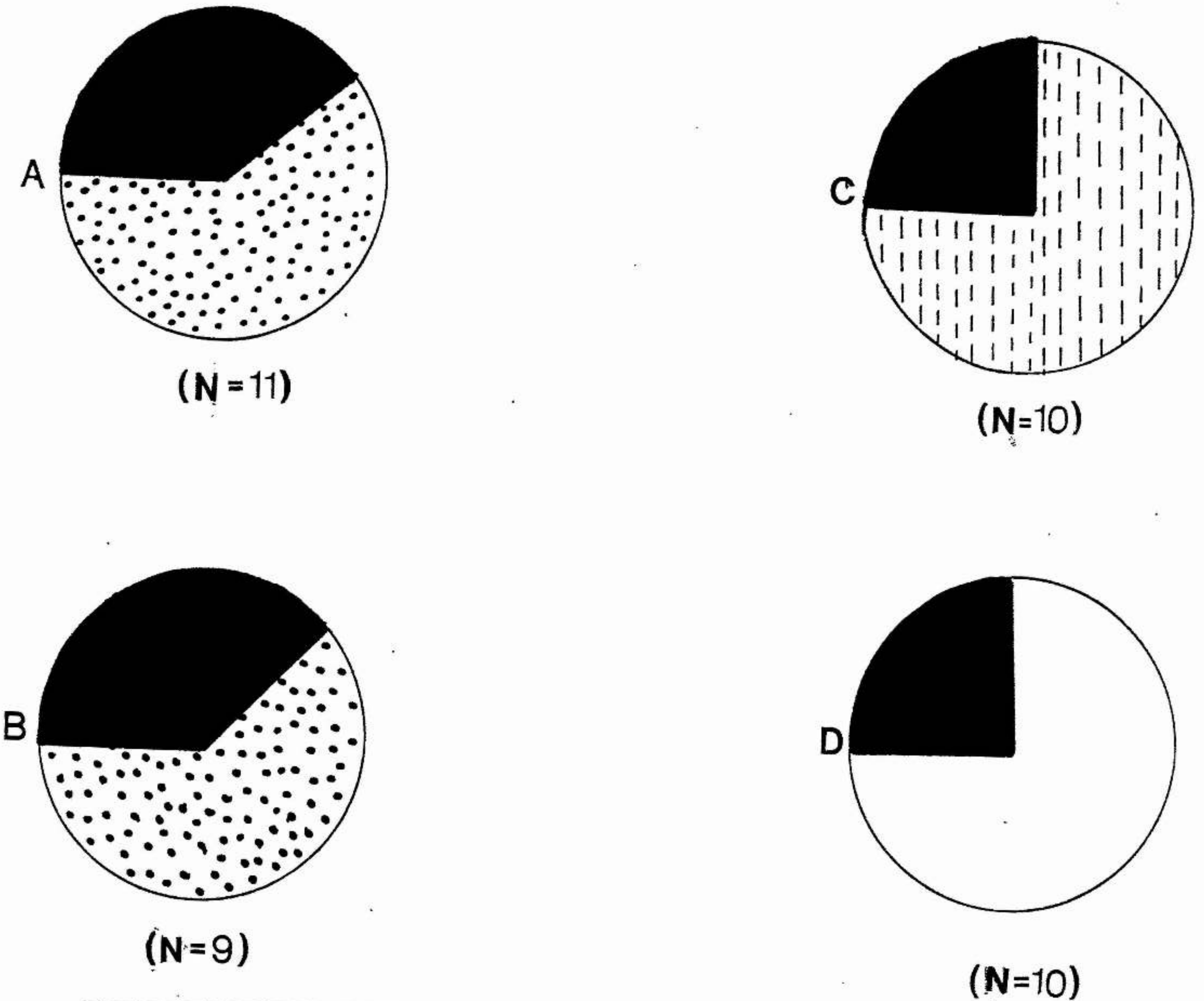


Figure 5.2:

Two sonagrams from B71, a young male from group A. The first sonagram (B71-1) was made at 4 months of age. Subsequently, the bird was housed with the Bengalese finch tutor, C, whose song he learnt (B71-2).

The letters denote portions of the song phrase common to both the young male and his tutor. For clarity individual song elements are not marked; each portion of song may contain one or several song elements.

FIG 5·2

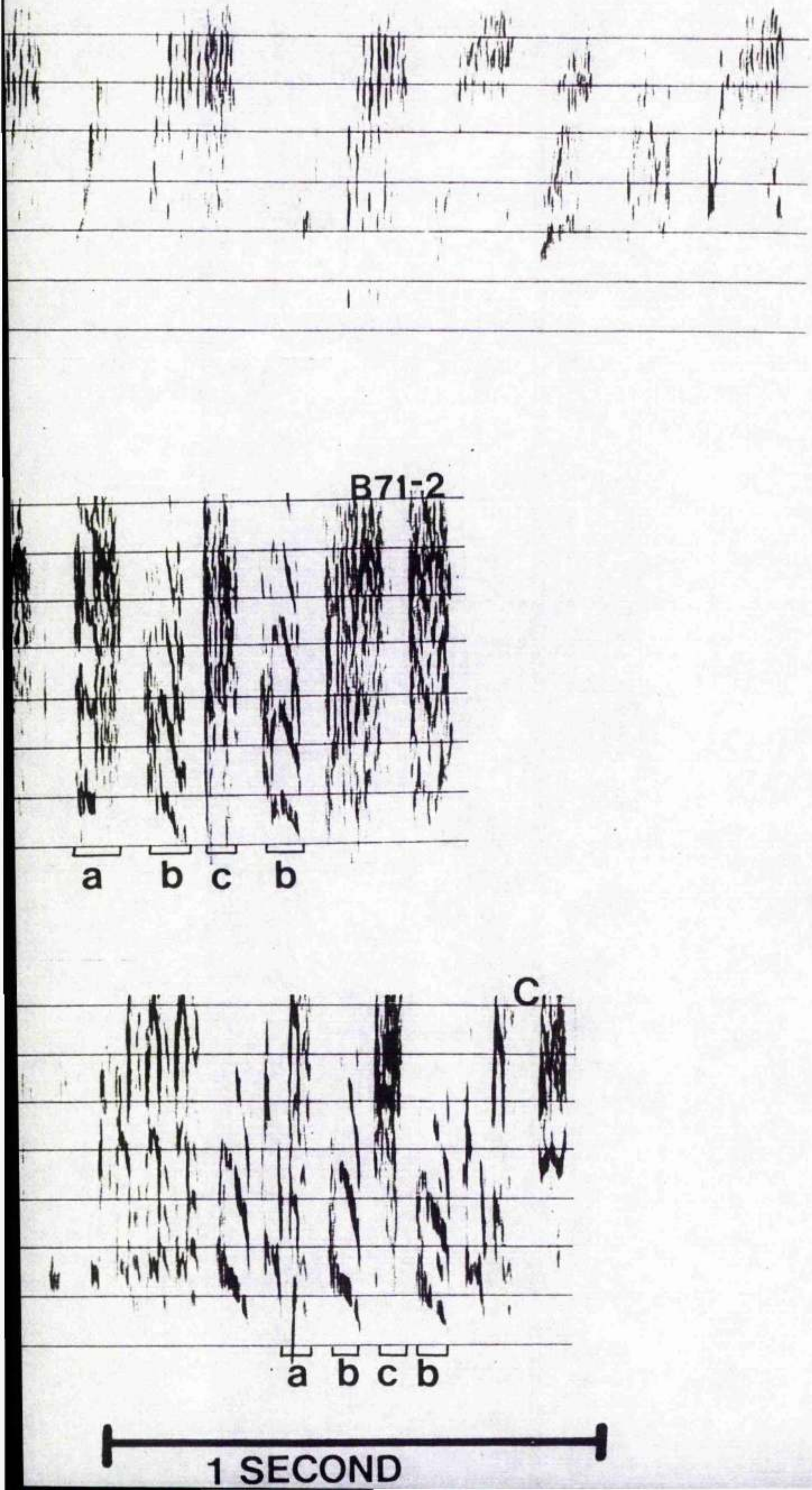


Figure 5.3:

B9 (group B) was raised with his parents until 35 days and then separated from his parents but housed with his siblings in the bird room until 4 months of age. At this stage (B9-1) his song was abnormal and a series of elements were produced but these lacked the typical zebra finch phrasing. The second sonagram (B9-2) shows the result of exposing the bird to a Bengalese finch tutor, P4, at 4-6 months of age. After this time B9 produced a normal song phrase based on that of P4.

Letters below the sonagrams show portions of song common to the two males.

FIG 5·3

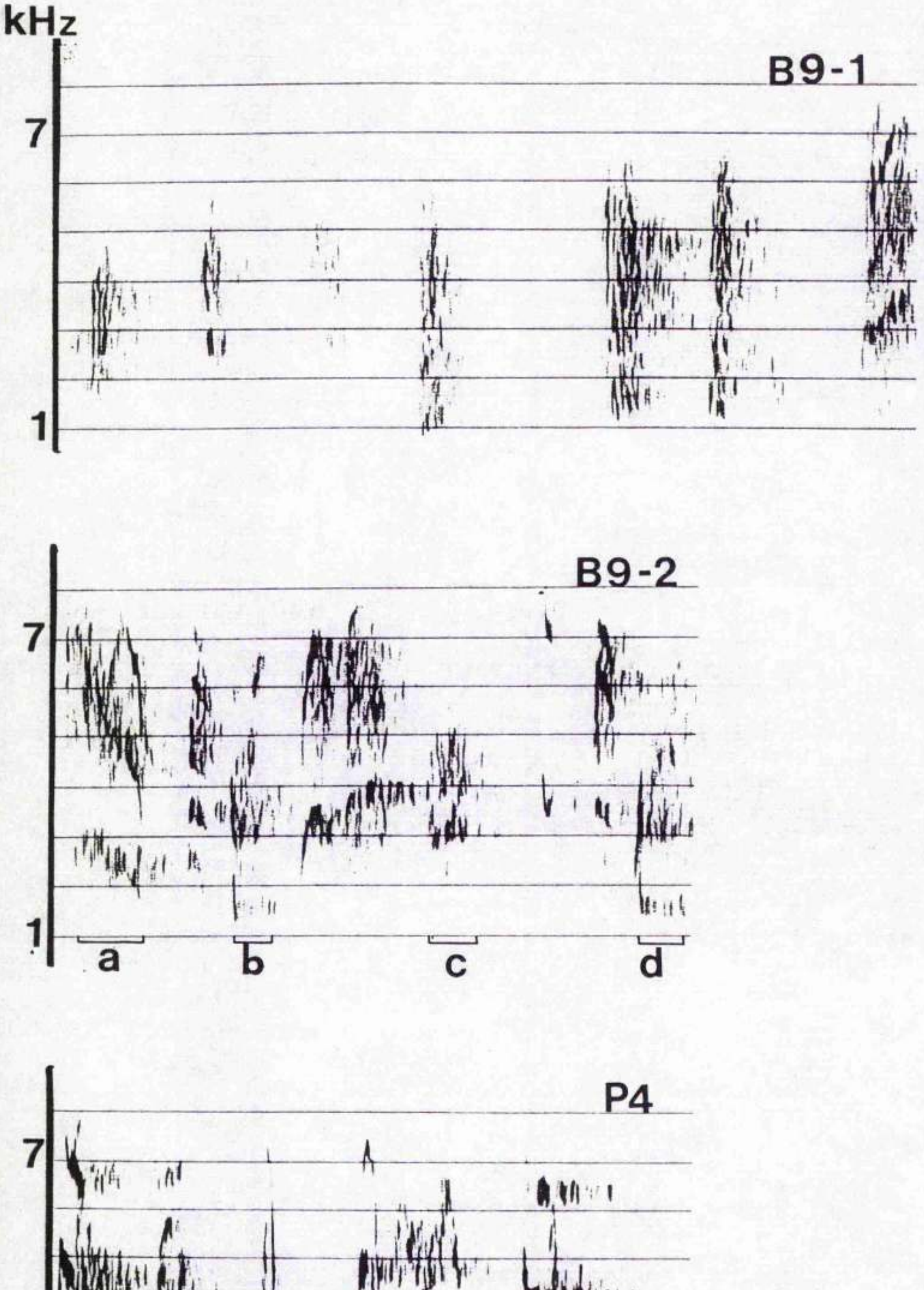


Figure 5.4:

Song phrases of PR and PW, two brothers who were housed with their father, CR, until 35 days and then given a new male, T, until 70 days old. Both males learnt from T. At 4 months they were given a second tutor, QK, but their songs did not change after this time.

Letters below the sonagrams show portions of song common to two or more males.

FIG 5·4

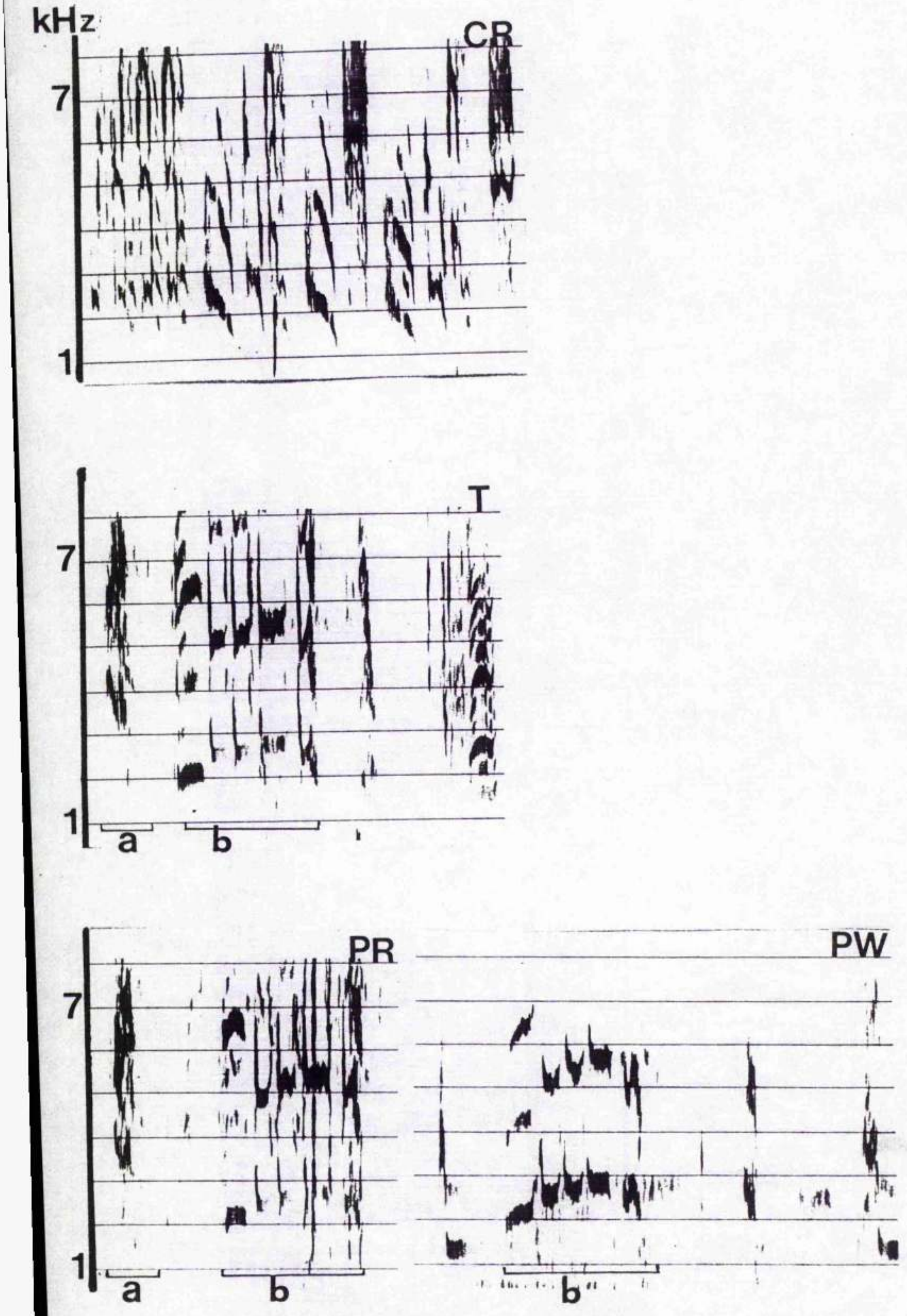
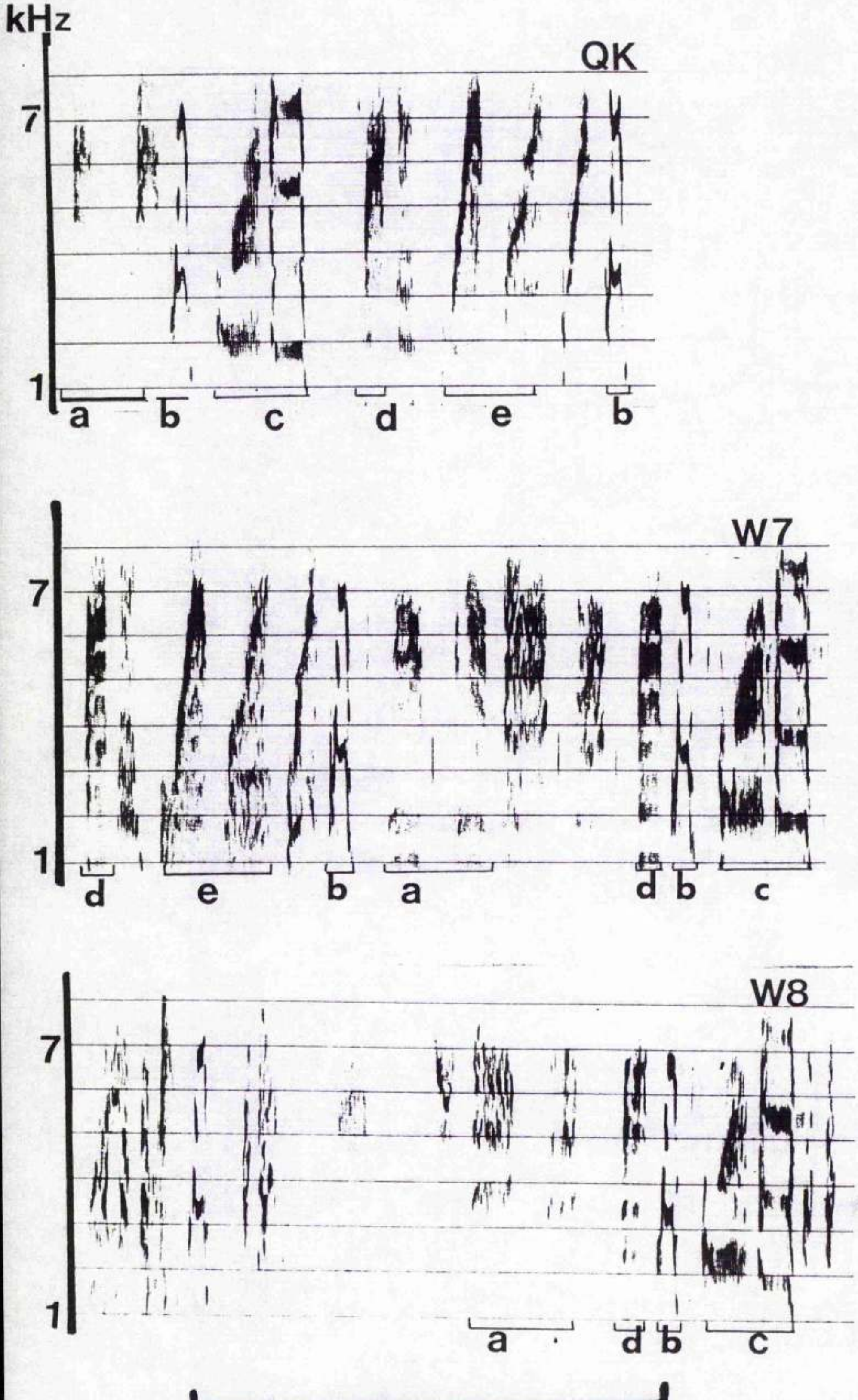


Figure 5.5:

W7 and W8 based their song on that of their father, Qk, with whom they were housed until 70 days old. At this stage their songs were stable: neither male learnt from the new tutor, T, at 4-6 months of age.

Letters below the sonagrams show portions of song common to two or more males.

FIG 5·5



Chapter 6.

THE EFFECTS OF CROSS-FOSTERING ON SELECTIVE SONG LEARNING IN ESTRILDID FINCHES.

ABSTRACT.

Male zebra finches which have been cross-fostered to Bengalese finches learn Bengalese finch song elements with as much accuracy as a male learning from his natural father. However, these elements are sung in phrases which are more nearly zebra finch length and lack the repetitiveness typical of the elements in a Bengalese finch phrase.

Male Bengalese finches are also capable of learning song from a zebra finch foster-father. Males vary substantially but they tend to produce fewer, more widely spaced zebra finch elements in a Bengalese finch-length phrase.

Both species show selective song learning and these results suggest that phrase length and the absence or presence of repeated elements might act as important cues for species-specific learning. Cross-fostered Bengalese finches seem to learn less than cross-fostered zebra finches and possible reasons for this are discussed.

INTRODUCTION.

In the laboratory many species will copy the song of their heterospecific foster-father and some species will even learn alien song from tutor tapes e.g. Thorpe (1958) trained a chaffinch to sing tree pipit, Anthus trivialis, song. In the wild non-conspecific songs are seldom copied, and one reason for this might be that instances of cross-fostering are rare in nature (but see Rowley and Chapman 1986). However, there are occasional cases of mimicry in species which do not normally mimic (e.g. Tasker 1955; Baptista 1972; Slater 1983b; Cooper and Murphy 1985).

The fact that many birds will copy alien song from a foster-father but not from tutor tapes (Baptista and Petrinovich 1984) illustrates the importance of social rules for selective song learning. For a number of species, however, constraints are also imposed on the structural and temporal patterning of song.

One of the best examples is in sparrows of the genus Melospiza. For song sparrows temporal organizatiion is important: these birds fail to copy ordinary swamp sparrow song but will learn the syllables if they are sung in song sparrow phrases. However, swamp sparrows use different rules: only swamp sparrow syllables are learnt but they will learn these even if edited as song sparrow phrases. Although swamp sparrows are largely unresponsive to temporal organization they prefer to learn syllables from the first half of two-part song phrases (Marler and Peters 1977, 1981). Swamp sparrow song learning consists of selecting the number, timing and sequence of notes from a limited set of note-types, whose structure is heavily constrained (Marler and Pickert 1984).

Song sparrows and swamp sparrows which are cross-fostered from the egg to female canaries show differences in singing behaviour, particularly in features of song organization such as element length, duration of the phrase and degree of segmentation (Marler and Sherman 1985).

Although a pretty clear picture emerges for song and swamp sparrows little is known of the extent to which these rules are used by other species. Immelmann (1969) found zebra finches could copy song from Bengalese finch foster-parents and vice-versa but the songs of these cross-fostered birds have not been analysed in detail.

This study examines the extent to which zebra finches and Bengalese finches copy the song of their foster-father and the nature of the structural and temporal constraints.

METHODS.

Birds and Housing Conditions.

Of the nineteen clutches of zebra finches which were used in this study ten clutches were normally-raised (ZZ) and the remainder were transferred as eggs to pairs of Bengalese finch parents, whose own eggs were removed (ZB). Eighteen clutches of Bengalese finches were also used; half the birds were normally-raised (BB), the rest were cross-fostered to zebra finch parents (BZ).

Some parents, particularly zebra finches raising Bengalese finches, did not start feeding the young until the third or fourth chick had hatched. Even then cross-fostered Bengalese finch chicks often received insufficient food, probably because they lacked the typical zebra finch mouth markings and begging behaviour (see Chapter

2), so these chicks were fed by hand. To control for the effects of human contact all the chicks were handled daily for the first ten days of life.

The birds remained with their parents in double breeding cages until 4 months of age when the males' songs were recorded and analysed.

Song Recording and Analysis.

The song structure of each male was compared with that of his father by making tracings of sonagrams of typical song phrase (further details in Chapter 3) and the number of different song elements the young male learnt from the father was calculated as a proportion of the different elements in the young male's song. To take into account the differences in the length and number of elements in zebra finch and Bengalese finch song phrases a second measure was used. The proportion of the father's song that the young male learnt was calculated as a proportion of the number of different song elements the father sang in a typical song phrase.

In addition to song copying accuracy five other parameters were used to compare the song structure of the four groups:- (1). duration of a typical song phrase for each male, (2). total number of elements in the song phrase, (3). tempo, calculated as the number of elements per second, (4). number of repeated elements during the song phrase, (5). element structure, classified as either "zebra finch" or "Bengalese finch".

Zebra finch elements tend to possess a series of stressed harmonics not present in Bengalese finch song phrases. There may be as many as eight harmonics in a zebra finch song element but rarely more than four in a Bengalese finch element. A further difference lies in whether call notes are incorporated into the song phrase: these are particularly common in zebra finches and the long calls involved may be more than twice the length of other elements in the phrase. In view of these differences it is possible to classify song elements as either "zebra finch" or "Bengalese finch" and this is particularly useful in the case where a cross-fostered male's song elements are not obviously derived from the foster-father.

RESULTS.

The four groups were compared using the Kruskal Wallis test and the main differences are summarised in Table 6.I. Mann Whitney tests were then carried out to compare individual groups.

Differences Between Zebra Finch and Bengalese Finch Song.

Both species normally sing only one song phrase, repeated several times during any one song bout. For the 26 normally-raised zebra finches and 26 normally-raised Bengalese finches used in this study (i.e. 20 ZZ and 20 BB young and their fathers) the Bengalese finch song phrase was significantly longer ($z=4.5$, $P<0.01$), with more elements per song phrase ($z=4.2$, $P<0.01$) and more repeated elements ($z=4.7$, $P<0.01$). In both species the elements are usually sung in a fixed sequence, in the frequency range 0-8 kHz, and at about the same tempo.

There were no significant differences in the proportion of song learnt using either measure.

A Comparison of Song Learning in Normally-raised and Cross-fostered Males.

Table 6.II summarises the results of the Mann Whitney tests comparing cross-fostered zebra finches and Bengalese finches with normally-raised males of both species.

Zebra finches which had been cross-fostered to Bengalese finches sang phrases which were longer than normal zebra finch phrases but considerably shorter than those of their Bengalese finch foster-fathers, with fewer song elements per phrase. There were more repeated elements than appear in normal zebra finch song but significantly less than in Bengalese finch song.

Comparing cross-fostered zebra finches with both normally-raised zebra finches and Bengalese finches no significant differences were found in the proportion of song learnt from the father but ZB males did learn a significantly smaller proportion of the foster-father's song. This reflects the difference in phrase length of the Bengalese finch foster-father and zebra finch male.

Cross-fostered zebra finches tend to learn Bengalese finch song elements with as much accuracy as a zebra finch learning from his natural parents but these elements are usually sung in phrases which are more nearly zebra finch length (Fig. 6.1).

Bengalese Finches Learning Zebra Finch Song.

Cross-fostered Bengalese finches also tended to learn song elements from their foster-father but incorporated these into phrases typical of their species in length. However, they differed from both species in the total number of song elements and the number of repeats per phrase.

As a result of singing fewer, more widely spaced elements the tempo was also slower and the song resembled that of Bengalese finches which have been raised in a bird room but isolated from adult males (Chapter 5). These males learnt significantly less song than males from the other three groups. However, BZ males varied considerably: some learnt as accurately as normally-raised males learning from their Bengalese finch father whilst others learnt virtually nothing and improvised song elements or sang a series of call notes (Fig. 6.2). One male produced only subsong as an adult; the song was very quiet, with poorly formed elements which were not organized into song phrases.

DISCUSSION.

Common to both zebra finches and Bengalese finches is the tendency to organise song elements into species-specific phrases. In zebra finches this is achieved by repeating fewer Bengalese finch elements so that the phrase is only slightly longer than typical zebra finch song whereas Bengalese finches produce normal length song by repeating zebra finch elements and singing them at a slower tempo.

Temporal constraints on what a bird will learn seem to be generally applicable to many species of bird. One example is the chaffinch which will learn the song of a greenfinch or canary but will sing this in chaffinch phrases (Conrads 1977; Slater 1983b). One of the most remarkable examples is the marsh warbler which copies the songs from as many as 214 different species. However, the species-specific qualities of marsh warbler song are retained in the temporal and sequential patterning of these elements (Lemaire 1975).

For some species, e.g. the swamp sparrow, element structure acts as an important constraint for song learning (Marler and Peters 1977; Marler and Pickert 1984). In zebra finches this does not seem to be the case but it might be crucial for Bengalese finches: cross-fostered males learn fewer elements from the foster-father than normally-raised males which suggests that zebra finch elements are more difficult for a Bengalese finch to learn.

There are a number of reasons which might explain why cross-fostered Bengalese finches do not learn as accurately. The two species might simply use different rules to constrain what a young male can learn. Alternatively, differences in the structure of the two species' song might account for differences in accuracy. Bengalese finch song might be generally easier for a bird to learn because of the repetitiveness of the song elements. The length of the song phrase might also influence copying accuracy: it might be easier to learn alien song if the phrase is of a similar length to normal conspecific song; alternatively, a longer phrase might act as a supernormal stimulus and a shorter phrase might be suboptimal.

Behavioural differences could be important. Both Bengalese finches and zebra finches have similar song outputs (see Chapter 2) and unless song output falls to an abnormally low level there appears to be no affect on song learning (Bohner 1983; Chapter 3). Bengalese finches spend more time clumping, show less parental care, especially around the time of fledging, and are less aggressive (ten Cate 1982, Chapter 2): these differences might have important consequences for song learning.

A consequence of the difficulties in using zebra finches as foster-parents is that the cross-fostered Bengalese finch clutches tended to be smaller and, if the number of siblings influences how accurately birds learn song then this introduces a bias into the results. Young males might stimulate each other to practise: this appears to be the case for males isolated from adult song during the sensitive phase for song learning (Eales 1987b for zebra finches; Chapter 5 for Bengalese finches). Brothers might learn from each other, although this seems less likely in view of the fact that males which have been raised by their mother alone often develop quite different songs (Eales 1987b). Sisters and other females with whom the males can interact might influence song learning; this is certainly true for brown-headed cowbirds, Molothrus ater (King and West 1983; West and King 1985) and red-winged blackbirds, Agelaius phoenicus (Marler et al 1972) where social stimulation from the females biases the young males against learning alien species' songs. Visual imprinting on siblings could also sway the preference away from the foster-father (see ten Cate et al 1984 for its effect on sibling recognition).

Comparing normally-raised and cross-fostered zebra finches and Bengalese finches reveals some of the rules which constrain song learning and the extent to which the young males are biased towards learning conspecific song. It is also instructive to compare these results with males raised in absence of a song tutor, either Kaspar Hauser or by the mother alone. Males of both species produce highly abnormal song when denied a song tutor during the sensitive phase for song learning: their songs tend to be of a slower tempo, with fewer elements and little, if any, normal phrasing (Eales 1987b for zebra finches, Chapter 5 for Bengalese finches). This comparison shows that interaction with either a conspecific or a heterospecific male affects song acquisition and illustrates how certain rules can be modified by experience. In zebra finches, for example, exposure to any adult male is sufficient for a young male to organise his song elements into phrases. In this sense, the adult male acts as a non-specific stimulus for selective song development.

The following four chapters consider which aspects of adult males make them suitable stimuli by examining the relative importance of visual and vocal cues for what a bird learns and when.

TABLE 6.I: A comparison of cross-fostered and normally-raised zebra finches and Bengalese finches, showing median values for each group.

Parameter.	ZZ	BB	ZB	BB	Kruskal Walli value
Duration of song phrase.	0.7	1.2	0.8	1.2	38.0***
No. elements per phrase.	8.5	14.0	9.0	11.0	21.0***
Tempo	13.8	13.8	13.8	8.9	31.0***
No. repeats per phrase.	0	4	2	3.5	35.0***
Prop. song learnt from father.	0.83	0.79	0.80	0.47	ns
Prop. father's song learnt.	0.73	0.68	0.69	0.36	8.4*

TABLE 6.II: The results of Mann Whitney tests (U values) comparing parameters of song in cross-fostered and normally-raised males of both species.

Parameter	Group comparison:	ZZ (n=20)	BB (n=20)
Duration of song phrase.	ZB (n=15)	84 *	59 ***
	BZ (n=10)	42 **	ns
No. elements per phrase.	ZB	ns	17.5 ***
	BZ	47 **	37 **
Tempo.	ZB	ns	ns
	BZ	11.5 ***	5 ***
No. repeats per phrase.	ZB	40.5 **	88 *
	BZ	15.5 ***	56 *
Prop. song learnt from father.	ZB	ns	ns
	BZ	45 **	53 *
Prop. father's song learnt.	ZB	70.5 **	89.5 *
	BZ	39.5 **	52.5 *

Figure 6.1:

Sonagrams of the Bengalese finch father (BF), C, his zebra finch son (Z), YB2, and his Bengalese finch son (B), P8.

YB2 learnt from the foster-father. Only one of the sections (e) was repeated.

P8 also copied his father's song. His song contains 4 repeated sections (a, b, c and d) and the father repeats 3 sections (section c is repeated once, d is repeated twice and e is repeated once).

Letters below the sonagrams show sections of song common to two or more males.

FIG 6·1

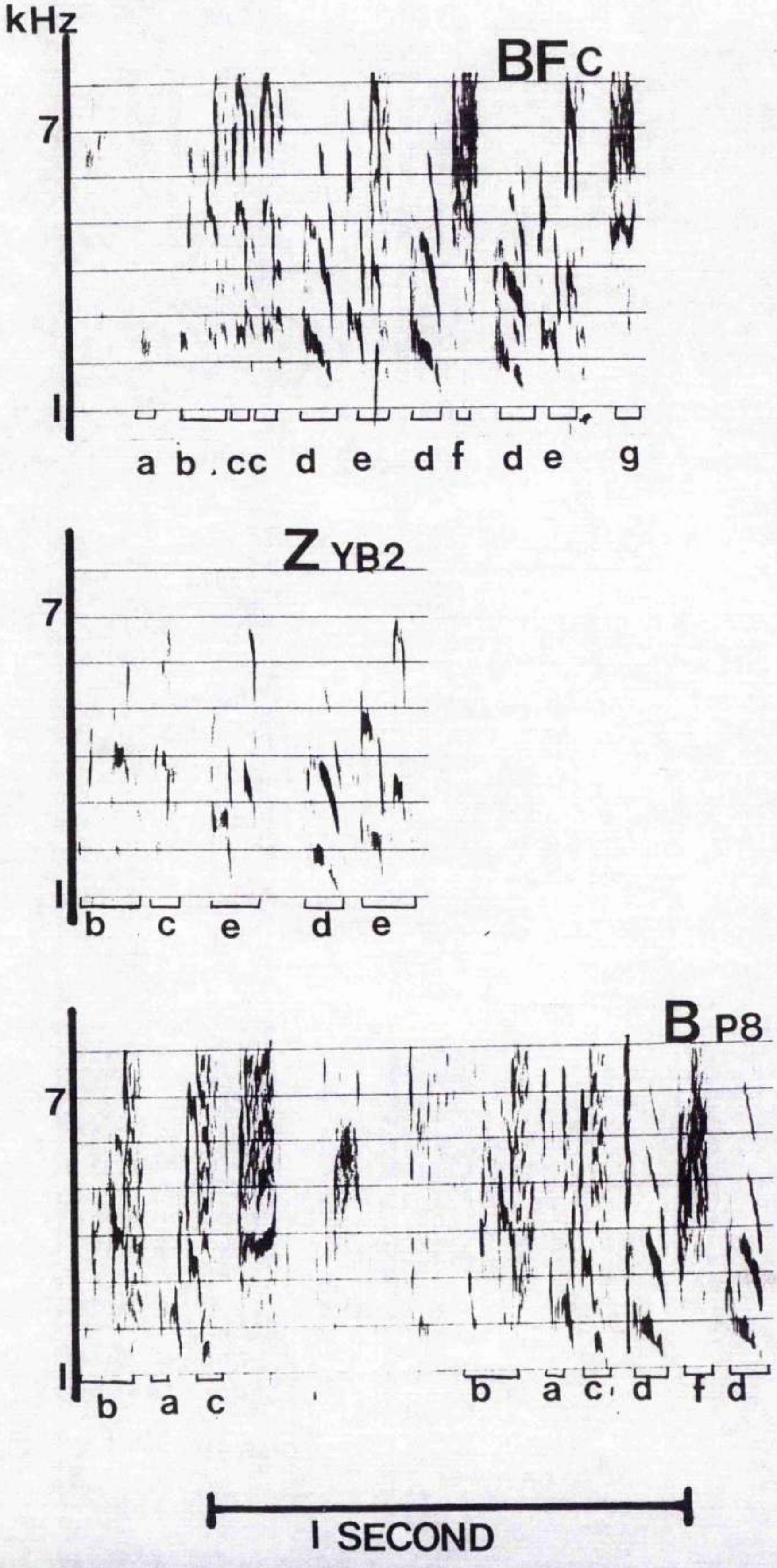

kHz
7
1
BF C
a b . cc d e d f d e g
Z YB2
7
1
b c e d e
B P8
7
1
b a c
b a c d f d
1 SECOND

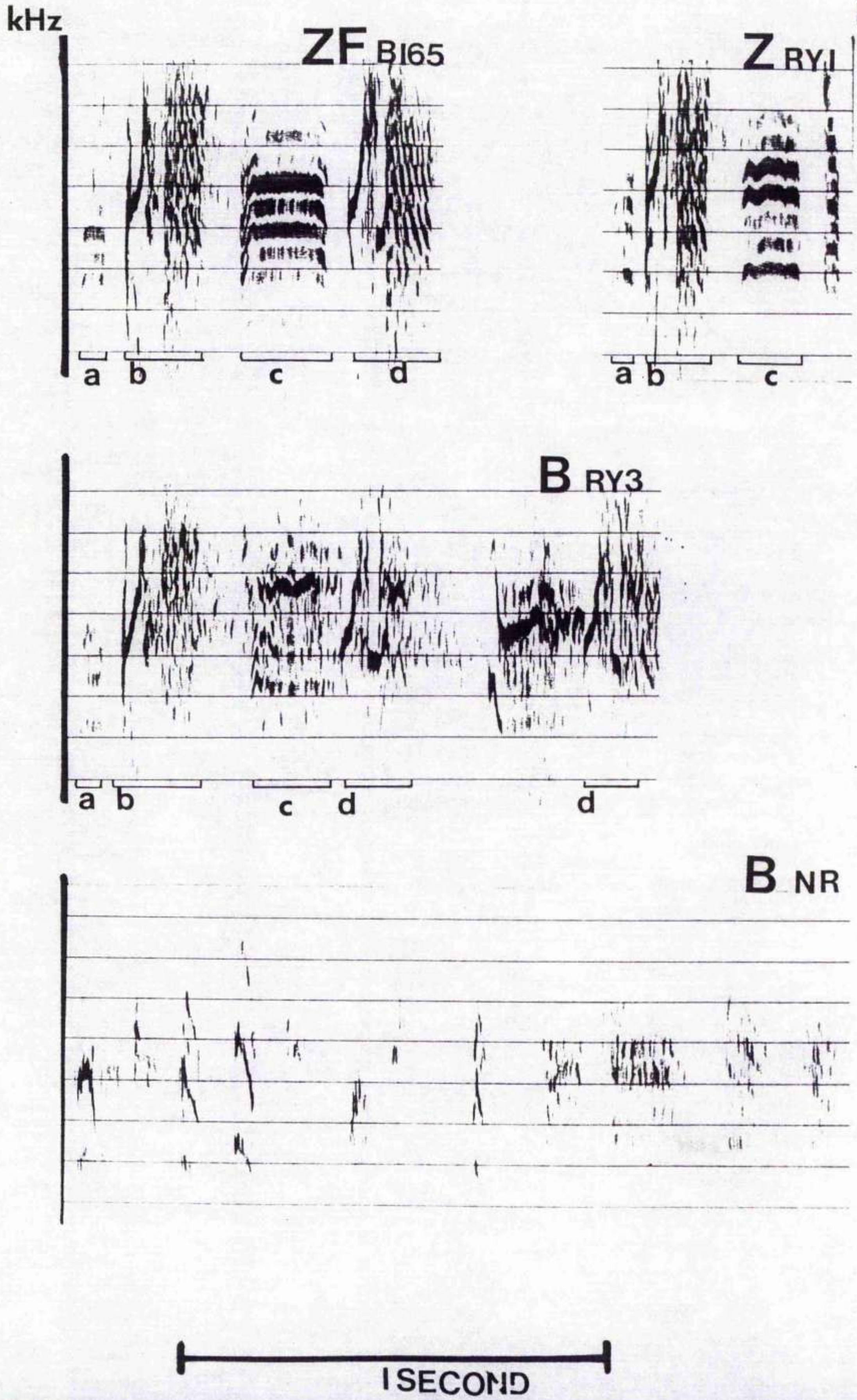
Figure 6.2:

Sonagrams of the zebra finch father (ZF), B165, his zebra finch son (Z), RW1, and two Bengalese finch sons (B), RY3 and NR.

Both RW1 and RY3 based their songs on the father but RY3 repeated section d; repeating elements within a song phrase is a feature typical of Bengalese finches. NR sang a series of very quiet elements which were not split up into phrases and resembled subsong.

Letters below the sonagrams show sections of song common to two or more males.

FIG 6·2



Chapter 7.

SONG TUTOR CHOICE IN ZEBRA FINCHES AND BENGALESE FINCHES: THE IMPORTANCE OF VISUAL AND VOCAL CUES.

ABSTRACT.

This chapter examines the relative importance of visual and vocal cues for song tutor choice in zebra finches and Bengalese finches by exposing young males of each species to two song tutors at independence, a zebra finch singing Bengalese finch song and a Bengalese finch singing zebra finch song. All the males tended to learn from the conspecific song tutor, irrespective of whether they had been raised by a pair of conspecifics, the female alone or cross-fostered to a pair of the other species. These results suggest that visual differences, both in appearance and behaviour, are important in biasing a young male in favour of learning from the conspecific tutor. However, there are also vocal differences between the two species which might account for the own-species bias. Parental influences before independence appear to be relatively uninfluential but siblings may be important, both the species and number per clutch: this is a factor which has been overlooked in previous studies of song learning.

Chapters 7 and 8 jointly form a paper which is due to appear in Behaviour (in press).

INTRODUCTION.

One of the most important points to emerge from the past ten years of research on bird song learning is that, for a number of species, the young bird must interact with a live song tutor if song is to develop normally.

The method of song model presentation plays a crucial role in determining what a bird will learn and from whom (Baptista and Petrinovich, 1984). A song tutor who behaves abnormally may fail to be recognised as a suitable model for copying and, for a number of species including the zebra finch playback tapes are insufficient for song learning (Eales 1985). Even in species which do learn from tutor tapes anomalous results may be obtained which do not match interactions with live song tutors in the wild. One example is the marsh wren : Kroodsma and Pickert (1984) showed that young males will only learn from tutor tapes in the autumn but are capable of learning from adult males both then and in the following spring. Waser and Marler (1977) found that canaries learn fewer song elements from tape recordings than from live song tutors.

Social interactions with non-singing females may also influence what a bird will learn. This is certainly true for cowbirds: M.a.ater males who are reared with females alone develop different repertoires when they are housed with M.a.ater females from those housed with M.a.obscura females even if they are simultaneously exposed to tutor tapes of M.a.ater song. Since females do not sing these differences in male song cannot result from copying adult song (King and West 1983; West and King 1985). This also seems to be the case for red-winged blackbirds which only learn northern oriole, Icterus galbula, song if they are isolated without female conspecifics (Marler et al 1972).

A recent study by Eales (1985) on zebra finches suggests that the mother might influence a young male's choice of song tutor: female-raised zebra finches which are subsequently housed with the father and an unrelated male during the sensitive phase for song learning prefer to learn from the father even though they had no previous experience with him provided the mother is still present. Normally-raised zebra finches also prefer to copy the father's song (Bohner 1983). However, if he is not one of the two tutors they experience during the sensitive phase, they tend to base their songs on that of the tutor whose song is most similar to the father (Chapter 3).

Both visual and vocal cues are likely to influence what a bird will learn and from whom. Physical interactions might also be important. In indigo buntings males copy the songs of individuals they interact with socially and aggressive encounters seem particularly important (Payne 1981). Aggression also appears to influence zebra finch song tutor choice: when housed with two song tutors males tend to learn from the tutor who is most aggressive towards them (Chapter 3). However, physical contact is not essential and zebra finch song development will proceed normally provided visual and vocal interaction with the tutor is maintained throughout the sensitive phase for song learning (Eales 1985).

Visual cues are crucial for song learning in several species including nightingales (Todt et al 1977; Todt and Hultsch 1985), canaries (Waser and Marler 1979) and indigo buntings (Payne 1981). Vocal interactions are also likely to be important, and for zebra finches (Price 1979) and Bengalese finches (Dietrich 1981) calls might act as markers of species-specificity.

The question of the relative importance of visual and vocal cues for song learning still remains, as well as that of the extent to which these are affected by social interactions with the mother and father before the sensitive phase for song learning. This study examines these questions in zebra finches and Bengalese finches by providing young males with the opportunity to learn from two song tutors, a zebra finch that sings Bengalese finch song elements and a Bengalese finch that sings zebra finch song elements.

METHODS.

Birds and Housing Conditions.

Thirteen clutches of zebra finches and fourteen clutches of Bengalese finches were raised in one of three conditions: by a pair of conspecifics (groups A and D), by a conspecific female (groups B and E) or cross-fostered to a pair of the other species (groups C and F). Table 7.I summarises the conditions for the six groups.

To control for the effects of egg swopping the eggs from each pair of birds were removed and replaced by a fresh clutch of conspecific (groups A,B,D and E) or heterospecific eggs (groups C and F). All the birds were raised with their foster-parents until independence (mean age of the brood = 35 days).

During the normal sensitive phase for song learning at about 5 to 10 weeks of age, the young males were housed with two song tutors which, as a result of having been cross-fostered from the day before hatching until sexual maturity, had copied the alien song of their fost-father: the zebra finch tutor sang Bengalese finch song elements and the Bengalese finch tutor sang zebra finch song elements (Figs. 7.1 and 7.2 and Chapter 6).

The tutors were separated from each other and from the young birds by wire mesh screens which divided the cages into three portions so preventing physical encounters. After 70 days the tutors were removed and the young males remained with other members of their brood until 4 months of age when their songs were recorded and analysed on the sonagraph.

Method of Song Analysis.

Song elements were classified as either common to both a tutor and the young male or as unrelated in structure on the basis of visual similarity of the sonagraphed elements and the sequence in which they occurred (see Chapter 3 for further details). This allowed poorly copied elements to be assigned to a particular category on the basis of context and where ambiguities arose independent observers were used to make the assessment. It was not always possible to calculate the amount of song a young bird learnt because the standard of copying was very poor in some cases, and so a qualitative assessment was made of whether the male learnt at least one element from either, both or neither tutor. In Fig. 7.3, for example, male H has a very poor song with some zebra finch elements copied from the Bengalese finch tutor and a zebra finch distance call.

RESULTS.

The results are summarised in Table 7.II, which shows the number of males in each group which learnt from each tutor. In all the groups males tended to learn from the conspecific tutor (further details in Appendix 7a).

Of the eight normally-raised zebra finches (group A) six copied Bengalese finch elements from the zebra finch tutor, one produced a hybrid song containing elements from both tutors and one male improvised his song with a series of zebra finch distance calls (Fig. 7.4). One zebra finch in group B also sang a series of improvised elements and conspecific call notes; the remaining nine, which had been raised by their "mother" alone, learnt Bengalese finch elements from the conspecific and two of these also learnt zebra finch elements from the Bengalese finch tutor. One of the cross-fostered males in group C based his song exclusively on the Bengalese finch, while seven copied Bengalese finch elements from the zebra finch and the remaining two sang hybrid songs (see Fig. 7.3).

A similar pattern of song learning was shown by the Bengalese finches. Six males in both groups D and E learnt from the conspecific while the remainder produced hybrid songs. Of the cross-fostered birds in group F two sang hybrid songs, four learnt zebra finch elements from the conspecific and two learnt Bengalese finch elements from the zebra finch . These results indicate a bias towards learning from the conspecific tutor, despite the inappropriate song elements which that male produces, or of previous experience with the "parents" (Fig. 7.5).

Although there was no significant difference betweeen the groups in the number of males who learnt at least one element from each tutor (Fisher exact test for A vs B, A vs C, D vs E, D vs F), the groups varied considerably in the accuracy with which they copied individual elements. Copying accuracy was poor in both cross-fostered groups; this was particularly so for the Bengalese finches in group F. Some of these males tended to produce a series of elements which were not divided up into phrases (n=2), songs which contained more widely spaced elements (n=3 - see bird G in Fig. 7.3), and songs with portions of subsong (n=1).

The males which had been cross-fostered to a pair of heterospecifics tended to base their song on the heterospecific song tutor as well as the conspecific. Three males in group C and six males in group F learnt at least one element from the heterospecific compared with one normally-raised zebra finch and three normally-raised Bengalese finches but this difference was not statistically significant. Nonetheless it does suggest some influence of the foster-parents before the chicks gain independence at about 35 days of age. It is interesting that none of the birds copied elements from their "father" which they had only heard before this time.

At least one male in all six groups produced a hybrid song. Bengalese finches had a greater tendency to copy portions of their song from both tutors but the difference between the two species did not reach statistical significance (χ^2 test, n.s. for A,B,C vs D,E,F).

DISCUSSION.

Zebra finches and Bengalese finches which are exposed to two tutors, a zebra finch singing Bengalese finch song and a Bengalese finch singing zebra finch song, immediately after independence show a tendency to learn from the conspecific irrespective of which species raised them.

One possible reason for this apparent "own species bias" is that young males may learn from a tutor who has the visual appearance of their species. For zebra finches visual interaction with a song tutor is required for learning to take place (Eales 1985): the same is likely to be true for other estrildids including the Bengalese finch. Estrildid finches have a quiet song, which is high in frequency and rich in harmonics: these qualities place severe limits on the distance of sound transmission (Immelmann 1968), especially as different frequencies attenuate at different rates (Konishi 1970). For young birds to be able to hear details of such a quiet song the tutor would need to be close and therefore likely to be visible. This might explain why visual contact is important for song learning in zebra finches and Bengalese finches. For each species the groups did not differ significantly in tutor choice which suggests that visual cues from the parents are relatively uninfluential. However, siblings might bias song tutor choice, a factor which has often been overlooked in the past, but one which is known to be crucial in the development of sexual preference (Kruijt et al 1983). The number of birds in the clutch, and the number of each sex, might be important. A subtle point here is that, because of the difficulties in rearing birds by the other species, particularly for Bengalese finches cross-fostered to zebra finch parents, there tend to be fewer siblings per clutch. The greater tendency for cross-fostered Bengalese finches to learn from the zebra finch may be related to this.

Both visual appearance, especially plumage, and behavioural differences between the two species might bias learning in favour of the conspecific. Cross-fostered zebra finches receive less parental care from their Bengalese finch parents (ten Cate 1982; ten Cate et al 1984) and Bengalese finches are also less aggressive towards their young (Chapter 2). This last difference might be very important for song tutor choice (Chapter 3). As well as these basic differences between the species, adults may also differ in their reactions to chicks of their own species and those of the other. This is most obvious in mixed-species pairs (ten Cate 1982) where the conspecific parent tends to feed the chicks more and to direct more contact behaviour and aggression towards them. In mate choice tests the young males subsequently prefer a female of their own species (ten Cate 1985). Although it has not been tested, a preference for a conspecific song tutor could also be established through such behavioural interactions. Zebra finch chicks reared by a male of their own species and a Bengalese finch female will cease to prefer a female of their own species if interactions with the male that reared them are reduced, even though they can still see him. From this ten Cate et al (1984) argued that behavioural interaction, rather than just visual and vocal stimulation, is the important factor leading to mate preference. The same might also be true for song learning (see Chapter 3, 9 and 10)).

In this study behavioural interactions between the young males and their tutors were minimised by separating the two tutors from each other and from the young males by wire mesh screens. Nonetheless, previous interactions with the parents before independence might be important. In this situation, however, it seems unlikely since there was no significant difference in song learning between the normally-raised males and those which had been raised by the other species.

The results presented in this chapter might be taken to suggest that visual cues are more important than vocal ones for song tutor choice in zebra finches and Bengalese finches. However, another factor which might bias learning stems from species-specific differences in vocalizations. Zebra finches are capable of copying song from a Bengalese finch tutor but they tend to sing these Bengalese finch elements in phrases which are more nearly zebra finch in length (Chapter 6). Bengalese finches can also learn from the other species: these males tend to sing zebra finch elements in longer phrases, with elements being repeated in typical Bengalese finch fashion. These elements tend to be copied inaccurately and more widely spaced so that the song is sung at a slower tempo. These basic differences in the length of the song phrase, and the number and repetition of the elements might act as important markers of species-specificity. An additional feature is that species-specific call notes are often incorporated into song by zebra finches but not by Bengalese finches; they might serve as a label indicating the suitability of a song tutor.

If these factors are important for own-species bias in song tutor choice, an interesting question concerns the use of song elements: do males base their song on that of a normal conspecific when exposed to two tutors, one who sings a normal song and one who sings elements copied from the other species? This is the subject of Chapter 8.

Table 7.I: Housing conditions for the six groups.

Group.	Housing condition.		Total no. males.
	♂	♀	
(1). Zebra finch chicks.			
A	Z	Z	8
B		Z	10
C	B	B	10
(2). Bengalese finch chicks.			
D	B	B	9
E		B	10
F	Z	Z	8

Table 7.II: The no. of males which learnt from each tutor in the six group

Group	ZBS	BZS	Hybrid	Neither	Total
(1). Zebra finch chicks.					
A	6	0	1	1	8
B	7	0	2	1	10
C	7	1	2	0	10
(2). Bengalese finch chicks.					
D	0	6	3	0	9
E	0	6	4	0	10
F	2	4	2	0	8

Figure 7.1:

Sonagrams of a Bengalese finch male, Y3, learning zebra finch song elements (BZS) from his zebra finch foster-father (ZF), B165.

Letters below the sonagrams show sections of song (one or more elements) common to both males.

FIG 7·1

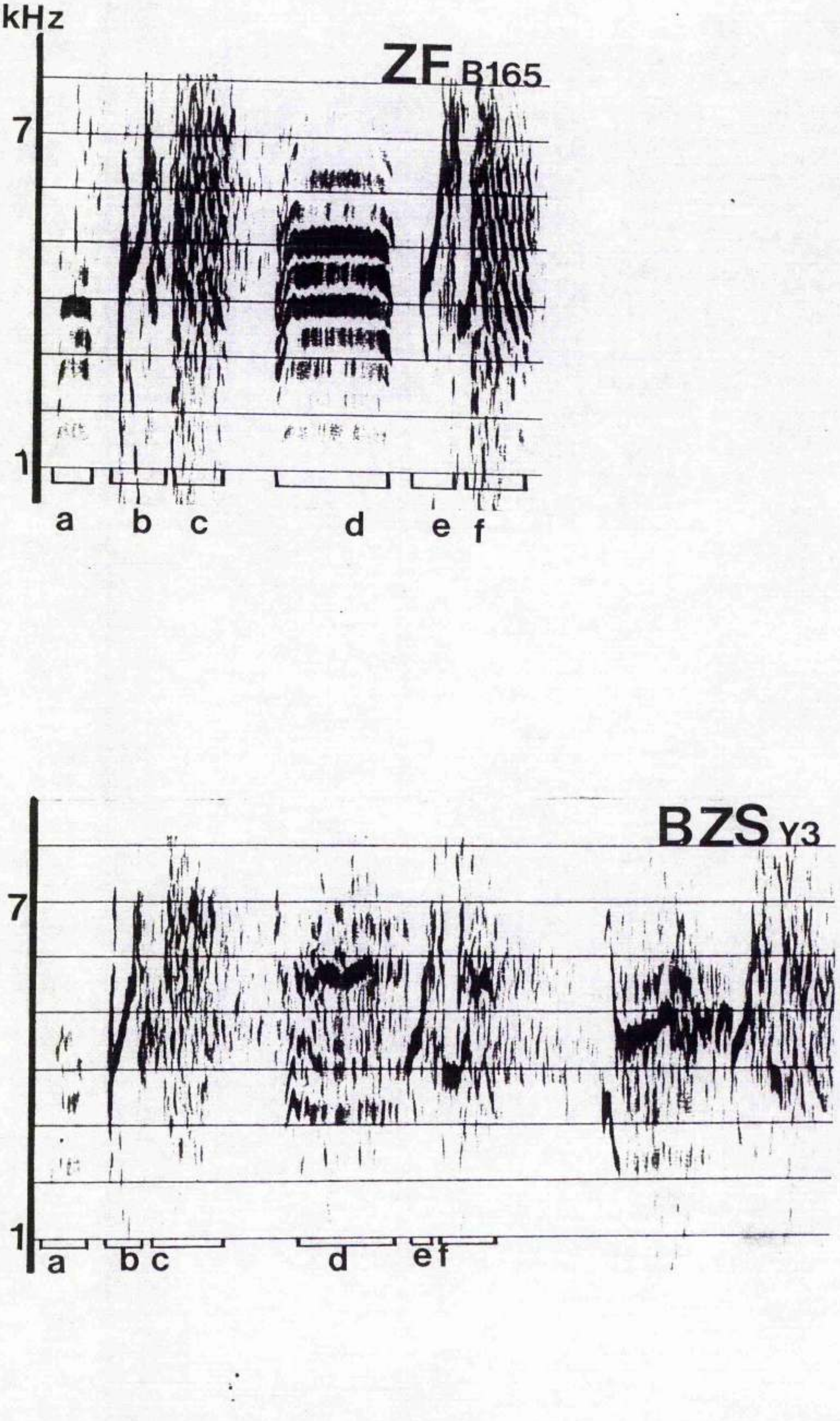


Figure 7.2:

Sonagrams of the zebra finch male, YB2, learning Bengalese finch song elements (ZBS) from his Bengalese finch foster-father (BF), P40.

Letters below the sonagrams show sections of song common to both males.

FIG 7·2

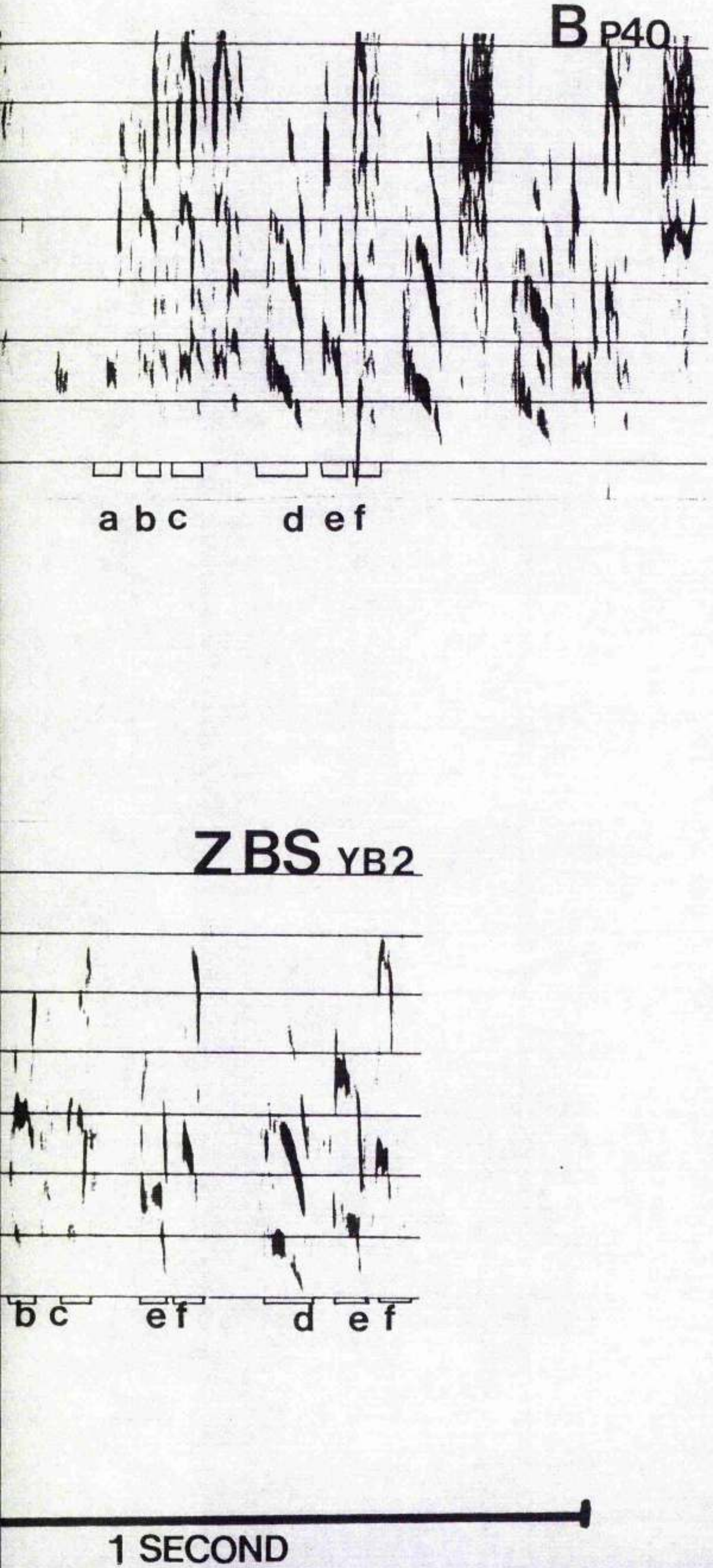


Figure 7.3:

Sonagrams of two Bengalese finch males (B), G and H, who were housed with B1, a zebra finch singing Bengalese finch song elements (ZBS), and PB10, a Bengalese finch singing zebra finch song elements (BZS). Bird G (group F) learnt elements from both the tutors and adds a long zebra finch distance call (zc) which is similar to that present in PB10's song. Bird H (group E) has a very poor song containing a zebra finch distance call (zc) and inaccurately copied elements from PB10's song.

Letters below the sonagrams represent portions of song common to two or more males.

FIG 7·3

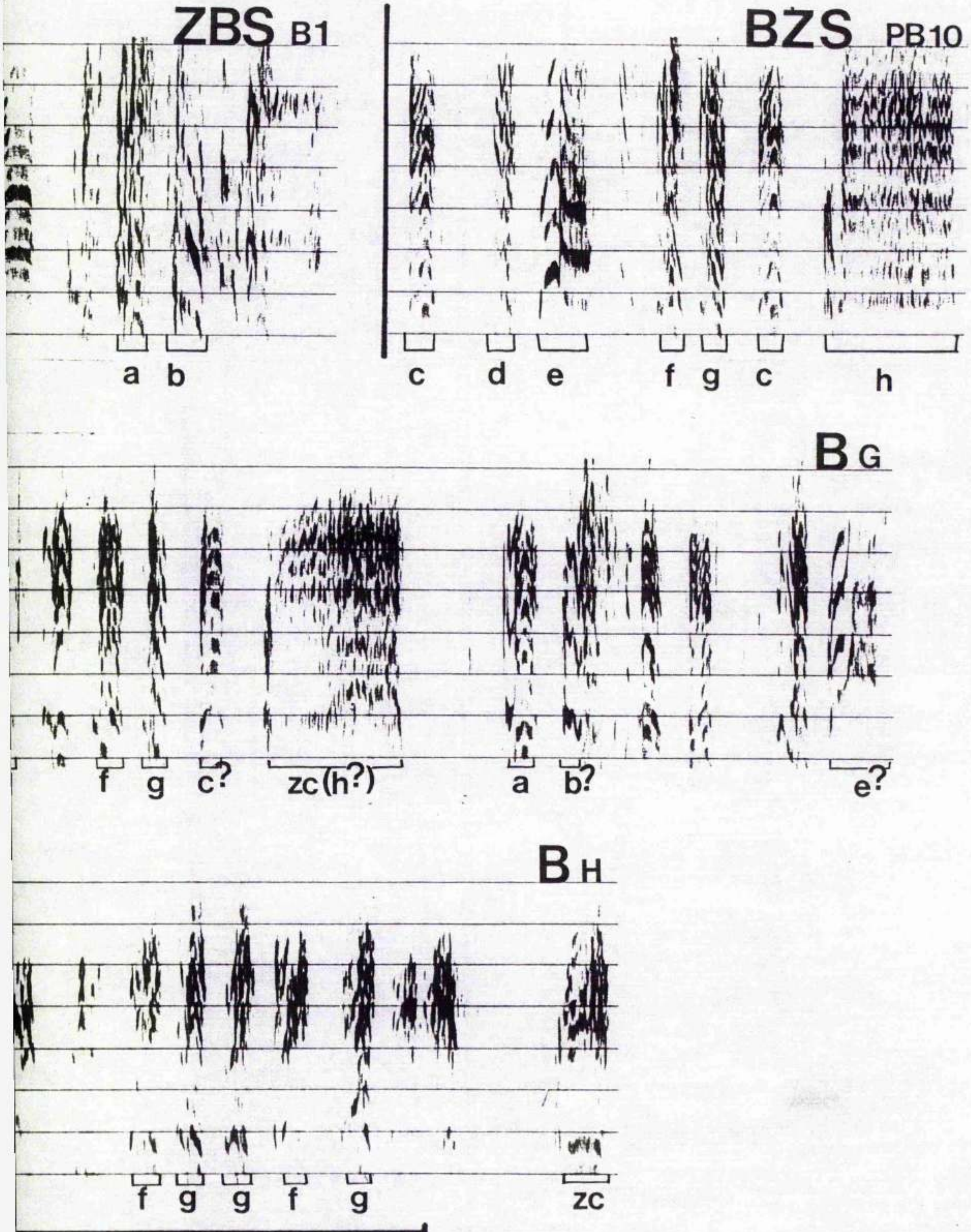


Figure 7.4:

Sonagrams of B142 and B146, two zebra finch males (Z) from group A, and those of their zebra finch tutor Y408 (ZBS). Fig. 7.1 shows a sonagram of their Bengalese finch tutor's song (Y3). B146 based his song on that of the conspecific whereas B142 improvised his song with a series of zebra finch distance calls (zc).

Letters below the sonagrams show portions of song common to two or more males.

FIG 7·4

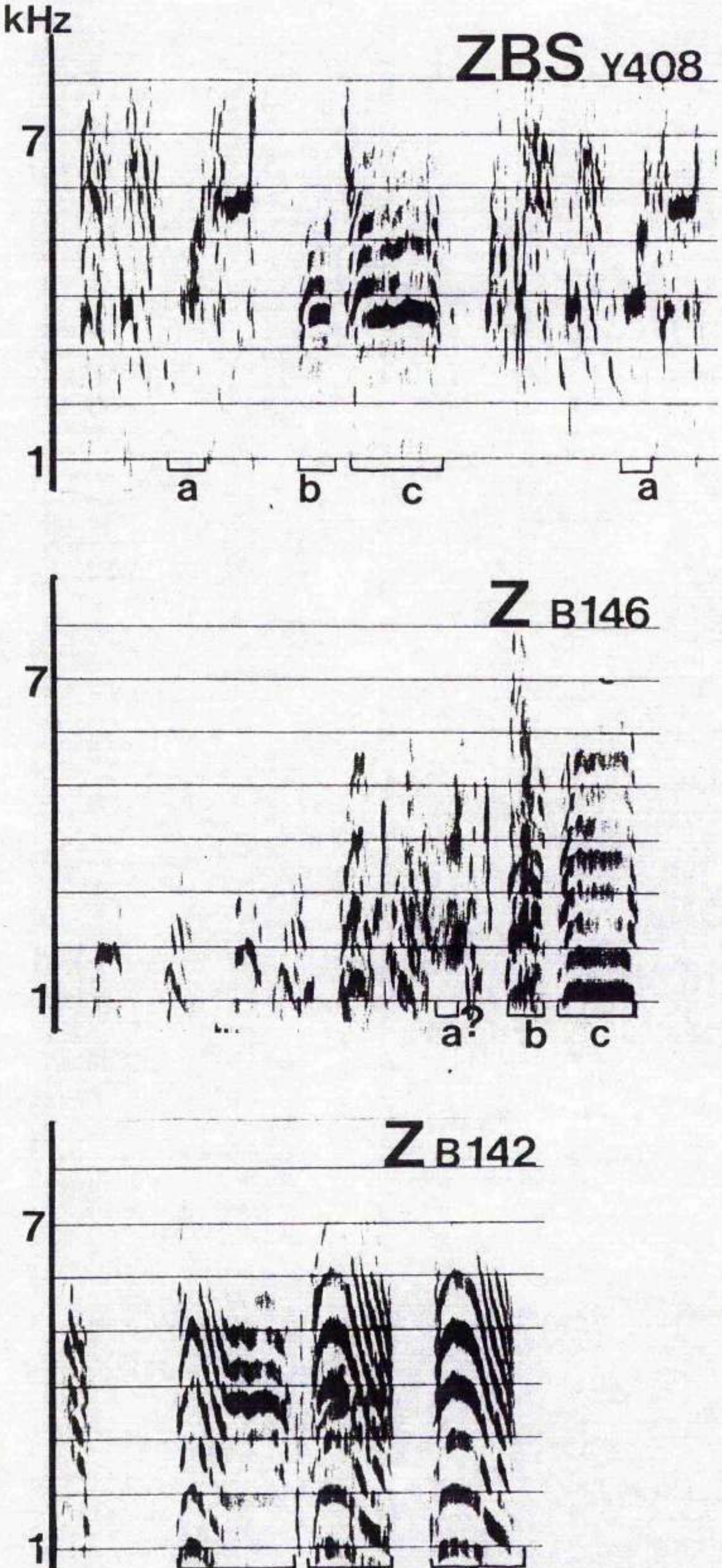


Figure 7.5:

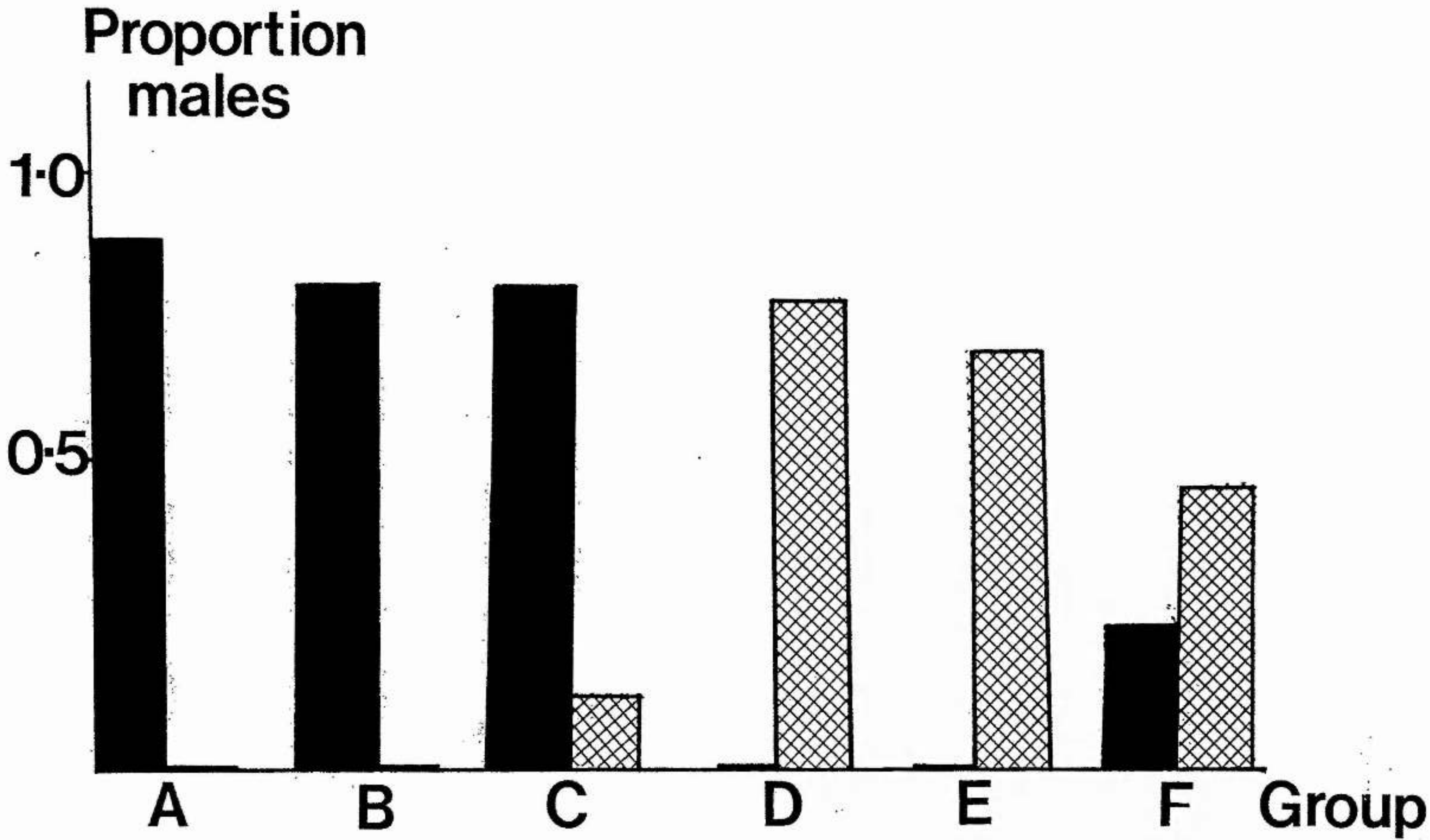
A histogram of the proportion of males in each group who learnt from the two tutors.

Key:-

■ ZBS Tutor

□ BZS Tutor

FIG 7·5



Chapter 8.

HOW IMPORTANT ARE SONG ELEMENTS FOR SELECTIVE VOCAL LEARNING IN THE ZEBRA FINCH?

ABSTRACT.

This study considers whether song elements are important for selective vocal learning in the zebra finch. Young males were given the choice of two conspecific song tutors at independence, one who sang normal zebra finch song and one who sang Bengalese finch elements. There was no tendency to learn zebra finch elements; this was irrespective of whether the males had been raised by a pair of zebra finches, the female alone, or cross-fostered to a pair of Bengalese finches. The most likely explanation is that element-type is not important for song tutor choice in zebra finches. There is even the hint that males raised by a conspecific female or cross-fostered to Bengalese finches prefer to learn from the ZBS tutor and it is suggested that Bengalese finch elements might provide a super-normal song stimulus.

Chapters 7 and 8 jointly form a paper which is due to appear in Behaviour (in press).

INTRODUCTION.

For the vast majority of passerines constraints on song learning ensure that only species-specific songs are sung in the wild and, in many species, structural and social rules go hand in hand to ensure normal song learning. In the white-crowned sparrow for example, there are strict structural constraints; despite extensive tutoring from tapes at suitable times, young males will not sing the songs of alien species even if these are similar to their own (Marler 1970). With social tutoring, however, these structural constraints are slackened and young white-crowned sparrows will even learn the song of a strawberry finch with which they are housed from 50 days (Baptista and Petrinovich 1984).

Zebra finches can also learn elements from a strawberry finch or a Bengalese finch foster-father (Price 1979; Immelmann 1969) but these song elements are sung in shorter phrases which are more nearly zebra finch in length (see Chapter 6). They copy Bengalese finch elements quite accurately but tend to repeat them less frequently within a song phrase: normally-raised zebra finches tend not to repeat elements whereas Bengalese finches may repeat two or three elements several times per phrase. Another species-specific characteristic of zebra finches is the inclusion of call notes into the song phrase. These call notes might be one means of recognising conspecifics because most of the call repertoire develops without learning. However, the male distance call does require learning: males which do not gain normal experience during the first 40 days of life are unlikely to produce a normal distance call and males which have been cross-fostered to Bengalese finches tend to lack the sexually dimorphic noise element at the end of the distance call or to sing a Bengalese finch call note (Zann 1985).

Given these structural constraints on the temporal patterning of zebra finch song a crucial question concerns the significance, if any, of learning species-specific song elements. The results in Chapter 7 suggest that the visual features of a song tutor are more important than the type of song elements which he sings: zebra finches prefer to learn from a zebra finch singing Bengalese finch song rather than a Bengalese finch singing zebra finch song. But, is the distinction between a zebra finch singing Bengalese finch song and one which sings typical zebra finch elements a functional one? The present study examines whether species-specific song elements influence song tutor choice by giving young males the choice of two zebra finch tutors, one who sings a normal song and one who sings Bengalese finch song elements, during the sensitive phase for song learning. The extent to which parental influence before the sensitive phase influences song element selection can be evaluated by comparing normally-raised birds with those which have been cross-fostered during the first five weeks of life.

To investigate whether there is any auditory predisposition to learn certain types of element normally-raised males are also compared with those raised by the mother alone. Female-raised zebra finches which are housed with a song tutor during the sensitive phase will learn as accurately as those raised by both parents. However, if normally-raised males are subsequently housed with two different tutors at independence, one who has at least 75% of his song elements in common with the father and one who has a very different song, they prefer to learn from the one whose song is similar to their father's (Chapter 3).

In the experiment described here specific song elements are not shared by the father and one of the tutors: the discrimination is at a grosser level. Do zebra finches prefer to learn conspecific song elements and to what extent is this influenced by previous experience with the father and mother?

METHODS.

Birds and Housing Conditions.

Zebra finches were raised in one of three conditions: by a pair of conspecifics (group A), by a conspecific female alone (group B), or cross-fostered to a pair of Bengalese finches (group C). The conditions for the three groups are summarised in Table 8.I.

To control for the effects of egg swopping the eggs from each pair were removed and replaced by a fresh clutch of conspecific or heterospecific eggs. All the birds were raised by their foster-parents until independence.

At 35 to 70 days, during the normal sensitive phase for song learning, the young males were housed with two zebra finch song tutors, one who had a typical zebra finch song (Z) and the other who sang Bengalese finch song elements (ZBS), as a result of having been raised by a pair of Bengalese finches until sexual maturity. Fig. 8.1 shows typical sonagrams of Z and ZBS song.

To control for the effects of differences between tutors, six Z and six ZBS males were used so that the same tutor pairs could be used for all groups, with one pair per clutch. However, one pair of tutors was used only once because there were six clutches of group A but only five clutches of groups B and C.

To prevent physical encounters the tutors were separated from each other and from the young birds by wire mesh screens which divided the cages into three identical portions. This is important because the ZBS tutors behave differently from normal Z males. As a result of having been raised by the other species they tend to be less aggressive and subject to more supplanting attacks and pecks by other, normally-raised males with whom they can interact. These behavioural differences are likely to confound the choice of song tutor (Chapter 9).

Songs and Sonagrams.

The songs of all the males were recorded when the birds were four months old. The tutors' distance calls were also recorded (Fig. 8.2). The songs and calls were analysed using the sonagraph (see Chapter 3 for details). The amount of song each male learnt was calculated in two ways and the mean value taken. The first measure calculated the number of different song elements the young male learnt from each tutor as a proportion of the different elements in the young male's song. The second measure took into account differences in the number of elements in the tutors' songs by taking the number of different elements a young male learnt as a proportion of the total number of different elements in each tutor's song.

RESULTS.

Table 8.II shows the number of males who based their song on Z, on ZBS and on both tutors (further details in Appendix 8a). Of the 11 normally-raised males in group A, five copied Z, four sang Bengalese finch elements from ZBS and one male produced a hybrid song with elements from both males. Two males in group B also sang a hybrid song. Of the other nine raised by their "mother" alone, seven based their songs on the ZBS tutor and two copied the Z tutor. Group C also tended to learn from the ZBS tutor: eight out of nine sang Bengalese elements from the ZBS but two of these also sang conspecific elements which they had learnt fron the Z tutor. Only one male in this group sang pure zebra finch song. The results of tests on the number of males in each group who learnt at least one zebra finch element from the Z tutor, and the number of males per group who learnt at least one Bengalese finch element from the ZBS tutor, give no significant differences between the three groups.

All the males tended to copy both zebra finch and Bengalese finch elements accurately. Fig. 8.1 shows sonagrams of a male in group A who learnt from the Z tutor and a male in group C who learnt from the ZBS tutor. There was considerable variation between males, however, in the amount of song they copied from each tutor. In one clutch from group A, for example, where all three brothers based their songs on the ZBS tutor, one male learnt 0.4 of his song, one learnt 0.58 and one learnt 0.8 of his song. The histograms in Fig. 8.3 show the mean proportion of song learnt from each tutor for the three groups. Kruskal Wallis tests on the proportion of song learnt from the Z and ZBS tutors respectively give no significant difference between the groups.

Only one of the Z tutors, G43, repeated any element within each song phrase whereas all the ZBS tutors repeated at least one element, although none repeated an element more than once. To test whether these repeated elements are more easily learnt the song learning results of the 22 males who sang ZBS song and the one male who learnt from G43 were analysed. A Wilcoxon test comparing, for each male, the proportion of learnt elements which the tutor had and had not repeated shows a significantly greater tendency to learn repeated elements ($T=68.5$, $n=23$, $p<0.05$ for a one-tailed test).

Table 8.III compares the number of males in each group who learnt from each pair of tutors and the type of distance call they sang to see whether males tended to learn from a tutor with a normal zebra finch distance call. The songs of each tutor was copied by at least one male and, although no control was made for variation in the calls of ZBS tutors, the results did not suggest a tendency to learn from specific tutors.

DISCUSSION.

The most important result presented in this chapter is that zebra finches show no tendency to learn conspecific song elements: normally-raised males are equally likely to copy Bengalese finch song elements provided they are sung by a zebra finch tutor and, for zebra finches raised by a conspecific female or cross-fostered to a pair of Bengalese finches, there is even the suggestion of a preference for the ZBS tutor.

The most likely explanation is that species-specific elements are not important for song tutor choice. The birds might use other vocal cues such as phrase length, the temporal patterning of elements within a phrase, and call notes. All the zebra finches which learnt Bengalese finch song added call notes to their vocal repertoire; these accompany the singing bouts and are often incorporated into the song phrase with other song elements. The results in the previous chapter suggest that other cues, primarily from visual interactions, are important for species-selectivity.

Chapter 3 suggested that song elements were important for tutor choice but this was at a much finer level of discrimination: males preferred to learn from a tutor whose song contained a large proportion of the father's song elements. This study used Z tutors whose songs were as dissimilar as possible from the fathers', yet still within the range of "normal" zebra finch song (Sossinka and Bohner 1980), in order to trace song copying unambiguously.

Although there was no significant difference between the three groups, there was a slight tendency to learn more from the ZBS tutor. With only six pairs of song tutors the possibility cannot be ruled out that the ZBS males were particularly good tutors to learn from. However, this seems unlikely: there was no indication that certain tutors were particularly likely to be chosen. One possibility is that Bengalese finch elements provide a super-normal stimulus. The results of this paper suggest that males find it easier to learn elements which have been repeated at least once per phrase. Since Bengalese finch elements are often repeated two or three times during each phrase this might explain why Bengalese finch elements tend to be learnt.

Table 8.I: Housing conditions for the three groups.

Group.	Housing condition.		Total no. males.
	♂	♀	
A	Z	Z	11
B		Z	10
C	B	B	9

Table 8.II: The no. of males which learnt from each tutor.

Group.	Z	ZBS	Hybrid.	Neither.	Total.
A	5	4	2	0	11
B	2	7	1	0	10
C	1	6	2	0	9

Table 8.III: No. males which learnt from each pair of tutors and the type of distance call (DC).

Group.	Z	ZBS	Hybrid.
(1).	P Normal DC	BkPk. ♀-like DC	
A	1	0	1
B	1	0	0
C	1	0	0
(2).	G43 Normal DC	0190 Normal DC	
A	1	0	0
B	0	3	0
C	0	3	0
(3).	B189 Normal DC	056 ♀-like DC	
A	0	3	0
B	1	0	0
C	0	1	0
(4).	G18 Normal DC	028 ♀-like DC	
A	1	0	0
B	0	1	0
C	0	1	1
(5).	B7,10 Normal DC	032 ♀-like DC	
A	1	0	0
B	0	3	1
C	0	1	1
(6).	B35 Normal DC	040 ♀-like DC	
A	1	1	1
B	-	-	-
C	-	-	-

Figure 8.1:

Sonagrams of typical song phrases of a normal zebra finch tutor (Z), G43, a zebra finch singing Bengalese finch song (ZBS), 0190, and two young males. B96 (group A) based his song on that of G43. B39 (group C) copied the 0190's song.

Letters below the sonagrams show portions of song common to two or more males.

FIG 8·1

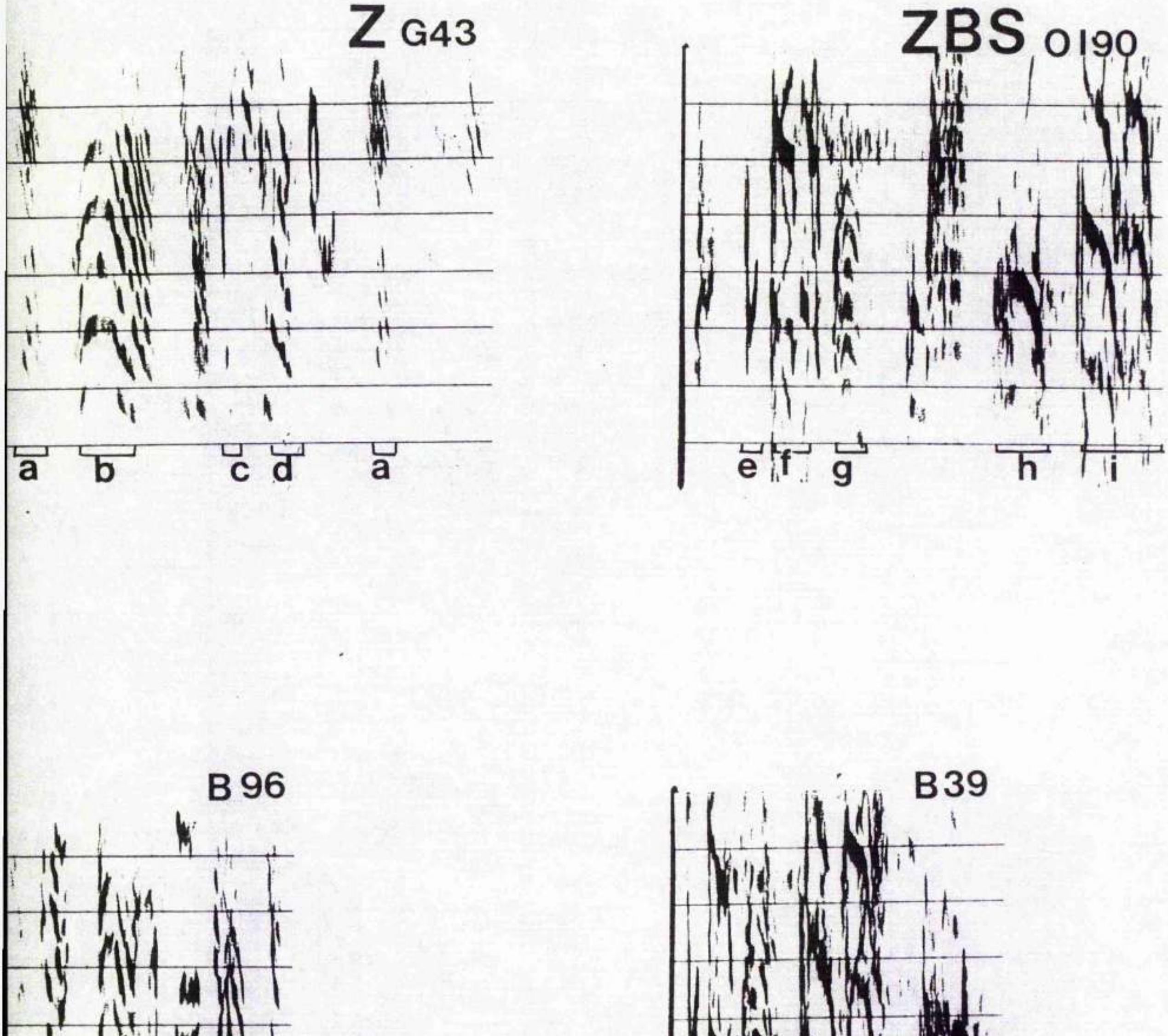


Figure 8.2:

Sonagrams of two normal distance calls and the distance calls of two ZBS tutors, 028 and 032. The normal male distance call consists of a tonal element (t) followed by a noise element (n). 028 lacks the tonal element; his call resembles a female zebra finch distance call. 032 sings a reversed distance call with the tonal element following the noise element.

FIG 8·2

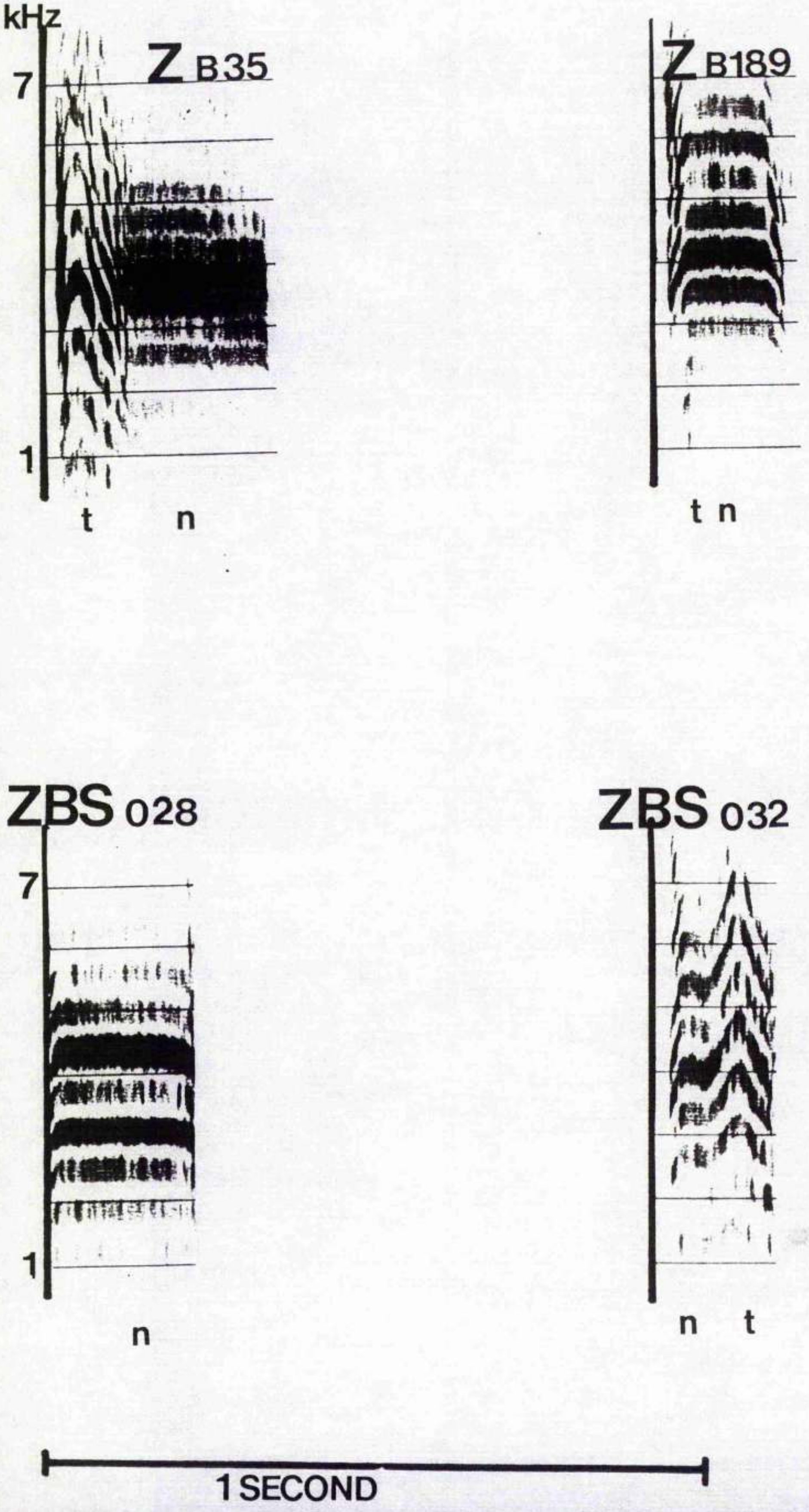


Figure 8.3:

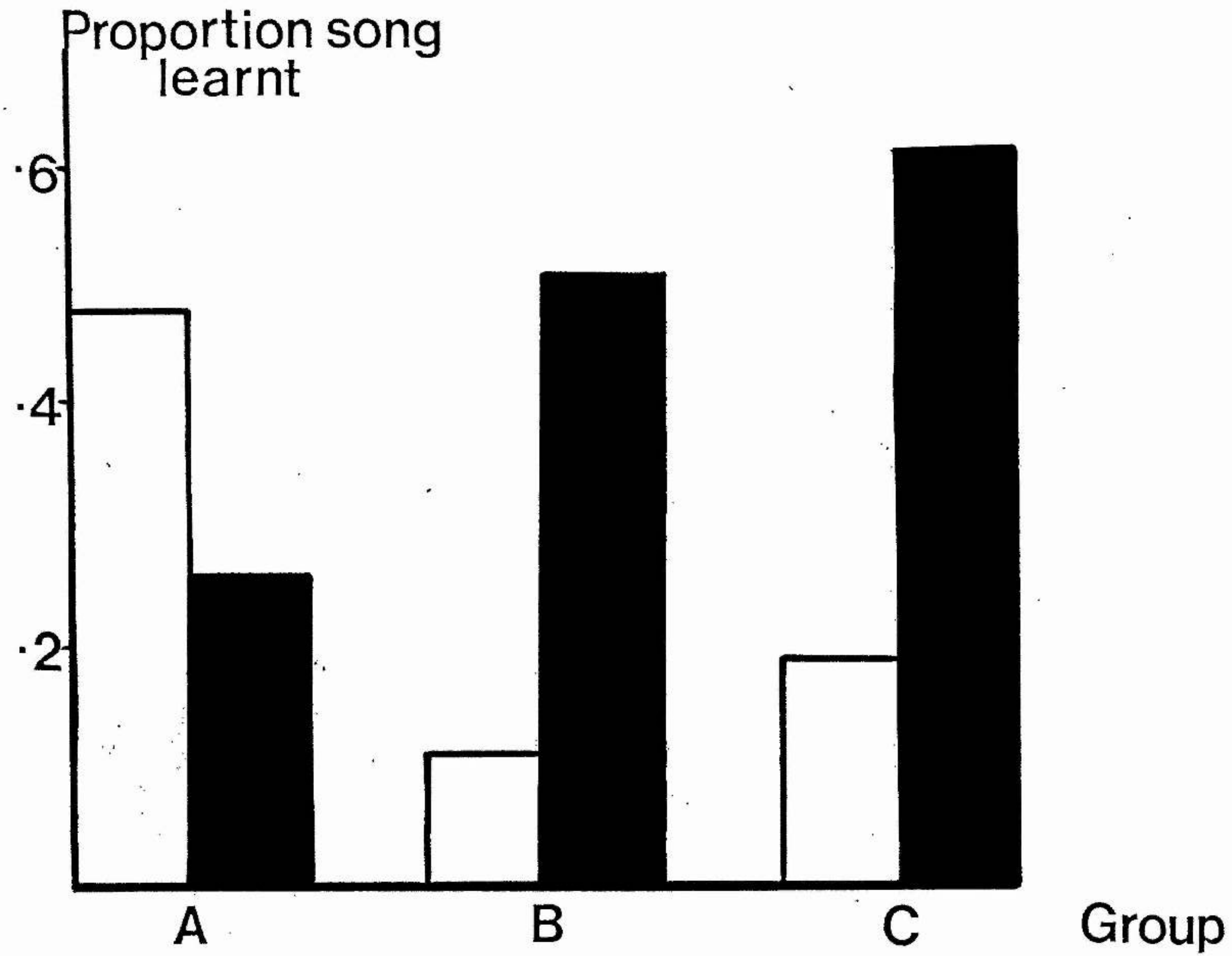
Histogram of the mean proportion of the young bird's song that was learnt from each tutor in the three groups.

Key:-

■ Z Tutor

□ ZBS Tutor

FIG 8·3



Chapter 9.

SONG LEARNING IN CROSS-FOSTERED ZEBRA FINCHES: A RE-EXAMINATION OF THE SENSITIVE PHASE.

ABSTRACT.

Male zebra finches which have have been normally-raised or cross-fostered to Bengalese finches learn from a song tutor with whom they are housed during the sensitive phase, between 35 to 70 days of age. If the tutor is a different species from the father or foster-father however, then the tendency to learn during this time is much less and some males will produce song heard before 35 days. None of the birds in this study learnt after 70 days, although some lost song elements or added improvised ones.

These results suggests that specific types of experience influence when a young bird learns its song. It seems that exposure to "poor" song during the sensitive phase stimulates the bird to remember song heard previously and blocks further learning after this time. These results are compared with those obtained in imprinting studies.

Based on a paper to appear in Behaviour (August, 1987).

INTRODUCTION.

Some bird species are capable of learning song throughout life e.g. canaries (Nottebohm and Nottebohm 1978) and green finches (Guttinger 1977). For many song birds, however, vocal learning is concentrated into a relatively brief period early in life. In zebra finches the sensitive phase for song learning normally begins when the young male gains independence from his parents, at about 35 days old, and continues until sexual maturity, at about 70 days of age. A suitable song tutor present during this time, that is one with whom the young male can visually and vocally interact, is likely to be copied accurately (Eales 1985a). This may be true even if the song tutor is a Bengalese finch. Immelmann (1969) reported that some zebra finches will learn song from a Bengalese finch foster-father with as much accuracy as a male copies his natural father. In most cases, however, the foster-father's song is not learnt in its entirety: only some Bengalese song elements are copied and these are organized into shorter, zebra finch phrases (Chapter 6).

Immelmann (1969) suggested that cross-fostered zebra finches will reproduce song from their Bengalese finch foster-father even if they are housed with conspecifics later in development. However, there are some interesting variations on this theme: whether a young male sings his foster-father's song seems to depend on the relative amount of social interaction he experiences with the foster-father and adult conspecifics during the sensitive phase (Eales 1987a).

Normally-raised zebra finches that are housed with conspecifics after independence copy their father's song, provided visual and vocal interaction with their father is maintained after independence, irrespective of the amount of interaction they experience with a second adult male zebra finch (Böhner 1983; Eales 1987a). This difference in song tutor preference between normal and cross-fostered zebra finches suggests some initial own species bias. This may be due to differences in the two species' vocalizations but it may also be the result of visual and behavioural differences (see ten Cate 1982 and Chapter 2). Immelmann (1969) states that "in the zebra finch there exists a double security: innate preferences both for the father's song and for the right tonal quality, and if the two do not coincide, the former is likely to be the stronger".

Immelmann (1969) believed that young zebra finches learn from their father or foster-father before independence and this prevents further learning from other adult males. In the wild the father is unlikely to be present during the sensitive phase for song learning (Eales 1985b) so it seems particularly important to consider the influence that experiences immediately after independence might have on song acquisition in the absence of the father, especially for cross-fostered young males denied the parental behaviour typical of their species.

Ten Cate et al (1984) found that normally-raised zebra finches can be influenced in their later sexual preference by exposure to Bengalese finches during the period immediately after independence: this also applies to song learning (Eales 1987a).

A zebra finch denied the opportunity to learn song during the normal sensitive phase may remain open to learning until a suitable song tutor is available. This suggests that suitable experience, rather than age, is the most important factor determining the end of the sensitive phase (Eales 1987b). This appears to be true for many species. For example, Kroodsma and Pickert (1984) found that marsh wrens will learn from live song tutors during their first spring but fail to learn from tutor tapes until the following autumn.

In view of the importance of social factors for song learning, and particularly of visual contact (see Chapter 8 and Eales 1985a), it seems probable that cross-fostering will also affect the timing of the sensitive phase. For example, a Bengalese-raised zebra finch might take longer to learn his foster-father's song than a zebra finch learning from his natural father. The copying could also be less accurate, particularly for Bengalese-raised zebra finches which are housed with a conspecific after independence or for normally-raised zebra finches presented with a Bengalese finch tutor at that stage. In addition, a young male denied the opportunity to hear conspecific song during the sensitive phase might tend to alter his song at a later stage, if a tutor of the same species as his foster-parents is available.

This study examines the influence of cross-fostering experience on when and what a young zebra finch learns.

METHODS.

Birds and Housing Conditions.

Nineteen clutches of zebra finches were used in this study; nine were raised by their natural parents (groups A and C), the rest were raised by Bengalese finch foster-parents, whose own clutches they replaced (groups B and D). All the birds were removed from their parents or foster-parents at the age of independence (mean clutch age of 35 days) and housed with a pair of non-breeding adults until 70 days.

Following 10 days of isolation, from day 70 to 80, during which the young males' songs were recorded, they were housed with a third pair of adults for 5 weeks and then recorded once more. They were then housed in groups and their songs were recorded again at 6 months of age to determine whether the songs had changed after the normal sensitive phase.

The conditions for the four groups are summarised in Table 9.I.

Method of Song Analysis.

The song structure of each young male was compared with that of his tutors by making tracings of sonagrams of typical song phrases (see Chapter 3 for further details).

Figure 9.1 illustrates the main differences between zebra finch and Bengalese finch song (see Chapter 6 for a more detailed account). In view of these differences it is possible to classify some song elements as either "zebra finch" or "Bengalese finch". This is particularly useful in the case where a young male's song elements are not obviously derived from the three song tutors present during the study.

The amount of song a young male learnt was calculated as the number of different song elements the young male learnt from each tutor as a proportion of the different elements in the young male's song. A second measure, the proportion of each tutor's song that the young male learnt, took into account differences in the length and number of elements in zebra finch and Bengalese finch song phrases. This was calculated as the number of different elements in the tutor's song which were learnt, as a proportion of the number of different song elements each tutor sang in a typical song phrase.

To look for changes in each young male's song structure the three sets of song recordings were compared. A change in the structure of a song phrase is defined here as the loss or addition of one or more elements in the song phrase, rather than the modification of a pre-existing song element.

RESULTS.

The Timing of the Sensitive Phase.

Table 9.II shows the number of young males who learnt one or more song elements from each of the three successive tutors (further details in Appendix 9a). All the young males in the zebra finch control group (A) learnt only from the tutor with whom they were housed from 35 to 70 days (see Fig. 9.2): this agrees with previous work (Eales 1985b). All the cross-fostered young males in group B also learnt from the tutor present at this time (see Fig. 9.3). Not all the birds in groups C and D learnt during this sensitive phase and

group C differed significantly from the other groups in its pattern of song learning (Fisher exact test, P<0.01 for C vs D; P<0.001 for C vs A,B combined as all the birds in these two groups learnt only from the second tutor). Only one male in group C and eight males in group D based their song solely on the second tutor (Figs. 9.4 and 9.5). With the exception of three males who sang a series of call notes, the remainder of group C learnt at least one element from the father or foster-father. In groups A and B none of the birds produced a hybrid song based on both the father (tutor 1) and tutor (tutor 2) whereas in group C 4 out of 10 sang a hybrid song compared with 2 out of 10 in group D (Fisher exact test for C vs A,B, P<0.02; C vs D, P<0.1; A,B vs D, P<0.1).

None of the birds learnt from the third tutor with whom they were housed after the sensitive phase, from 80 to 115 days of age. Although three males in group C and 1 male in group D did change their songs during this period, the difference between the groups was not significant (Fisher exact test). In group C PB2, who sang a hybrid song, replaced the last two zebra finch elements with two Bengalese finch elements; none of these elements appeared to be derived from any of the song tutors. PB1 and P33, whose songs consisted of a series of call notes, became more zebra finch like: PB1 added three improvised zebra finch elements and P33 gained two more zebra finch call notes. In group D P29, whose song was based on the zebra finch tutor, lost two of his improvised zebra finch elements (Fig. 9.6). With only four males no statistical conclusions can de drawn, but these results do not suggest any tendency to lose or gain either type of element.

None of the changes were reversed and none of the young males altered their songs at 115 days or by the time of final song recording at 6 months.

Copying Accuracy.

Individuals vary considerably in their accuracy of song learning but within a clutch birds tend to produce similar songs; presumably this reflects exposure to similar sorts of experiences, although young males may also influence each other in their choice of song tutor. In spite of these inter-clutch differences, the four groups differ significantly in the proportion of song elements learnt from the three tutors (χ^2=76.91, df=6, P<0.01). Figure 9.7 shows that the young males in group A produce the most accurate copies of tutor 2's song and those in group C the least.

DISCUSSION.

The results in this study agree with Eales (1985b) that captive male zebra finches normally learn their song at about 35 to 70 days of age. Young males cross-fostered to Bengalese finches at hatching also learn their song during this time which suggests that cross-fostering per se does not alter the timing of the sensitive phase.

The partially cross-fostered young males in groups C and D showed a rather different pattern of song learning. If the father or foster-father is a different species from the tutor present during the sensitive phase then the tendency to learn the tutor's song is not so great. This is particularly true for normally-raised young males given a Bengalese finch tutor: only 5 out of 10 of the birds in group C learnt some song elements from the Bengalese tutor while 6 out of 9 learnt at least one element from their father. Most of the cross-fostered young males in group D did base their songs on the zebra finch tutor but two of them also learnt from the foster-father.

Presumably, the preference for a zebra finch tutor reflects own species bias. This may be the result of the different experiences a young male receives in the nest. For example, Bengalese-raised zebra finches receive less parental care during the first three weeks of life (ten Cate 1982, 1984). Bengalese finch parents also direct considerably less aggression to their young (see Chapter 2) and recent findings suggest that aggression is important in a zebra finch's choice of song tutor (see Chapter 3). Genetic differences could also be responsible for the species bias. Kroodsma and Canady (1986) demonstrated that differences in repertoire size among populations of marsh wrens have a genetic basis. The longer Bengalese finch song phrase may be more difficult for a zebra finch to learn. There are certainly few cases of wild birds learning the wrong species' songs (but see Baptista 1972; Rowley and Chapman 1986).

It is becoming increasingly apparent that the timing of the sensitive phase is much more flexible than originally thought: this applies to the development of other behaviour patterns as well as song learning (e.g. Guiton 1959 for filial imprinting in chicks; Immelmann 1972 for sexual imprinting in zebra finches; Kroodsma and Pickert 1980 for song learning in marsh wrens). In zebra finches it is experience rather than age which determines when a song is learnt, so that a young male remains open to learning until a suitable song tutor is available (Eales 1987b).

The results of this study suggest that specific types of experience influence what a bird learns and when. If the tutor heard during the time when they normally learn is of a different species from the "father" then the young males are less likely to copy their tutor's song; of the young males in group C some produced only elements heard before 35 days old, some sang a hybrid song with elements from both males and some learnt from neither male.

Exposure to poor song during the sensitive phase seems to stimulate the bird to recall and reproduce song heard before 35 days. This is true for the birds in both groups C and D; and for those denied visual contact during the tutoring period (see Eales 1985a). For zebra finches living in mixed species flocks this may ensure that species-specific song is produced.

Zebra finches deprived of any song during this time are likely to learn from a tutor with whom they are housed after 70 days (Eales 1987b). It is interesting to compare this with the behaviour of the young males in groups C and D. Although some of these birds did change their song, particularly those in group C which sang a series of call notes, none reproduced any of the elements heard after 70 days. This might be an example of proactive interference in which stimulating a bird to remember song heard before 35 days of age prevents the learning of new song elements after 70 days, once a suitable song tutor is made available once more. If proactive memory interference is important in zebra finch song learning then young which are denied song before independence should remain open to learning after 70 days. Eales (1987a) found this to be the case for female-raised zebra finches. Proactive memory interference is also thought to affect song learning in great tits: the ability to recognise new neighbours is inversely related to the number and similarity of songs heard previously (McGregor and Avery, 1986).

The results in this chapter and those of Eales (1985b) suggest that secondary song learning is extremely stable in zebra finches. It is instructive to compare these results with various forms of prior experience on the development of secondary imprinting. There are several examples of young birds imprinting onto a second object, but in contrast to the song learning results, secondary imprinting is relatively unstable (Cherfas and Scott 1981).

Great caution must be exercised when considering the results of secondary imprinting. Most studies provide only inanimate objects for the animals to imprint on. The anomalous results accrued from using tape recordings rather than real birds for song tutoring should serve as a caveat (e.g. Kroodsma and Pickert 1984). A recent imprinting study (Boakes and Panter 1985) lends further support to this claim: chicks exposed to a live hen rather than an artificially moving windmill failed to show any secondary imprinting. It is important to realise, however, that the preference will depend on the relative length of exposure to the different stimuli (see Bateson 1983).

The results in this chapter fit "updating" model of imprinting quite well (Bateson, ms.). Bateson suggests that the effect of exposing a bird to one stimulus eventually makes it impossible for other stimuli to exert an effect, and the rate at which this occurs depends on how effective the first stimulus is. If a bird is exposed to two stimuli then the second should update the first, provided the differences between stimuli are small and the second has a greater stimulus value than the first. However, if the two stimuli are quite different then two separate standards are stored. This begs the question of how different the stimuli should be for separate standards to be created.

According to this hypothesis, the birds in groups A and B update their songs with elements present in the second tutor's song but no updating occurs after 70 days because the birds have had sufficient song learning experience by this time. For group C, however, the stimulus value of the Bengalese finch tutor is not great enough to exclude song learnt from the zebra finch tutor. In group D the conspecific (tutor 2) would have a higher stimulus value but, since two males copied elements from tutor 1, the difference between the two stimuli may not have been sufficiently great for complete updating of the first.

It is interesting to note that only birds in groups C and D produced hybrid songs composed of elements from both tutor 1 and tutor 2. These birds were exposed to the stimuli of two different species: this large stimulus difference, relative to the birds in groups A and B, might result in the creation of two separate standards so that the birds "dither" in their choice of song tutor. This bears striking similarity to the sexual preference of zebra finches exposed to both species: ten Cate (1986b) found that some males would court both zebra finch and Bengalese finch females and, if given the choice of both species and a hybrid, they would show a greater preference for the hybrid female. This point is taken up in more detail in Chapter 10 which examines the effect of simultaneous exposure to both species and compares these song learning results with the ones in this chapter.

where males are successively exposed to both zebra finches and Bengalese finches.

TABLE 9.I: Conditions of song tutoring for the four experimental groups of male zebra finches

Group	Treatment during					
	0-35 days		35-70 days		80-115 days	
	♂	♀	♂	♀	♂	♀
A (n=8)	Z	Z	Z	Z	Z	Z
B (n=6)	B	B	B	B	B	B
C (n=10)	Z	Z	B	B	Z	Z
D (n=10)	B	B	Z	Z	B	B

TABLE 9.II: No birds in each group who learnt one or more song elements from the three song tutors (T_1, T_2 and T_3)

Group	No. males who learnt from T_1 (0-35 days)	T_2 (35-70 days)	T_3 (80-115 days)	No. males who did not learn from any tutor	Total no males
A	0	8	0	0	8
B	0	6	0	0	6
C	6	5	0	3	10
D	2	10	0	0	10

Figure 9.1:

Sonagrams of typical zebra finch and Bengalese finch song phrases. In this example the zebra finch sings six elements (Z 1-6), including a long call note added to the end of the phrase. The Bengalese finch song phrase consists of seven elements (B 1-7), four of which were repeated.

FIG 9·1

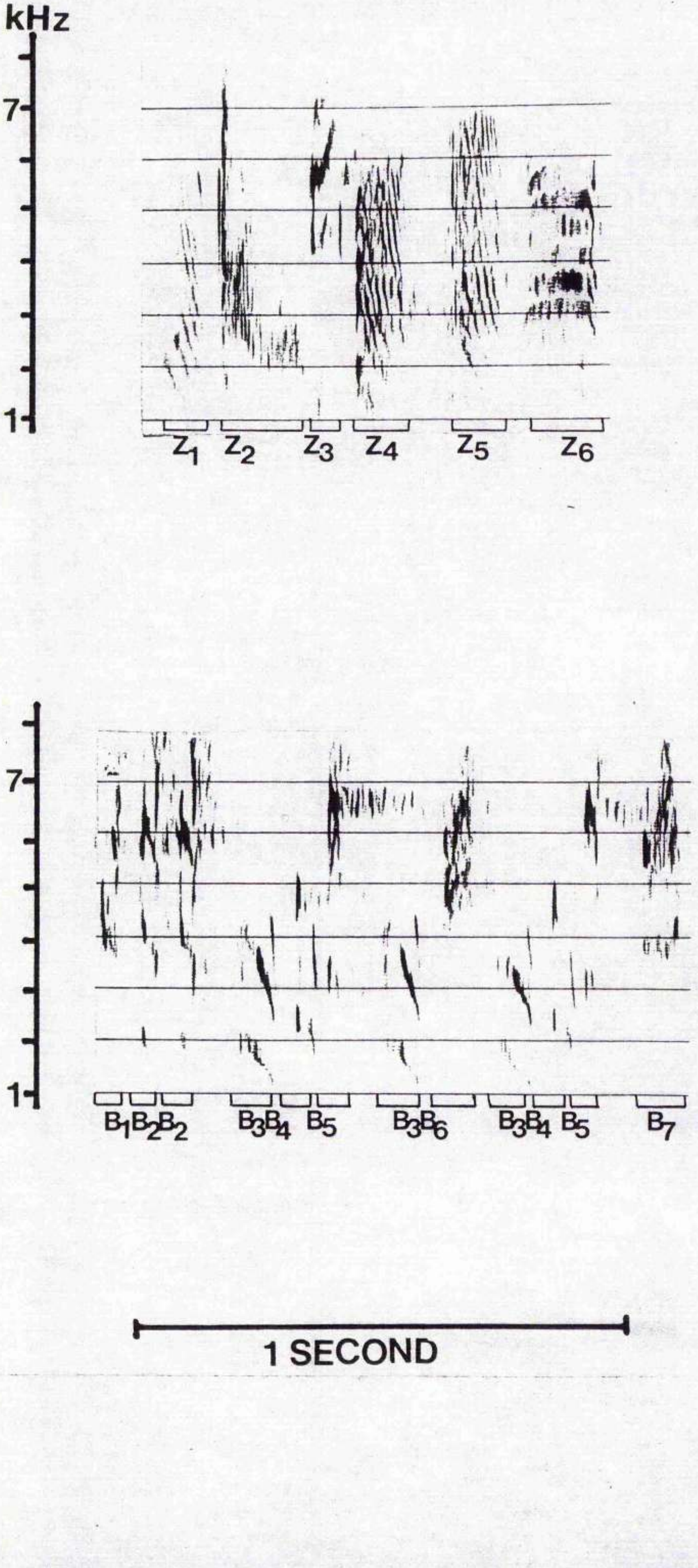

kHz
7
1
Z1
Z2
Z3
Z4
Z5
Z6
7
1
B1
B2
B2
B3
B4
B5
B3
B6
B3
B4
B5
B7
1 SECOND

Figure 9.2:

Sonagrams of the songs of three young males from one clutch of normally-raised zebra finches in group A (R1, Y5 and B3), with their song tutors, O180, B165 and G18. The youngsters were raised by O180 until independence and then housed with a second zebra finch tutor, B165, at 35 to 70 days of age. They were then housed with a third tutor, G18, for a further five weeks.

R1, Y5 and B3 learnt their song elements from B165. There was no change in song structure after 70 days.

Letters below the sonagrams represent sections of the tutors' songs which are copied by one or more youngsters.

FIG 9·2

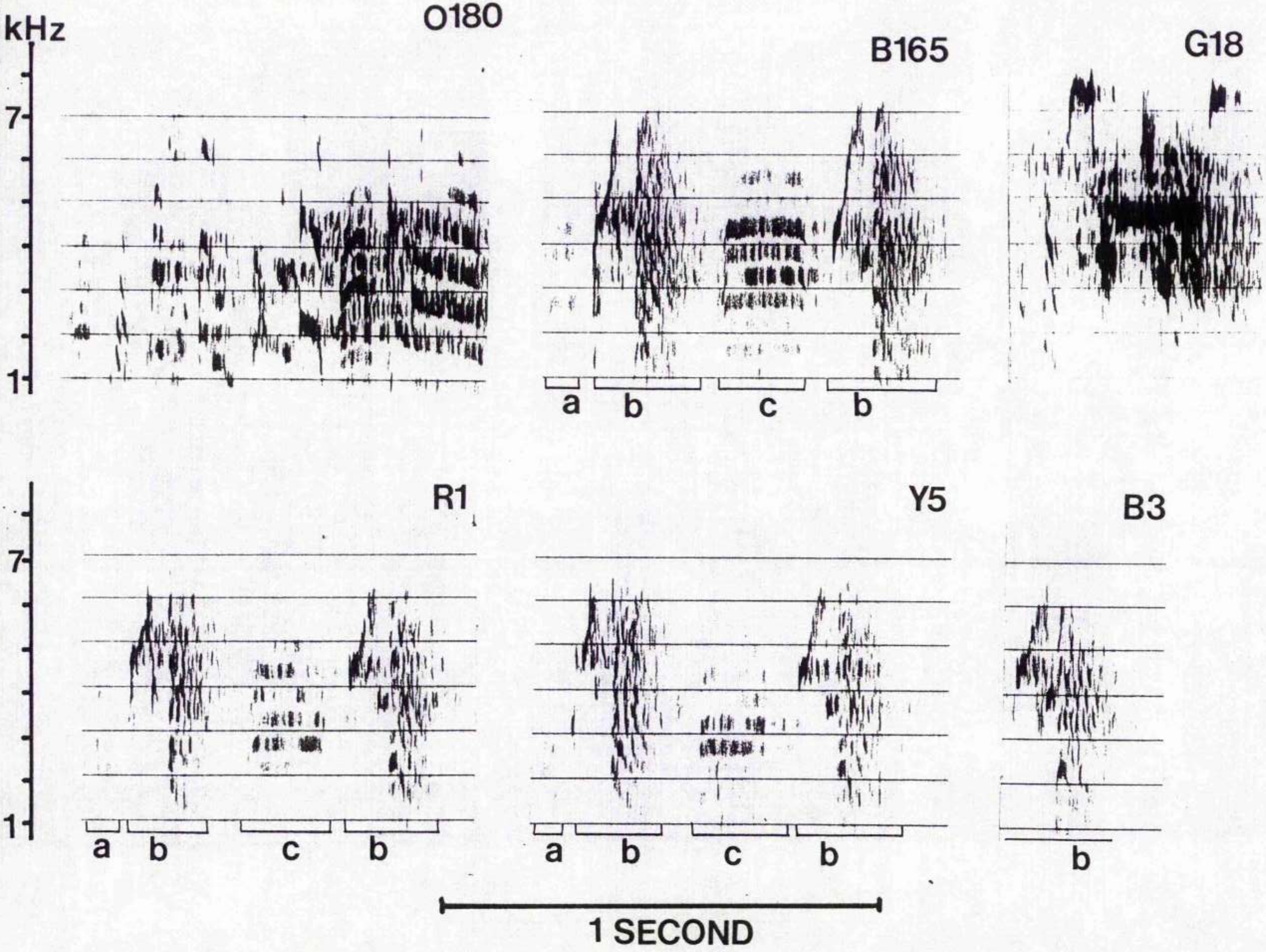


Figure 9.3:

Sonagrams of YB 5's song (group B) and the songs of his Bengalese finch tutors, P, WBd and D. The youngster learnt from WBd, the tutor with whom he was housed at 35 to 70 days. His song did not change after this time.

Letters below the sonagrams show portions of song common to two or more males.

FIG9·3

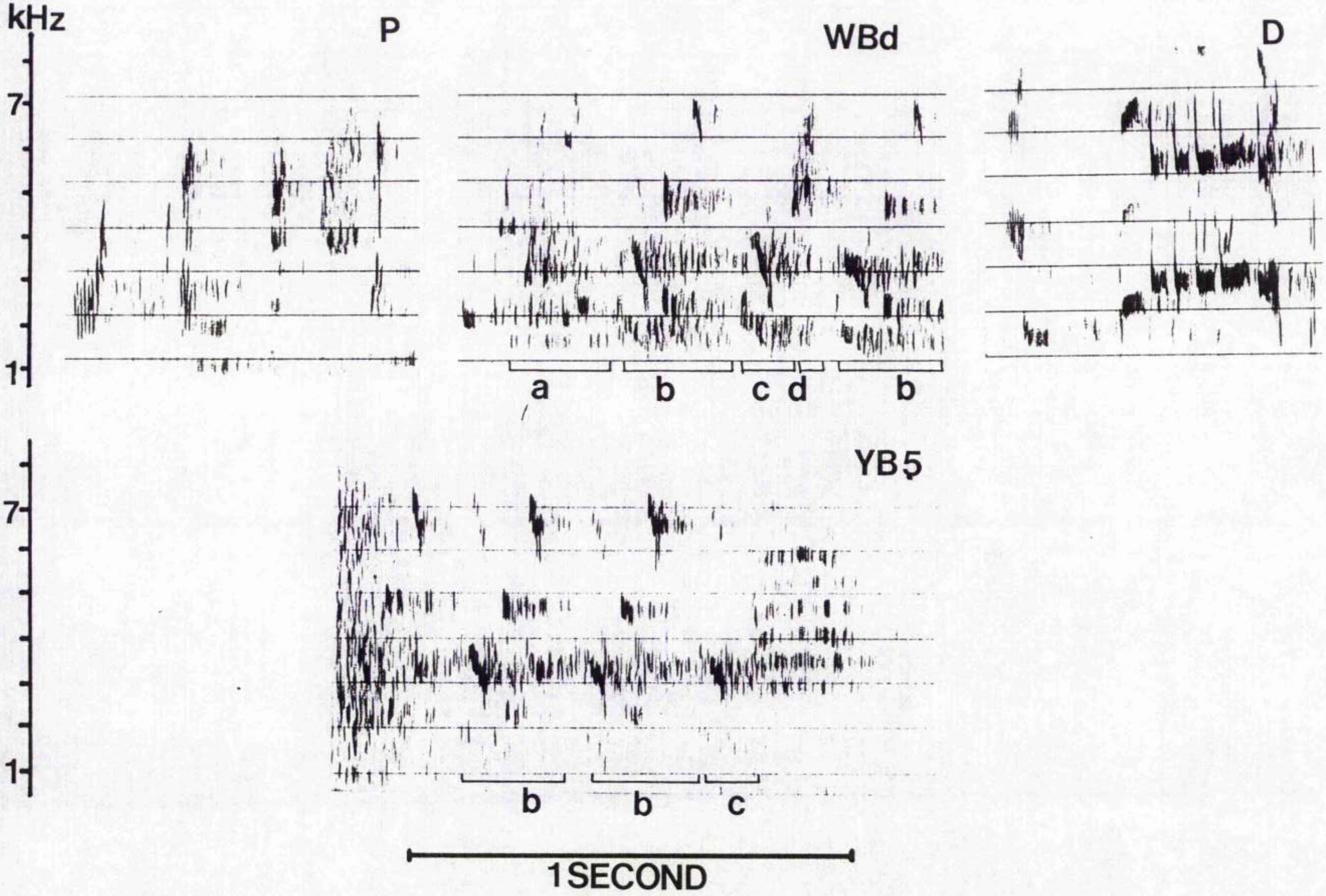


Figure 9.4:

Sonagrams of the songs of P35 (group C) and those of his two zebra finch song tutors (Z), Y8 and B165 and the Bengalese finch tutor (B), W. P35 did not learn any song elements from his tutors.

At 70 days (sonagram 1) his song phrase consisted of 4 zebra finch call notes. By 115 days (sonagram 2) P35 had incorporated two more call notes into his song phrase (x). There was no further change in song structure.

Letters below the sonagrams show portions of song common to two or more males.

FIG 9·4

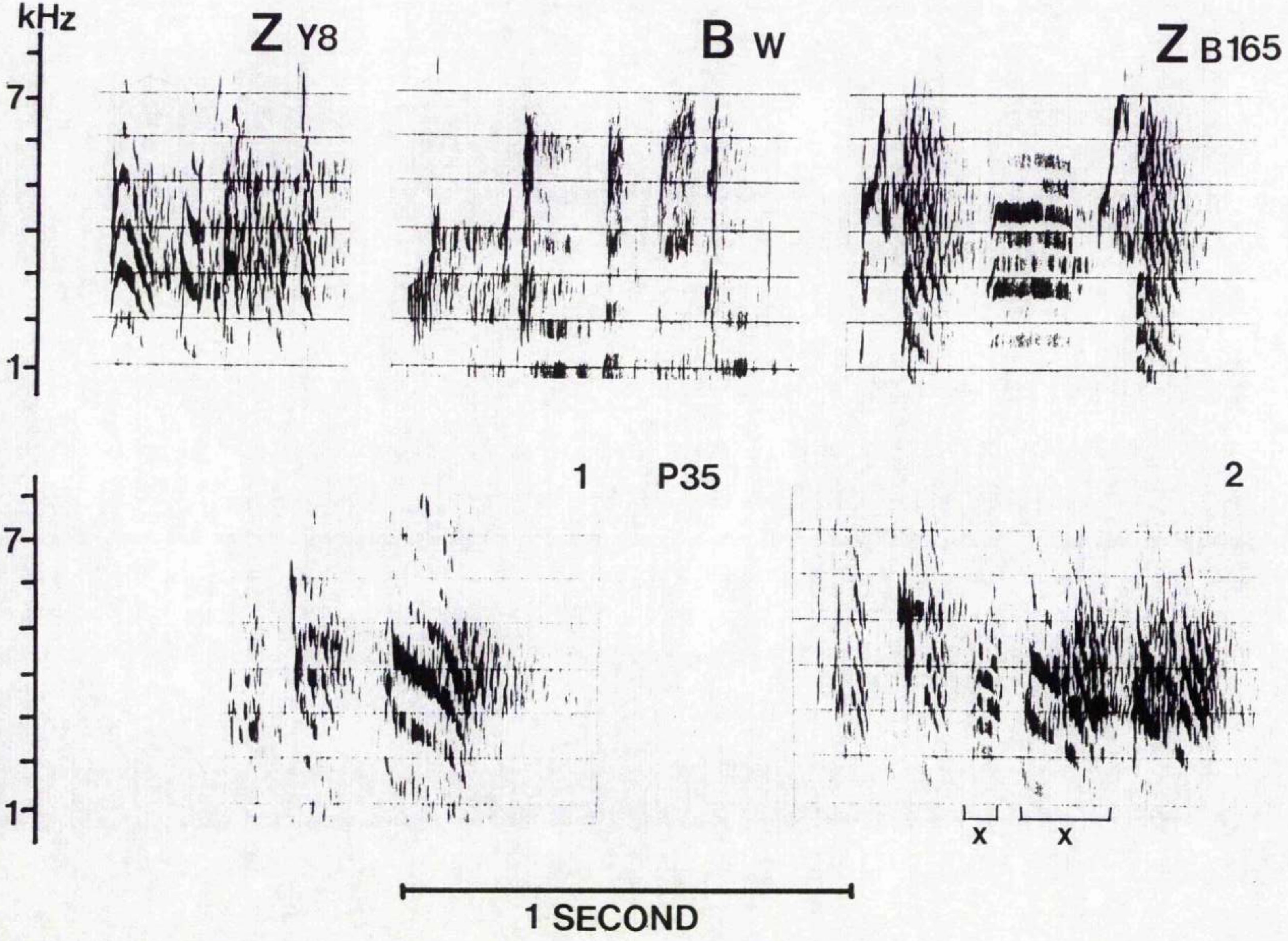


Figure 9.5:

YB 8 (group D) learnt from the Bengalese finch foster-father (B), WB. A zebra finch call note was repeated at the end of the song phrase. 085, the zebra finch tutor (Z) present at 35 to 70 days of age, had a very similar call note at the end of his song. No song learning occurred after this time.

Letters below the sonagrams show portions of song common to two or more males.

FIG 9·5

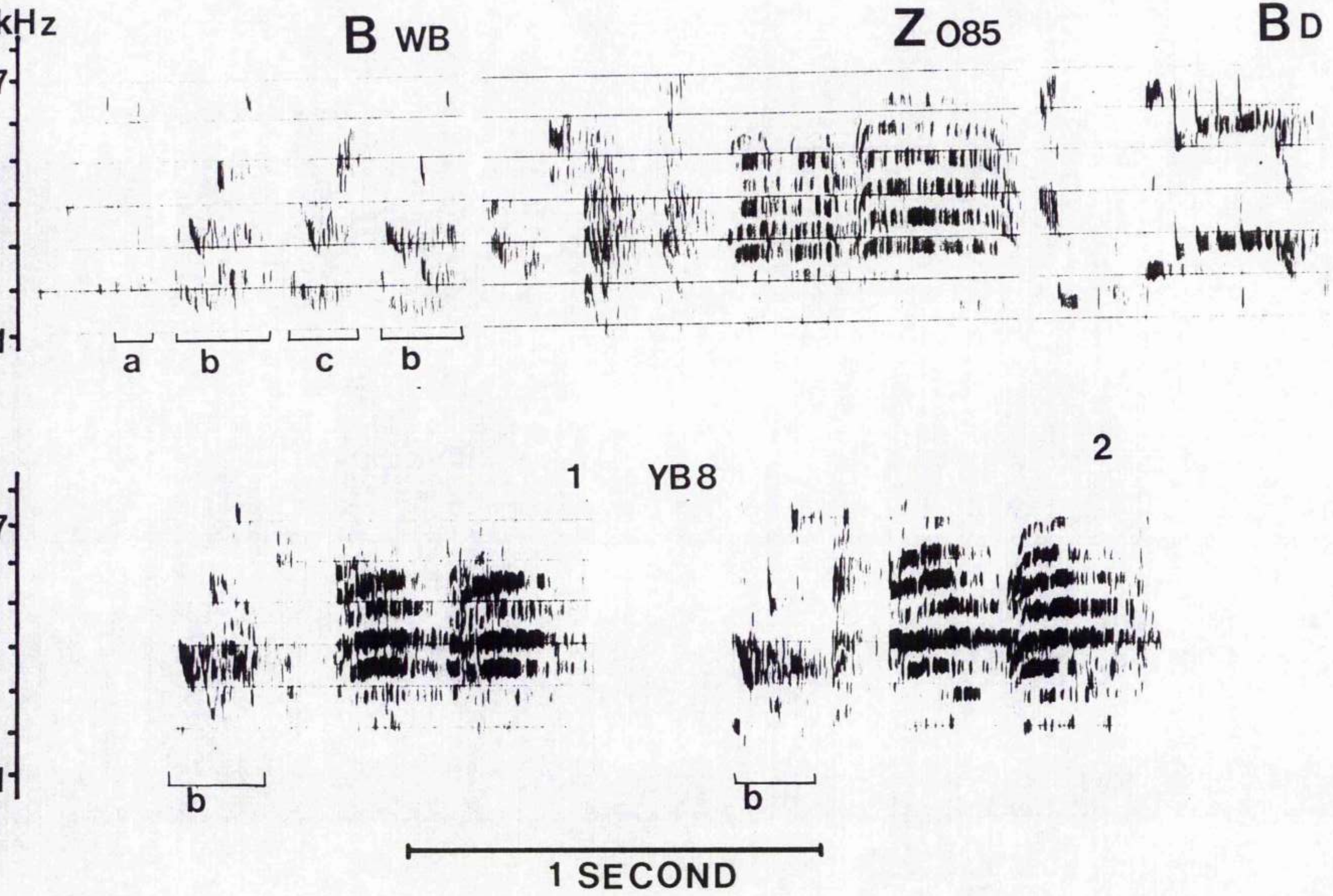


Figure 9.6:

P29 from group D learnt sections b and d from the zebra finch (Z), B217 at 35 to 70 days of age. He did not learn from T, his Bengalese finch foster-father (B) or the Bengalese finch tutor (B), W after 70 days. However, his song did change: two of the improvised song elements were lost. There was no further change after 115 days of age.

Letters below the sonagrams show portions of song common to two or more males.

FIG 9·6

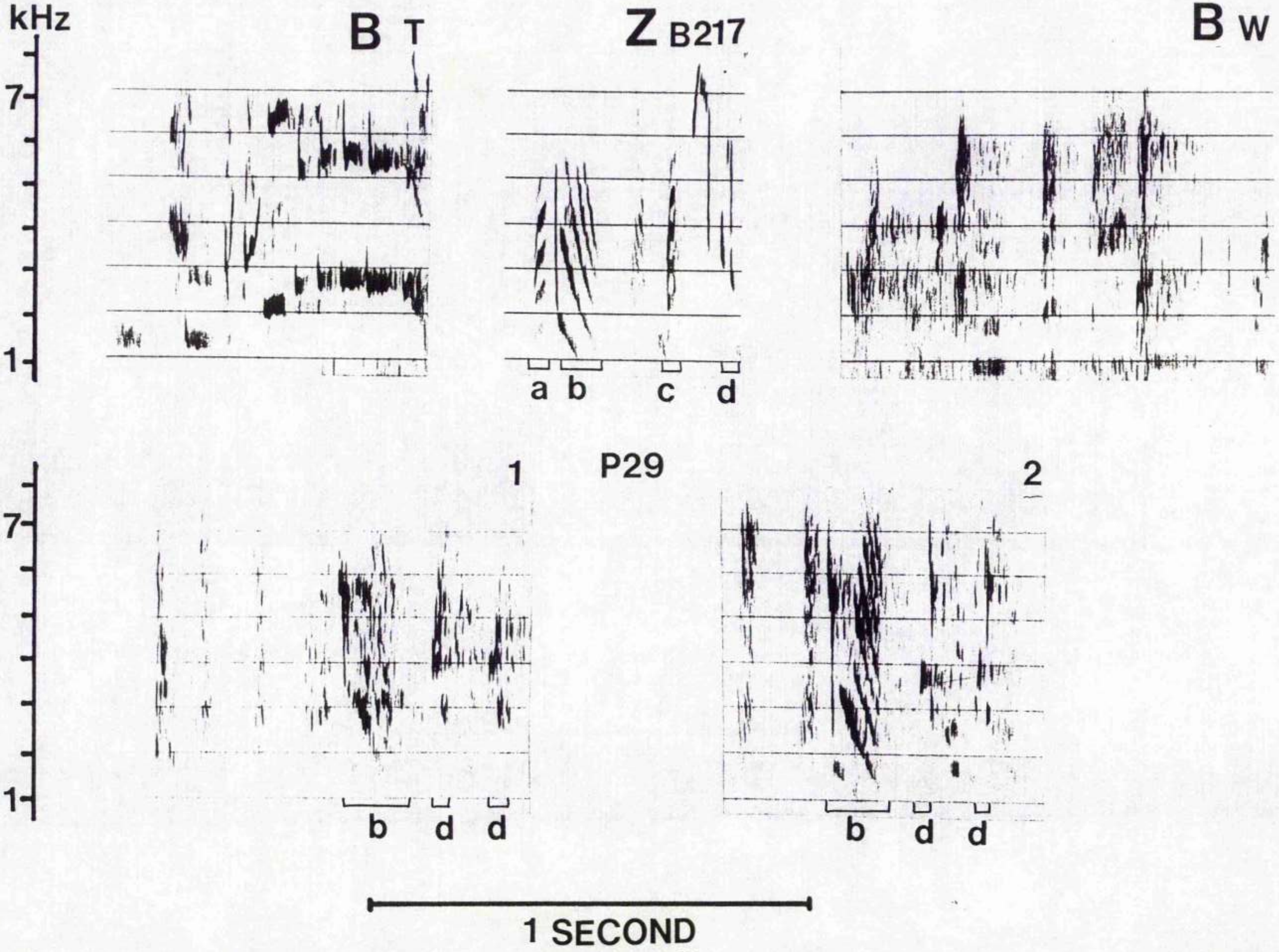


Figure 9.7:

Pie charts of the results of song learning at six months of age for the four groups of birds (A - D), showing the proportion of improvised elements and the proportion of song learnt from the three tutors.

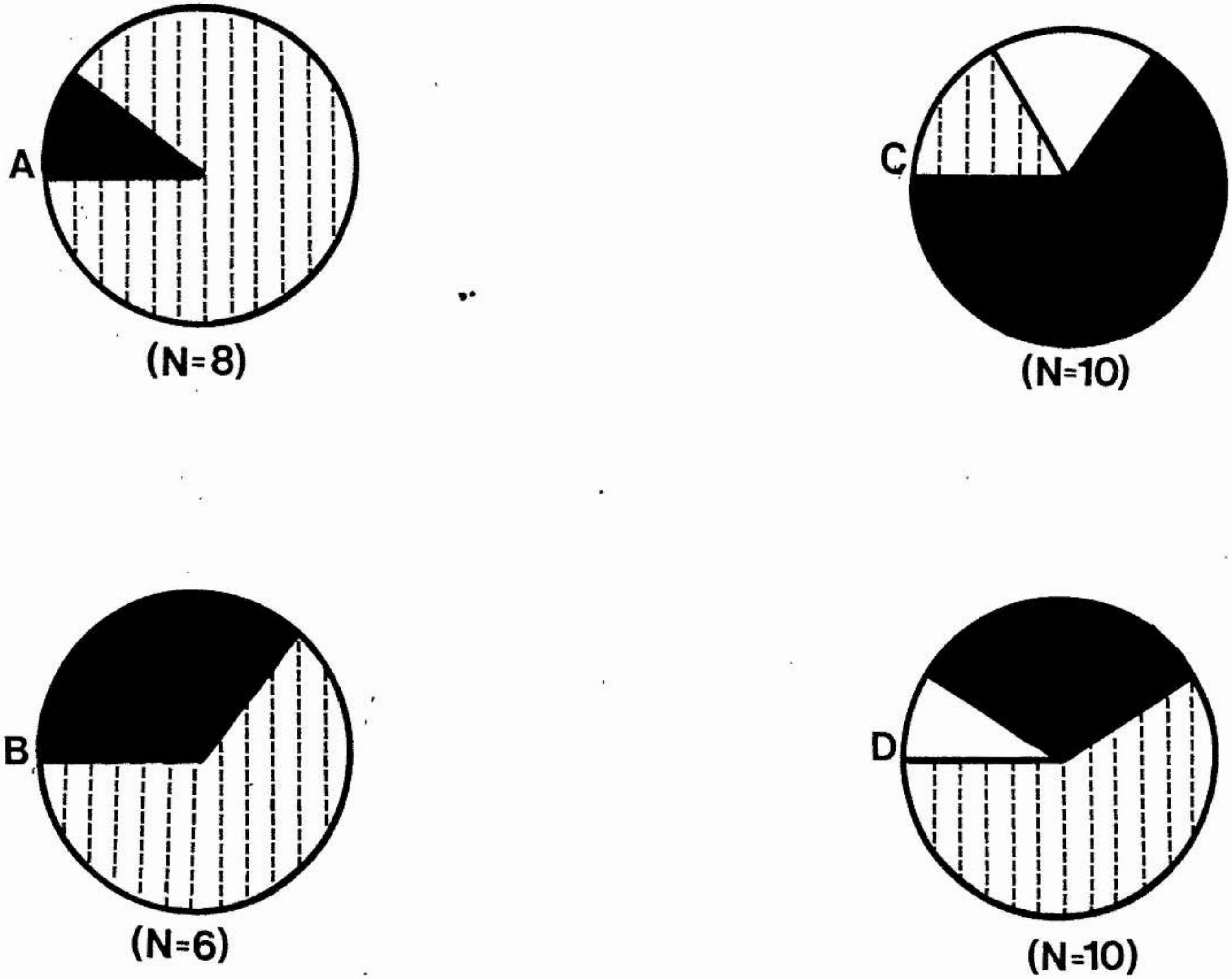
Key:-

■ Proportion of song improvised

□ Proportion of song learnt from tutor 1

▥ Proportion of song learnt from tutor 2

FIG9-7



Chapter 10.

SONG LEARNING IN ESTRILDIDS RAISED BY TWO SPECIES: EQUAL RIGHT FOR MUM AND DAD!

ABSTRACT.

Male zebra finches and Bengalese finches were normally-raised or cross-fostered to the other species until 35 days and then housed until 70 days with two song tutors, one from each species. Normally-raised males base their song on that of the conspecific tutor whereas cross-fostered birds also learn from the other tutor, reflecting both own-species bias and a tendency to learn from the tutor whose song is similar to the father's. Males raised by one of each species tend to learn from the father or foster-father as well as the tutor(s) but there is no significant difference between males which have been raised by a zebra finch foster-father and a bengalese finch foster-mother and vice-versa.

Based on a paper to appear in Anim. Behav. (in press).

INTRODUCTION.

Based on a series of studies of zebra finches Immelmann (1969) concluded that young males learn their song from tutors "with which a strong personal bond exists" and in some cases, this may override species-specificity since zebra finches which are raised by Bengalese finch parents will copy their foster-father's song even if conspecific males can be heard in the vicinity. However, if the cross-fostered males can socially interact with conspecifics then the tendency to learn from the Bengalese finch is less great. In Immelmann's study zebra finches which were raised in an aviary, and fed by a pair of conspecifics in addition to their Bengalese finch foster-parents, produced a hybrid song composed of elements learnt from both males.

More recent work by Eales (1987b) illustrates how influential these social bonds can be. Zebra finches were raised by Bengalese finch foster-parents until independence and then housed with both a conspecific song tutor and their foster-father. In one group the young zebra finches could freely interact with their foster-father but were separated from the zebra finch male by a wire screen; in another group the young males were separated from their foster-father by the screen but could freely interact with the conspecific tutor. Whether a zebra finch sang his foster-father's song depended on the relative amount of social interaction he experienced with the foster-father and adult conspecifics during the sensitive phase for song learning.

Normally-raised zebra finches and Bengalese finches which are housed with two tutors at independence, their father and an unrelated male, tend to copy their father's song (Bohner 1983; Dietrich 1980), irrespective of the amount of social interaction they have with the two tutors (Eales 1987b). However, behavioural differences between song tutors are also important; zebra finches which have been raised by the mother alone prefer to learn from the tutor who is most aggressive to them (Chapter 3).

Clearly social interactions immediately after independence are important in governing what is learnt and from whom but parental influences established before independence also play an important role. Zebra finches which have been raised by their mother alone selectively learn from their father if they are housed with both parents and another male from independence until sexual maturity (Eales 1985a). Vocalizations produced by the father also influence song tutor choice: normally-raised zebra finches which are housed with two conspecific song tutors at independence prefer to copy song from the tutor with a similar song to their father (Chapter 3).

The importance of behavioural interactions with the parents is particularly apparent in zebra finches and Bengalese finches which are raised by mixed-species pairs, i.e. a zebra finch "father" and a Bengalese finch "mother" or vice-versa. In this situation there is a tendency for the parents to feed conspecific chicks more frequently and to direct more aggression and contact behaviour towards them; this is correlated with a tendency to prefer a conspecific female in mate choice tests (ten Cate 1985).

If physical interactions between the zebra finch father and chicks are progressively suppressed while visual contact with the father is maintained, zebra finch males show a progressive shift in preference towards a Bengalese finch in mate choice tests when adult (ten Cate 1984a). From these results ten Cate argued that behavioural interactions with the parents and other birds, rather than merely visual and vocal exposure, might explain the tendency to prefer a conspecific mate. The results also suggest that the "mother" is slightly more influential: zebra finches raised by a zebra finch mother and a Bengalese finch father show a greater tendency to be more zebra finch-directed in their preference than those raised by a Bengalese finch mother and a conspecific father but the result is not statistically significant.

This study addresses these questions from the song learning point of view by raising broods of zebra finches and Bengalese finches with mixed-species parents and then housing individual broods with a zebra finch and a Bengalese finch song tutor during the song learning phase. What is the effect on subsequent song tutor choice of raising birds by mixed-species parents and what is the relative importance of the two parents? By comparing these results with those of males which have been normally-raised or cross-fostered to a pair of heterospecifics the influence of own species bias can be determined. How do these four rearing regimes affect what is learnt and when?

METHODS.

Birds and Housing Conditions.

Eight mixed-species pairs were established (4 Z♂B♀ and 4 B♂Z♀). These birds had been raised by foster-parents of the other species until 35 days but were then housed with conspecifics to obtain males with species-specific song phrases and distance calls but which directed some of their courtship towards females of the foster species (see Chapters 9 and 11). None of the birds had had previous breeding experience and each pair raised a brood of zebra finches (group A for

Z♂B♀ or group B for B♂Z♀) and a brood of Bengalese finches (group E or F).

If a female in a mixed pair laid eggs these were removed after a complete clutch had been laid and replaced by a fertile clutch of zebra finch or Bengalese finch eggs.

Four pairs of zebra finches (Z♂Z♀) and four pairs of Bengalese finches (B♂B♀) were also established. These birds had been raised by a pair of conspecifics but were sexually inexperienced. Each pair raised a brood of zebra finches and a brood of Bengalese finches. To control for the effects of egg-swopping, the eggs of these were removed and replaced by a fresh clutch of conspecific (the normally-raised control groups, C and G) or heterospecific eggs (the cross-fostered groups, D and H).

The conditions for the eight groups are summarised in Table 10.I.

All the birds remained with their foster-parents until independence (mean age of the brood = 35 days). During the normal sensitive phase for song learning at 35 to 70 days of age (Eales 1985b) each brood was housed with a zebra finch and a Bengalese finch song tutor. All the tutors had been normally-raised and housed with conspecifics until the time of the study. The tutors were separated from each other and from the young birds by wire mesh screens which divided the cage into three identical portions; these prevent physical encounters while maintaining visual and vocal interaction, thereby permitting normal song learning to occur (Eales 1987b). It also reduces the probability that behavioural differences between the tutors, and in the way they interact with conspecific versus heterospecific young, affect song tutor choice. After 70 days the tutors were removed and the young males remained with other members of their brood until four months of age when their songs were recorded and their sexual preference tested.

Songs and Sonagrams.

The songs of all the males were recorded when the young birds were four months old and their songs were compared by making tracings of sonagrams of typical song phrases (see Chapter 3 for further details). Song elements were classified as either common to both a tutor (or father) and the young male or as unrelated in structure on the basis of visual similarity of the sonagraphed elements and the sequence in which they occurred. This allowed poorly copied elements to be assigned to a particular category (Father, Zebra finch, Bengalese finch) on the basis of context and where ambiguities arose independent observers were used to make the assessment. It was not always possible to calculate the amount of song a young bird learnt from the three adult males: some elements were very poor copies which might have been derived from any one of the three or might have been a "blend" of two different elements (see Fig. 10.1). For this reason a qualitative assessment was made. In Fig. 10.1, for example, the young zebra finch (Y9B6) learnt from the zebra finch tutor and also included conspecific call notes in the song phrase. These calls were probably derived from the father since the father also incorporated similar calls into his song phrase. The young Bengalese finch (B60) learnt from both tutors and possibly made poor copies of two of his foster-father's elements.

RESULTS.

Song Learning: What is Learnt and When?

The song learning results are summarised in Table 10.II, which shows the number of males who learnt at least one of their song elements from their foster-father, the zebra finch and the Bengalese finch tutor respectively. Examples for each group are illustrated in Figs. 10.1 - 10.4. Further details are found in Appendix 10a.

All the groups tended to learn from the conspecific song tutor at 35 to 70 days of age. Of the 18 zebra finches which had been raised by mixed-species parents, 11 sang only zebra finch elements and the other seven produced hybrid songs containing zebra finch and Bengalese finch elements. A similar pattern was shown by the 17 Bengalese finches raised by mixed-species pairs: 11 sang pure Bengalese song, five learnt elements from both species and one learnt nothing from any of the adult males and produced a series of improvised elements. Of the 20 cross-fostered males eight out of ten zebra finches incorporated elements from the zebra finch tutor into their songs and seven of the Bengalese finches sang Bengalese elements and all 20 normally-raised males learnt only conspecific song. These results indicate a bias towards learning from conspecifics, irrespective of previous experience.

However, whereas the normally-raised birds in groups C and G based their songs entirely on the conspecific tutor, males in the other six groups showed a different pattern of learning. In group D eight cross-fostered zebra finches produced hybrid songs with elements copied from both tutors; this gives a significant difference from the ten controls in group C ($\chi^2=10.2$, df=1, $p<0.01$). Although some of the cross-fostered Bengalese finches also produced mixed songs the difference from the controls was not statistically significant. Zebra finches and Bengalese finches raised by mixed-species parents also tended to sing mixed-species songs ($\chi^2=5.25$, df=1, $p<0.05$; n.s. respectively). These results are summarised in Fig. 10.5.

A further difference lies in the tendency to learn from the father before 35 days of age (Fig. 10.6). None of the cross-fostered zebra finches sang any of their Bengalese finch father's elements but two cross-fostered Bengalese finches did so. In the mixed-species pairs nine zebra finches and eight Bengalese finches learnt from their foster-father and so differed significantly from the control groups ($\chi^2=5.25$, df=1, $P<0.05$; $\chi^2=4.62$, df=1, $p<0.05$ respectively).

In the mixed-species pairs there was no significant difference between the two groups of zebra finches (A versus B) or Bengalese finches (E versus F) in their pattern of song learning (Fisher exact tests). For both species, birds raised by mixed-species pairs were compared with those raised by two members of the same species. There was no significant between normally-raised and mixed-pairs in the proportion of zebra finches learning song from the conspecific tutor. There is also no significant difference between cross-fostered zebra finches and those raised by mixed pairs in the proportion which learn from the Bengalese finch tutor; the results for the Bengalese finch comparisons are also not significant. Nonetheless, as Fig. 10.7 shows, a greater proportion of the birds raised by two heterospecifics copied elements from the heterospecific song tutor.

DISCUSSION.

Normally-raised zebra finches which are housed with one or more different zebra finch males after independence produce a song based on that of one of the males which they heard at 35 to 70 days of age (Eales 1985b, Chapter 3). Zebra finches which have been cross-fostered to Bengalese finches also learn at this time (Chapter 9), as do normally-raised Bengalese finches (Chapter 5). The results presented in this chapter show that normally-raised zebra finches and Bengalese finches which are housed with both a zebra finch and a Bengalese finch song tutor at 35 to 70 days base their song entirely on that of the conspecific tutor. Even in groups in which birds were raised by the other species, males tended to base their songs, at least in part, on those of conspecifics which indicates some own-species bias.

There are a number of factors which might account for this "own species" bias. Differences in the two species' vocalizations might be important (see Chapter 9), making Bengalese finch song more difficult for a zebra finch to learn and vice-versa. In species such as the zebra finch, where vocalizations are quiet and so only effective at short range it also seems likely that visual factors may be important in tutor choice. In this respect siblings may play a crucial role: cross-fostered zebra finches raised with zebra finch siblings may be biased as a result in favour of learning from a zebra finch. This is certainly the case for sexual preference (Kruijt et al 1983; ten Cate et al 1984).

Bengalese finches vary considerably in their plumage and so there might be less tendency to learn from the Bengalese tutor if he differs markedly from the Bengalese finch foster-father. Previous experiments with Bengalese finches show no suggestion of this (Chapter 5). Equally, zebra finches are sexually dimorphic whereas Bengalese finches do not show sexual variation in plumage. Thus, if plumage details were important, males in groups B and F should have learnt less from their tutors than those in groups A and E since both tutors would show substantial plumage differences from the parents in the B♂Z♀ groups compared with the Z♂B♀ groups.

The preference for a conspecific might also result from different experiences that a young male has received in the nest. For example, cross-fostered zebra finches receive less parental care than normal from their Bengalese finch foster-parents during the first three weeks of life (ten Cate 1982, 1984). Bengalese finch parents also direct considerably less aggression towards their young (Chapter 2; ten Cate 1982) and recent findings suggest that aggression is important in a zebra finch's choice of song tutor (Chapter 3).

It is interesting that two cross-fostered Bengalese finches incorporated some of their foster-father's elements into their songs whereas the cross-fostered zebra finches based their songs on males heard after 35 days. With only two males it is not possible to assess whether the difference is a real one. However, one possible explanation is that the zebra finch is a "better" father, showing more parental care in the first three weeks and more aggression thereafter, and this stimulates the male to learn earlier than would normally be the case.

In addition to species differences in behaviour there are also differences between zebra finches and Bengalese finches in the way they behave towards normal and heterospecific young (ten Cate 1982). The greater number of interactions with the conspecific parent might account for the own species bias in song tutor choice in groups with mixed-species parents. Although physical interactions between the tutors and the young males after independence were minimised by the wire cage dividers some interactions either side of the cage were inevitable. One factor leading to own-species bias could simply be that the conspecific tutor is more stimulating.

Despite the own species bias most of the cross-fostered birds did learn from the heterospecific song tutor. In an earlier study zebra finches based their song on that of the conspecific whose song was similar to their father's (Chapter 3). A similar influence may have been at work in this experiment so that males which have been raised by a zebra finch father learn from the zebra finch tutor while those raised by a Bengalese finch father learn from the Bengalese finch tutor.

The mother may also be influential and one way of assessing the relative importance of the two parents is to raise young in mixed species pairs. For both species, males raised by Z♂B♀ and B♂Z♀ developed similar songs and sexual preferences which might be taken to suggest that both the mother and father are influential. However, this is confounded by differences in the effectiveness of the two tutors as song stimuli. If the conspecific tutor is in some way more stimulating then groups A and B would tend to learn zebra finch song and groups E and F would tend to learn Bengalese finch song. These two factors need not be alternatives. Hearing the father or foster-father's song may influence song learning but other vocal cues such as call notes, and visual and behavioural factors might be important too. King and West (1983, 1984) have also found females to be important for song learning in cowbirds, where social feedback from both males and females plays a crucial role.

An interesting feature of the cross-fostered males and those raised by mixed species pairs is the tendency to learn song from both species. This is also true of males successively exposed to two species, i.e. normally-raised zebra finches which are housed with Bengalese finches after independence and males which are raised by Bengalese foster-parents until independence and then housed with conspecifics (Chapter 9).

Ten Cate (1984) found that these birds which have been raised successively or simultaneously by both species also tend to court females of both species in choice tests. He suggests that this "dithering" is the result of sexual imprinting on both species (ten Cate 1986b). Ten Cate used white zebra finch and silverbill females in addition to zebra finch and Bengalese finch females in choice tests. The zebra finch males showed an exclusive preference for females of both the two parental species, a preference which was stable over a period of six months or more. Although the specificity of song preference has not been tested it seems likely that this is also reflects a specific tendency to learn from a zebra finch and a Bengalese finch tutor. Concerning the mechanism of sexual imprinting, ten Cate (1987) suggested that double imprinting results in a mixed standard being created to explain why ditherers prefer a hybrid female in choice tests between it and a female of one of the two species. For song tutor choice experiments males which have been raised by two species might also prefer to base their song on a tutor who sings a hybrid song containing elements from both species.

A preference for learning hybrid song might explain why Z♂B♀and B♂ Z♀ males tend to learn from their foster-father. Although the adult males used to form mixed-species pairs produced "normal" songs in terms of element-type and length, they may well have contained abnormal features as a result of having been raised by the foster-species. Call notes might be important in this respect: Zann (1985) found that cross-fostered male zebra finches tend to produce abnormal distance calls. These calls are often incorporated into the song phrase and frequently follow a bout of singing. Price (1979) suggests that they are used for species recognition. However, a preference for learning hybrid song fails to explain why zebra finches experiencing the two species in succession (i.e. Z-B or B-Z in Chapter 9) tend to copy song heard before 35 days since the foster-father had been normally-raised. In both cases, when male zebra finches are exposed to a tutor or tutors whose song is in some way inadequate for learning but sufficient to stimulate normal song development, there is a tendency to reproduce song which has been heard before 35 days. For young zebra finches, this might be a safeguard to ensure that only species-specific song is produced (for further discussion see Chapter 9).

To summarize, normally-raised zebra finches and Bengalese finches will learn their song at about 35 to 70 days of age. Birds denied suitable experience, either because they fail to hear any song during this time or because they are exposed simultaneously or successively to both species, can learn before or after the normal sensitive phase. However, it may take them longer, the copying may be less accurate and the song less stable.

Table 10.I: Housing conditions for the four groups of zebra finches and four groups of Bengalese finches.

GROUP.	YOUNG MALES.	PARENTS. (0-35 dys).	SONG TUTORS. (35-70 dys).	TOTAL.
A	Z	Z♂B♀	Z♂ & B♂	10
B	Z	B♂Z♀	"	8
C	Z	Z♂Z♀	"	10
D	Z	B♂B♀	"	10
E	B	Z♂B♀	"	9
F	B	B♂Z♀	"	8
G	B	B♂B♀	"	10
H	B	Z♂Z♀	"	10

(Key:- Z = Zebra finch; B = Bengalese finch).

Table 10.II: Number of males in each group which learnt their song from

GROUP	F ONLY	Z ONLY	B ONLY	F + Z	F + B	Z + B	F, Z + B	NONE	TOTAL
A	1	3	0	3	0	2	1	0	10
B	0	4	0	2	0	0	2	0	8
C	0	10	0	0	0	0	0	0	10
D	0	0	1	0	0	8	0	1	10
E	0	0	4	0	1	0	3	1	9
F	0	0	4	0	3	0	1	0	8
G	0	0	10	0	0	0	0	0	10
H	0	1	3	2	0	4	0	0	10

(Key:- F = Father; Z = Zebra finch; B = Bengalese finch).

Figure 10.1:

Sonagrams of a zebra finch (Z), Y9B6 and a Bengalese finch (B), B60 which were raised by a zebra finch father (ZF), Y5 and a Bengalese finch mother. At 35 days they were housed with a zebra finch (ZT), PB8 and a Bengalese finch tutor (B), W.

The zebra finch learnt his song from the conspecific tutor, incorporating zebra finch call notes (zc) which were similar to the father's. The Bengalese finch learnt from both tutors and possibly from the "father".

Letters under each sonagram denote portions of song (at least one element) common to two or more birds. Question marks indicate situations in which elements might have been poor copies or a blend from two males.

FIG 10·1

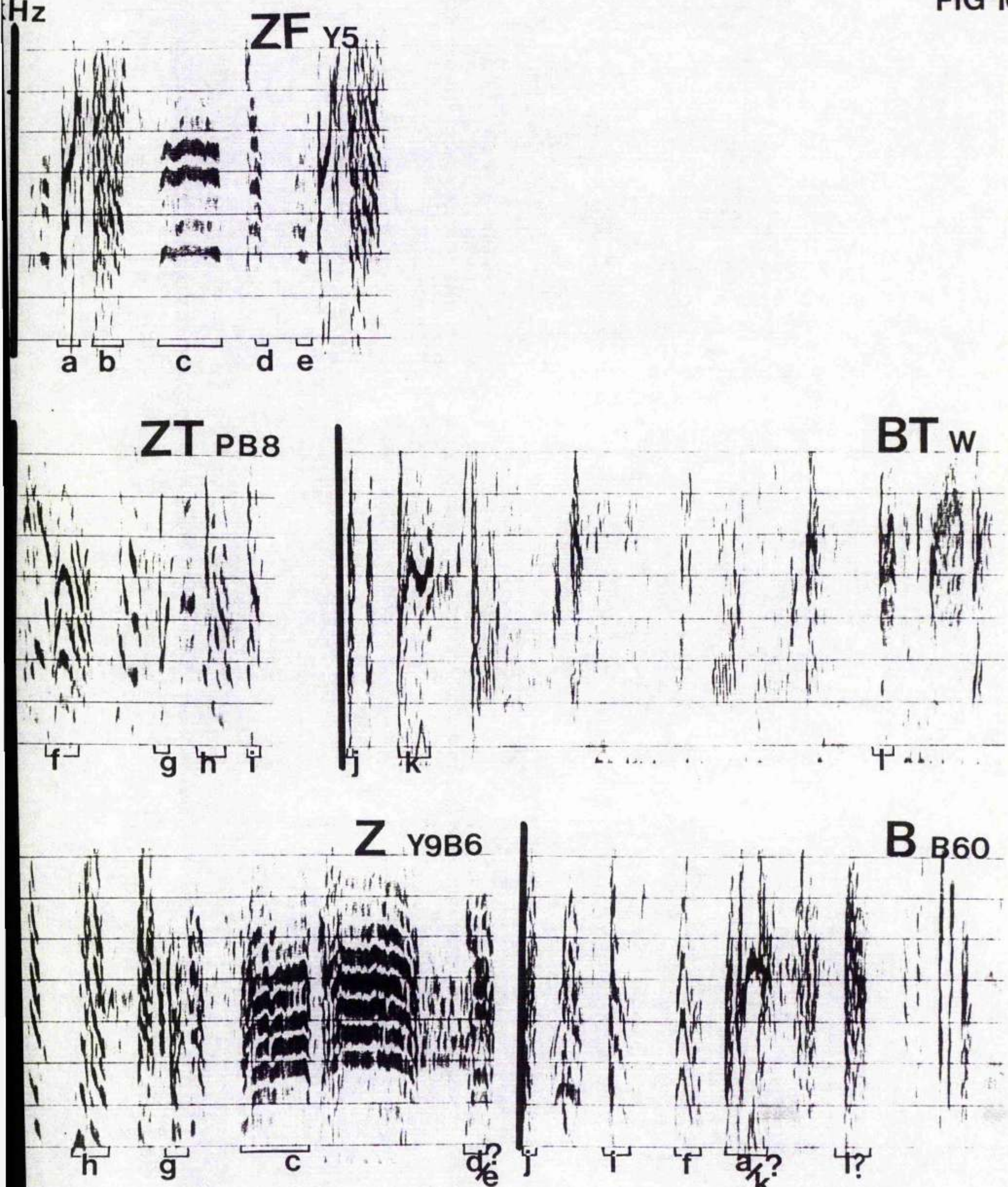

kHz
ZF Y5
a
b
c
d
e
ZT PB8
f
g
h
i
BT W
j
k
l
Z Y9B6
h
g
c
d?/e
B B60
j
i
f
a/k?
l?
1 SECOND

Figure 10.2:

Sonagrams of the zebra finch (Z), B79 and the Bengalese finch (B), B92 which were raised in a mixed species pair with a Bengalese father (B), 04. B79 copied song elements from both his father and the conspecific tutor (ZT), B259. B92 based his song entirely on the Bengalese finch tutor (BT), B.

Letters below the sonagrams represent sections of song common to two or more males.

FIG 10·2

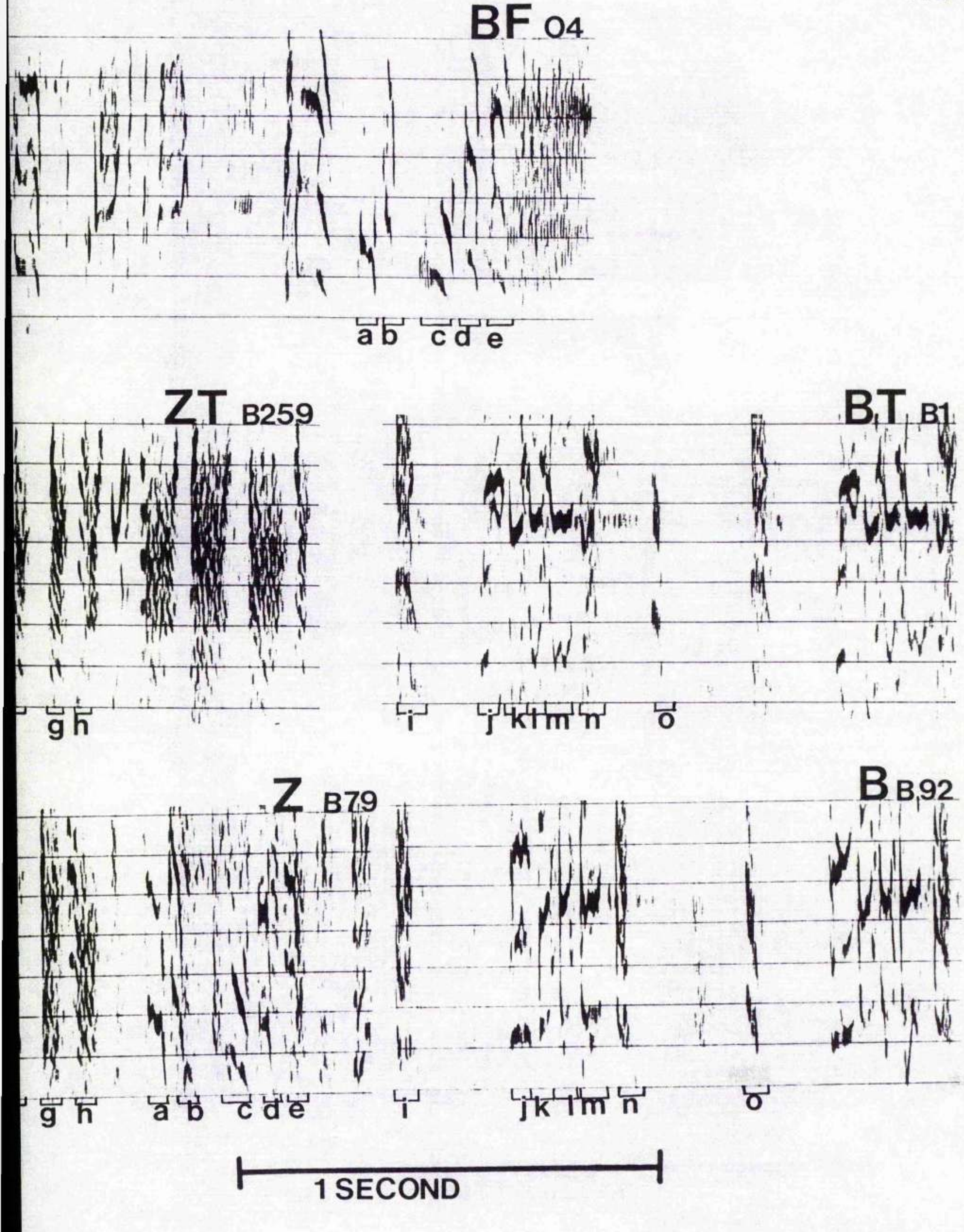

BF O4
a b c d e
ZT B259
g h
BT B1
i j k l m n o
Z B79
g h a b c d e
B B92
i j k l m n o
1 SECOND

Figure 10.3:

Sonagrams of a normally-raised zebra finch (Z), B8 and a Bengalese finch (B), B115 who had also been raised by the zebra finch (ZF), R1. B8 based his song on the zebra finch tutor (ZT), B207 whereas B115 learnt zebra finch call notes (zc), at least one of which (b) resembles that of the father, and song elements from the Bengalese tutor (BT), P7.

Letters bleow the sonagrams represent sections of song common to two or more males.

FIG 10·3

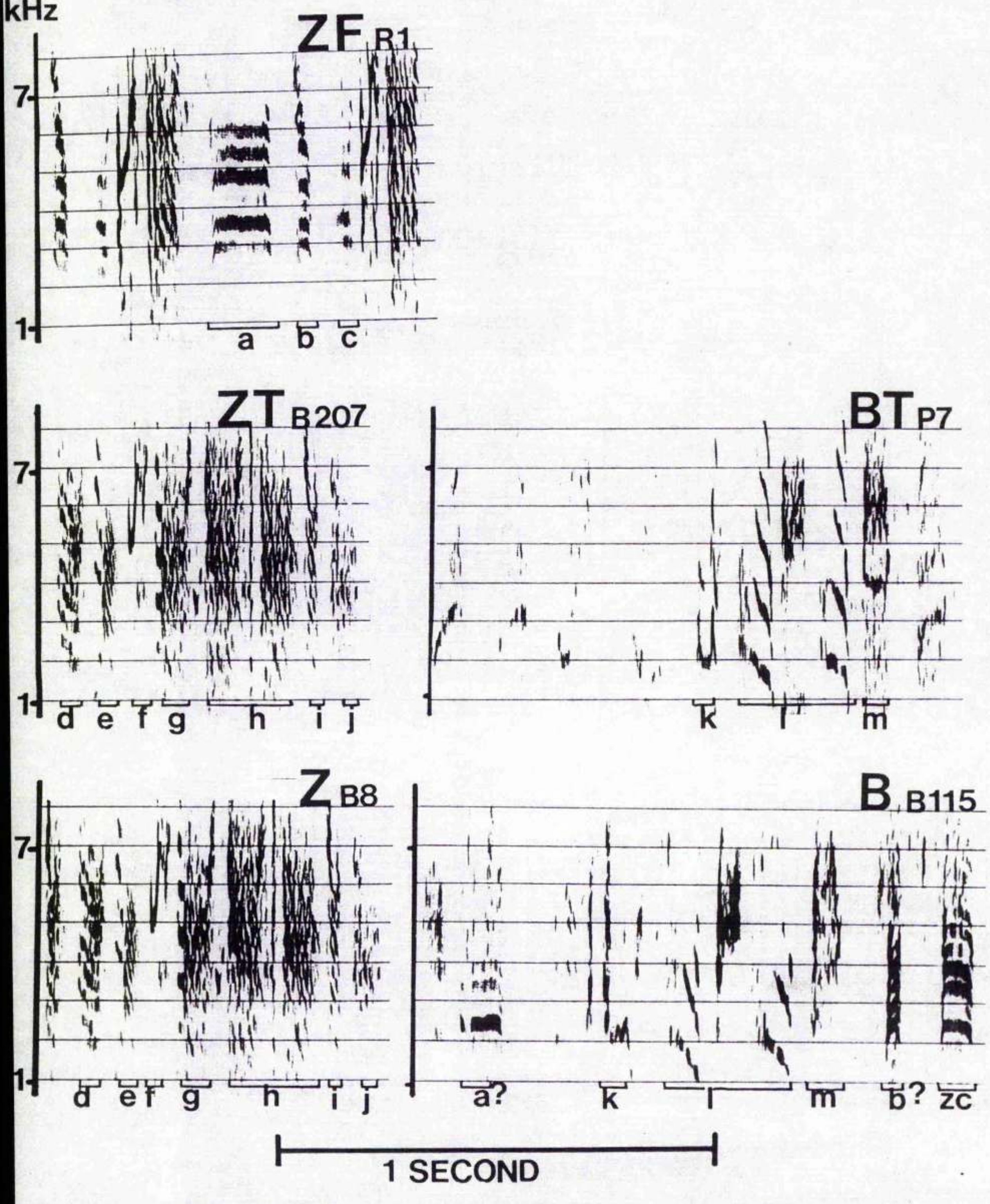
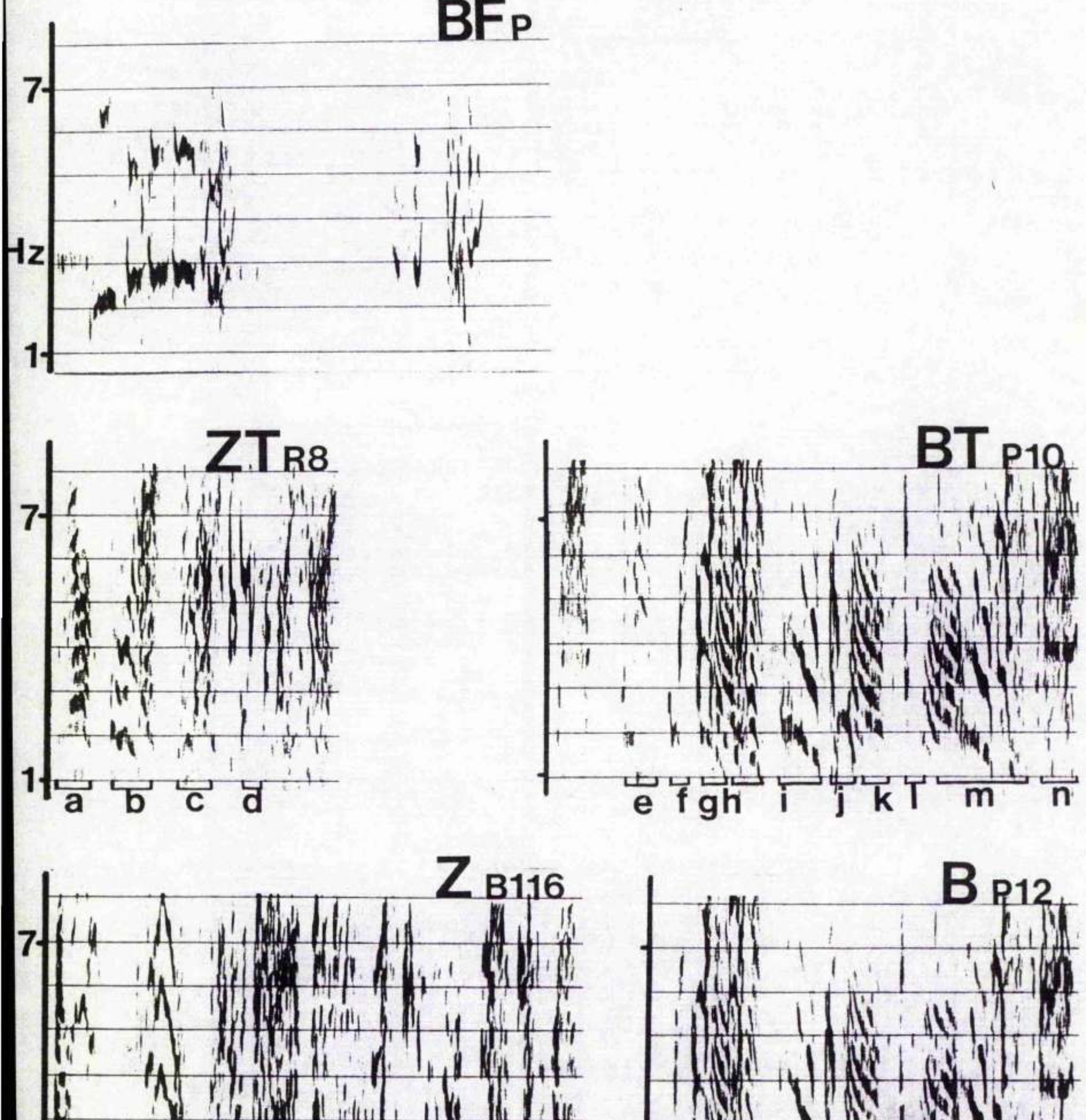

kHz
7
1
ZF B1
a
b
c
ZT B207
d
e
f
g
h
i
j
BT P7
k
l
m
Z B8
d
e
f
g
h
i
j
B B115
a?
k
l
m
b?
zc
1 SECOND

Figure 10.4:

Sonagrams of typical song phrases from a Bengalese finch (B), P12, a zebra finch (Z), B116 and their tutors P10 and R8. The normally-raised Bengalese finch (P12) copied his song from the Bengalese finch tutor (BT), P10 with whom he was housed from 35 to 70 days whereas the cross-fostered zebra finch (B116) learnt from the zebra finch tutor (ZT), R8 and the Bengalese finch tutor.

Lettters below the sonagrams show portions of song common to two or more males.

FIG 10·4



BFp
7
Hz
1
ZTR8
7
1
a
b
c
d
BT P10
e
f
g
h
i
j
k
l
m
n
Z B116
7
1
a
b?
c
e
d
i
j
B P12
f
g
h
i
j
k
l
m
n
1 SECOND

Figure 10.5:

Histograms of the proportion of males which learnt zebra finch and Bengalese finch elements for each group.

Key:-

NR normally-raised, i.e. by a pair of conspecifics.

XF cross-fostered to a pair of heterospecifics.

ZB raised by a zebra finch male and Bengalese finch female.

BZ raised by a Bengalese finch male and zebra finch female.

☐ zebra finch males.

■ Bengalese finch males.

FIG10·5

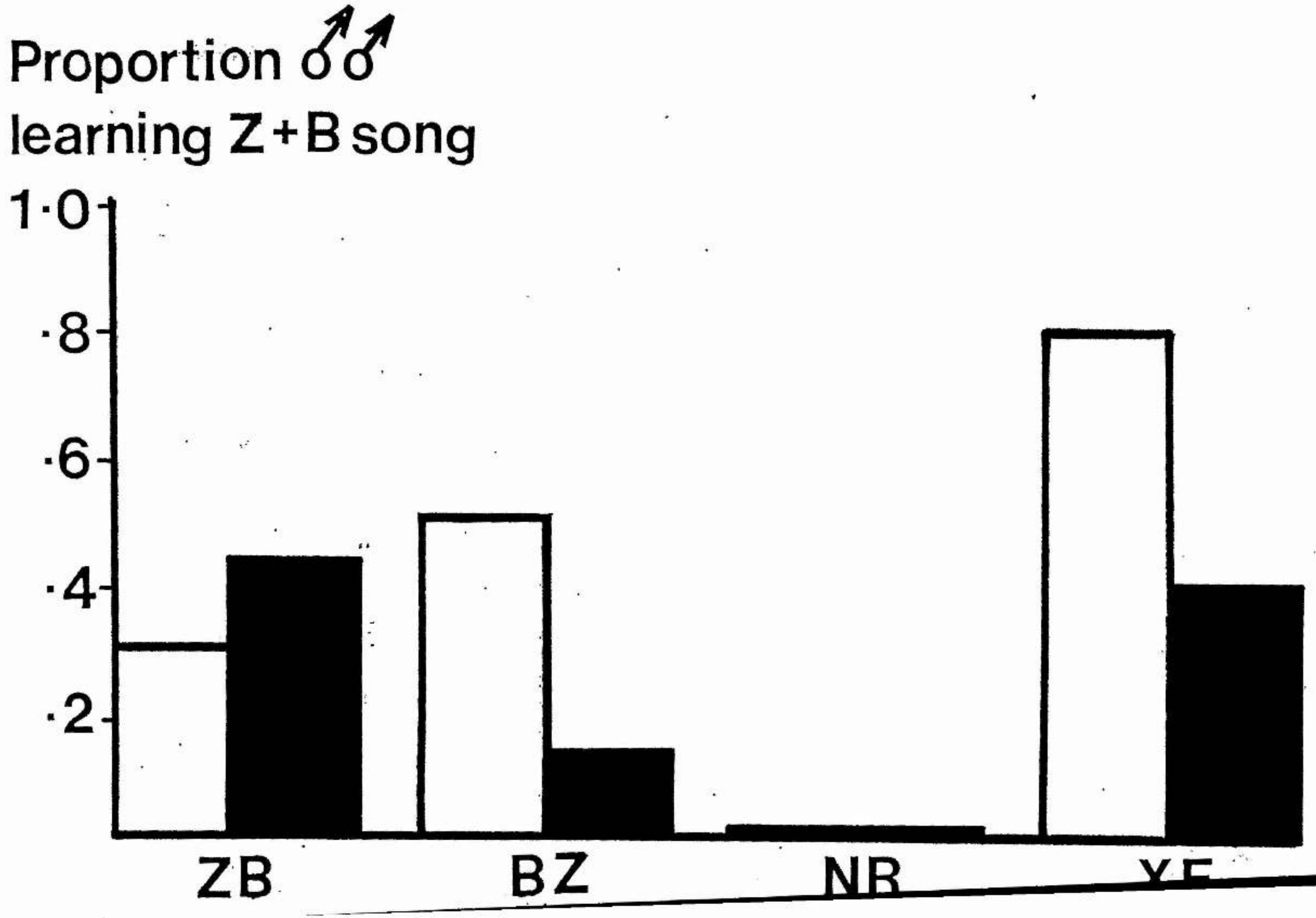


Figure 10.6:

Histograms for each group of the proportion of males which learnt some song elements from their father.

Key as for Fig. 10.5.

FIG 10·6

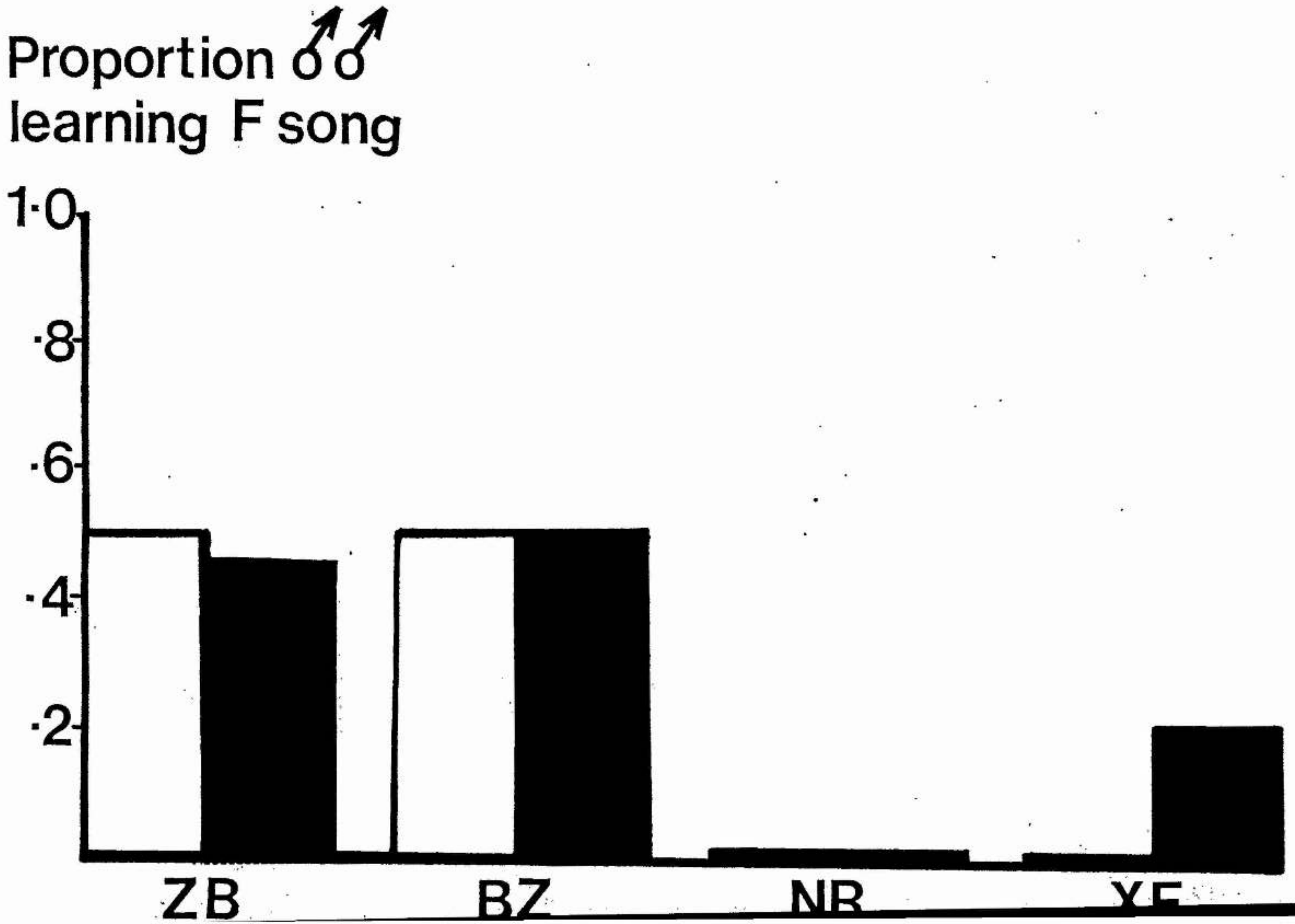
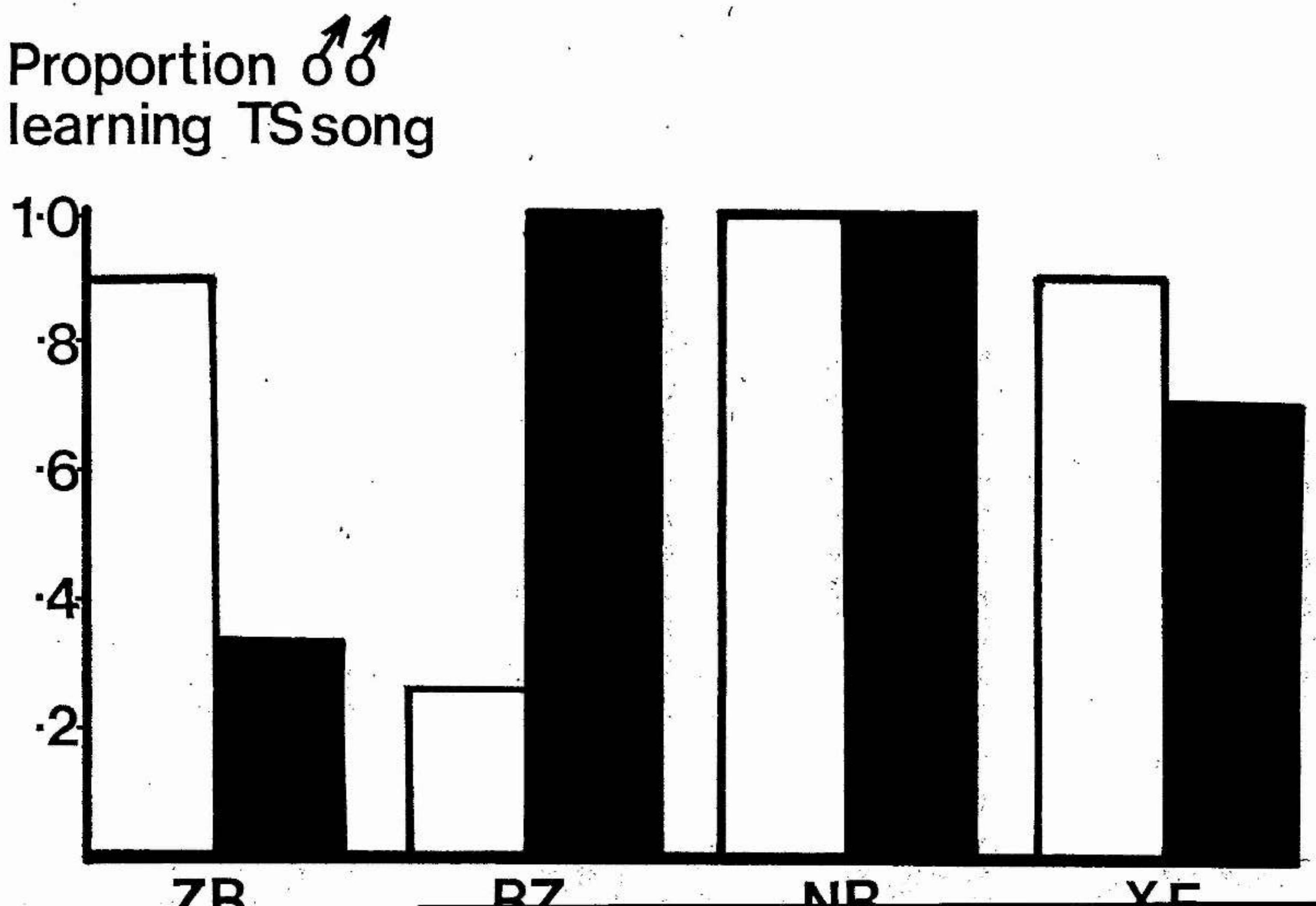


Figure 10.7:

Histograms are drawn of the proportion of males in each group which learnt at least one song element from the tutor who is of the same species as their "father" (TS).

Key as for Fig. 10.5.

FIG 10·7



Chapter 11.

SOME EFFECTS OF CROSS-FOSTERING ON THE DEVELOPMENT OF SEXUAL PREFERENCE IN MALE ZEBRA FINCHES AND BENGALESE FINCHES. HOW ARE SEXUAL IMPRINTING AND SONG LEARNING RELATED?

ABSTRACT.

Cross-fostering is an important technique for studying the extent to which early experience influences behavioural development. The results in Chapters 7 - 10 reflect just how crucial these social experiences can be for song acquisition. This chapter considers the effect of early experience on the development of sexual preference in male zebra finches and Bengalese finches.

Comparing these mate choice results with those obtained from the song learning studies suggests that there is no simple link between the two processes. Both are affected by the social experiences which a young male has early in life but the timing at which these operate and the relative weight of the various stimuli may be quite different.

INTRODUCTION.

Several studies have shown that male sexual preference in zebra finches is strongly influenced by early experience. Normally-raised zebra finches will only court the conspecific female but those which have been raised by Bengalese finches prefer females of the foster-species (Immelmann 1969, 1972; Kruijt et al 1983). Some males will court both females: these "ditherers" (ten Cate 1986b) are frequently found after exposure to their own and another species either successively or simultaneously. The former is achieved by raising zebra finch males with one species and then transferring them to the other before they are sexually mature (Immelmann 1979; Immelmann and Suomi 1981; ten Cate et al 1984). The latter can involve either raising by mixed-species pairs (Z♂ B♀ or B♂Z♀) or cross-fostering to Bengalese finches but with two or more conspecific siblings (ten Cate et al 1984; Kruijt et al 1983).

There are at least three experiential factors which determine sexual preference: the age at which the experience is obtained; the length of exposure to a particular condition; and the stimulus value of the conditions experienced. Because early social experiences are crucial to the development of sexual preference differences in experimental procedure can yield quite different results. This is shown by the work of Immelmann (1972) and ten Cate et al (1984) with zebra finches cross-fostered to Bengalese finches.

Acording to Immelmann sexual imprinting in zebra finches is normally complete by about day 20 and transfer to Bengalese finches should occur before this time if a previously established sexual preference is to be altered. However, in ten Cate et al's study one third of the zebra finches transferred to Bengalese finches at 30 to 60 days re-imprinted on the Bengalese finch female. As ten Cate et al point out, this variation probably results from differences in experimental design.

Ten Cate et al used cross-fostered Bengalese finch females in the mate choice tests so that females of both species would respond to the courting male; Immelmann used normally-raised Bengalese finch females. The female's response might be important, particularly for young males with a partial preference for both species.

Siblings, and other individuals with whom the birds were housed, could also affect the development of sexual preferences. Immelmann transferred whole clutches of birds to a pair of Bengalese finches whereas ten Cate et al placed individual males with a group of up to six Bengalese finches.

Another variable is the length of exposure to the second species. Ten Cate et al's birds were exposed to Bengalese finches for 28 or 29 days, in contrast to 16 days for Immelmann's birds. In the reverse situation, Immelmann and Suomi (1981) found that cross-fostered zebra finches which were subsequently transferred to conspecifics for 3 to 60 days, showed a greater preference for the zebra finch female the longer their exposure to conspecifics. The same is likely to apply in the case of normally-raised birds transferred to Bengalese finches: the longer the exposure to Bengalese finches the lower the preference for a conspecific mate.

Both of these research groups found that secondary exposure can influence mate preference. However, they place different interpretations on the results: Immelmann and Suomi believe that exposure to a second species temporarily interferes with a stable preference for the first, whereas ten Cate et al suggest that secondary exposure is stable, resulting in partial imprinting on the second stimulus.

In this chapter the stability of secondary exposure is tested in experiment I by giving the birds a third period of exposure with the first stimulus (the birds used being the same as in Chapter 9). If a recency effect operates then the preference for the second stimulus should disappear; if secondary exposure is stable the preference should be maintained. This assumes that no imprinting occurs during the third period of exposure. Although this cannot be ruled out completely, any effect would presumably be slight compared with exposure at an earlier age.

Experiment II compares the effect of successive exposure to the two species with simultaneous exposure, by raising both species in mixed-species pairs in the same way as ten Cate (1984) has done for zebra finches (see chapter 10 for details). Given the effect which subtle differences in experimental design can have on sexual preference this experiment therefore uses the same experimental procedure when comparing the effects of successive and simultaneous exposure to both species.

The third experiment considers the types of cue which might be important in the development of sexual preference. Males of both species were raised by conspecifics or cross-fostered to the other species. At independence they were then housed with a zebra finch male singing Bengalese finch song and a Bengalese finch singing zebra finch song (these are the males whose song learning was described in Chapter 7). To investigate the relative importance of visual and vocal cues the sexual preference values of these males are compared with the results in experiments I and II.

There are a number of interesting parallels between sexual imprinting and song learning. For both, social experience is critical in the learning process and, while learning occurs mainly during a relatively brief period early in life, the results are long lasting (Immelmann and Suomi 1981). However, song learning occurs later than sexual imprinting and so a young male might base his song on that of the male he has imprinted on. The final part of this chapter considers whether there is a direct link between song learning and sexual imprinting by comparing the song learning of each individual with the sexual preference results described here.

METHODS.

The males in Chapters 7, 9 and 10 were housed with their siblings in separate cages once the song learning studies had been completed (Table 11.I). At six months of age these males were tested for their sexual preference.

Each male was placed in the central portion of a double choice cage measuring 90 x 45 x 30 cm, which was separated from a 30 x 30 x 30 cm compartment at each end by a wire screen. For the zebra finch tests a female zebra finch was placed in one end compartment and a cross-fostered female Bengalese finch in the other: this ensured that both females preferred to solicit to a zebra finch male. Bengalese finch males were tested for their sexual preference using a normally-raised Bengalese finch and a cross-fostered zebra finch female. To reduce the influence of side preference the position of the females was changed at random from test to test.

Each male was given four 30 minute tests, with at least 24 hours between tests. To avoid preferences for particular females a male was offered the same female only once. The preference value for each male was calculated as the proportion of song phrases directed to the zebra finch female in choice tests with females of both species (see ten Cate 1984b).

RESULTS.

I: Successive Exposure to Both Species.

Fig. 11.1 illustrates the mean sexual preference for the four groups of zebra finches, shown as the proportion of courtship song phrases each male directed towards the zebra finch female in the choice tests. The four groups differed significantly in mate preference (Kruskal Wallis test, H=27.9, P<0.01). All the normally-raised birds in group A displayed an exclusive preference for the zebra finch (i.e. a preference value of 1.00) whereas those cross-fostered to Bengalese finches (group B) showed a definite, but not exclusive, preference for the Bengalese finch female. Groups C and D tended to court the zebra finch female but there was considerable variation between the individuals in groups B, C and D and a number of these males courted females of both species. This is reflected in Table 11.II which shows the number of males per group with preference values of 0, 0-0.5, 0.5-1 and 1.

Comparing group D with group B reveals that secondary exposure does influence final preference (Mann-Whitney U=0, $n_1=10$, $n_2=6$, $P<0.01$). Comparison of group C with group A also reflects this trend but the difference is much less (Mann Whitney U test, n.s.) indicating a bias towards the zebra finch. This own species bias is also reflected in the difference in response between groups A and B. Although group B birds had a significantly greater preference for the Bengalese finch female (U=0, $n_1=6$, $n_2=8$, $P<0.001$) this preference was not absolute: it is just that the Bengalese finch was a less effective stimulus.

II: Simultaneous Exposure to Both Species.

The mean sexual preferences for the eight groups of zebra finches and Bengalese finches (groups E-L) are shown in Fig. 11.2. All the normally-raised birds (groups E and I) displayed an exclusive preference for the conspecific female but individuals in the other six groups varied in their sexual preference and a number courted females of both species. Table 11.III shows the number of males in each group with preference values of 0, 0-0.5, 0.5-1 and 1.

The results of the normally-raised and cross-fostered (groups F and J) males show that sexual preference depends on the experiences which that male received during the first 35 days of life. A comparison of the preference values of cross-fostered zebra finches lends further support to this claim: males housed exclusively with Bengalese finches (group B) did not differ significantly in their sexual preference from those in group F which were cross-fostered to Bengalese finches until independence and then housed with both species (Mann Whitney U test, n.s.).

For the birds raised simultaneously by two species during the first 35 days of life (Z groups G and H, B groups K and L), however, males are biased towards a conspecific mate in subsequent mate choice tests. This own species bias is also reflected in the preference values of cross-fostered birds in this study: zebra finches in group F do not show an absolute preference for the Bengalese female but direct a small proportion of their song to the conspecific female, and the cross-fostered Bengalese finches in group J have a preference of 0.67 rather than an absolute preference for females of the foster-species.

The preference values for males raised by mixed-species pairs also show own species bias, although the preference is not absolute. Comparing groups G and H shows that, although males are slightly more Z-directed in their preference, if they have been raised by a zebra finch female, the difference is not significant and the Bengalese finches in groups K and L are slightly more B-directed if they have been raised by a Bengalese finch female rather than a bengalese finch male (Mann Whitney U tests, n.s.). Clearly, both parents are influential in guiding the development of sexual preference. For both species there is a significant difference in the preference values of males raised by one versus two heterospecific parents (U=0, n_1=18, n_2

=10, $P<0.001$ for zebra finches; $U=0$, $n_1=17$, $n_2=10$, $P<0.001$ for Bengalese finches).

III: The Importance of Visual Versus Vocal Cues.

Fig. 11.3 shows the mean sexual preference for the three groups of zebra finches (M, N and O) and the three groups of Bengalese finches (P, Q and R) which were housed with a zebra finch singing Bengalese song and a Bengalese finch singing zebra finch song during the five week period immediately following independence. All the normally-raised birds showed a complete preference for the conspecific in contrast to those males which had been cross-fostered to the other species ($U=0$, $n_1=8$, $n_2=10$, $P<0.001$ for M vs O; $U=0$, $n_1=9$, $n_2=10$, $P<0.001$ for P vs R). The cross-fostered males show considerable variation in their preference values: this is apparent in Table 11.IV which shows the number of males per group with preference values of 0, 0-0.5, 0.5-1 and 1. These results show the importance of early experience during the first 35 days and the bias towards learning from conspecifics, even for those birds raised by the mother alone (Mann Whitney U tests, n.s. for M vs N and P vs R).

Comparing groups M and O with normally-raised (group E) and cross-fostered (group F) zebra finches which were housed with a normal zebra finch and Bengalese finch male after independence gives no significant difference in sexual preference (Mann Whitney U tests). The same is true for Bengalese finches. This result suggests that visual factors are of prime importance for sexual imprinting. However, vocal cues can also have some influence: if males are housed after independence with males whose songs are inappropriate there is a greater tendency to court the conspecific female in subsequent mate choice tests but this difference does not reach statistical significance (groups M vs E, O vs F).

IV: The Relationship Between Song Learning and Sexual Imprinting.

Table 11.V examines the relationship between song learning and sexual preference. In Table 11.Va the number of zebra finches with an exclusive preference for a zebra finch mate, a zebra finch song tutor, both or neither is compared for all the groups (A-D, E-H, M-O). The results for Bengalese finches are given in Table 11.Vb (groups I-L, P-R). tests for the both species (excluding the normally-raised birds - groups A, E and M for zebra finches; B, F and P for Bengalese finches) indicate that there is no significant tendency for a male to copy song from a male of the species on which he is sexually imprinted (see Appendix 11a for details).

DISCUSSION.

A notable feature of the sexual preference results in all three studies is the tendency to court the conspecific female in mate choice tests, irrespective of previous experience. Even males which had been cross-fostered to the other species and remained with them after independence do not show an exclusive preference for females of the foster-species.

One possible reason for the bias is the influence of siblings. Kruijt et al (1983) found that cross-fostered zebra finches raised alone or with only one sibling court the Bengalese finch female exclusively: only males raised with two or more siblings direct 5% or more of their courtship song towards the conspecific female. Sibling bias might also explain the difference between ten Cate et al's results and those of Immelmann and the present study (experiment I), where siblings were transferred with the young male.

Immelmann (pers. comm.) suggests that aggressive interactions between siblings may influence mate preference. Other aggressive encounters might also be important. Ten Cate et al (1984) found Bengalese finches were less aggressive than zebra finches but, the greater the number of aggressive and non-aggressive initiatives by Bengalese finches towards the young, the greater the preference for Bengalese finch. Aggressive interactions between young zebra finches and their tutors appear to be important for song tutor choice: the males in Chapter 3 learnt from the zebra finch who was most aggressive towards them.

Behavioural interactions with the parents are also likely to be important. In mixed-species pairs (Z♂B♀ or B♂Z♀) ten Cate (1985) found that parents tended to feed conspecific chicks more frequently and to direct more aggression and contact behaviour towards them. These birds also tended to prefer a conspecific female in mate choice tests (ten Cate 1985). A further indication of the importance of parental interactions comes from Bohner's observations (pers. comm.) on normally-raised zebra finches. Bohner found a correlation between the father's singing activity and the frequency with which both parents feed their fledglings in the two weeks prior to independence.

The results in this chapter show that normally-raised zebra finches and Bengalese finches have become sexually imprinted by 35 days of age. This applies even if zebra finches are transferred to Bengalese finches at 35 days (group C), a result which agrees with

Immelmann (1972) but contrasts with the work of ten Cate et al (1984). It seems unlikely that this is simply because exposure to zebra finches was longer, since group D were housed with Bengalese finches for longer yet they also preferred conspecific females.

Cross-fostered males, however, are capable of becoming sexually imprinted after 35 days of age. Indeed, the males in group D showed a strong preference for the zebra finch female even though they had been raised by Bengalese finches for the first 35 days of life. Comparing group D with group B also shows the influence of secondary exposure on final preference. This effect is probably the result of partial imprinting rather than temporary interference. Ten Cate (1986) also found secondary imprinting to be relatively longlasting: zebra finch "ditherers", which court females of both species, continued to show dithering behaviour when they were retested six months later.

The results of experiments I and II indicate that successive exposure to both species has a greater influence on the development of sexual preference than housing the birds with both species simultaneously. With simultaneous exposure the birds show a strong preference for females of their own species although this preference is not 100%. Presumably this reflects the importance of behavioural interactions, particularly the difference in parental interactions with conspecific and heterospecific young.

For both species, males raised by Z♂B♀ and B♂Z♀ pairs developed similar sexual preferences. The "mother" may be slightly more influential: birds raised with a conspecific mother had a greater preference for the conspecific female than those raised by a conspecific father but the difference between the two did not reach statistical significance for either species. This agrees with ten Cate's (1985) results for zebra finches raised by mixed species pairs. A further indication that one conspecific parent is sufficient for a young male to develop a sexual preference for conspecific females comes from the results of experiment III where, for both zebra finches and Bengalese finches, males raised by their mother alone only courted the conspecific female in subsequent mate choice tests.

Experiments I and III also suggest that visual factors, both physical cues such as plumage characteristics and behavioural interactions with the parents and siblings, are of prime importance in the development of sexual preference. Vocal cues can also have a subtle effect: males which have been housed with tutors who sing inappropriate songs (experiment III) show a greater tendency to prefer conspecific females than those housed with normally-raised tutors after independence.

The overall results of these sexual imprinting studies bear striking similarity to the song learning results in Chapters 7, 9 and 10, and superficially, the two processes do appear to correlate: normally-raised males court conspecifics exclusively and only sing conspecific song; cross-fostered males prefer to court females of the foster-species and to learn from a song tutor of that species; and males raised by two species are intermediate between the two. However, the results in this chapter clearly indicate that, if one considers individual males, there is no direct link between the two.

TABLE 11.I: Housing conditions.

Group	0-35 days	35-70 days	80-105 days	Total No.
A (Z chicks)	Z♂Z♀	Z♂Z♀	Z♂Z♀	8
B (Z chicks)	B♂B♀	B♂B♀	B♂B♀	6
C (Z chicks)	Z♂ Z♀	B♂B♀	Z♂Z♀	10
D (Z chicks)	B♂B♀	Z♂Z♀	B♂B♀	10
E (Z chicks)	Z♂Z♀	Z♂+ B♂		10
F (Z chicks)	B♂B♀	Z♂+ B♂		10
G (Z chicks)	Z♂B♀	Z♂+ B♂		10
H (Z chicks)	B♂Z♀	Z♂+ B♂		8
I (B chicks)	B♂B♀	Z♂+ B♂		10
J (B chicks)	Z♂Z♀	Z♂+ B♂		10
K (B chicks)	Z♂B♀	Z♂+ B♂		9
L (B chicks)	B♂Z♀	Z♂+ B♂		8
M (Z chicks)	Z♂ Z♀	ZBS♂+ BZS♂		8
N (Z chicks)	B♂ B♀	ZBS♂+ BZS♂		10
O (Z chicks)	Z♀	ZBS♂+ BZS♂		10
P (B chicks)	B♂B♀	ZBS♂+ BZS♂		9
Q (B chicks)	Z♂Z♀	ZBS♂+ BZS♂		10
R (B chicks)	B♀	ZBS♂+ BZS♂		8

TABLE 11.II: Sexual preference for zebra finches in experiment I.

Group	No. males with a sexual preference value of:-				Total No.
	0	0-0.5	0.5-1	1	
A (Z-Z-Z)	0	0	0	8	8
B (B-B-B)	3	3	0	0	6
C (Z-B-Z)	0	0	4	6	10
D (B-Z-B)	0	0	10	0	10

TABLE 11.IV: Sexual preference in zebra finch and Bengalese finch males in experiment III.

Group	No males with a sexual preference value of:-				Total No.
	0	0-0.5	0.5-1	1	
M (Z♂Z♀)	0	0	0	8	8
N (Z♀)	0	0	0	10	10
O (B♂B♀)	2	8	0	0	10
P (B♂B♀)	9	0	0	0	9
Q (B♀)	10	0	0	0	10
R (Z♂Z♀)	0	2	6	0	8

TABLE 11.III: Sexual preference in zebra finch and Bengalese finch males in experiment II.

Group	No males with a sexual preference value of:-				Total No
	0	0-0.5	0.5-1	1	
E (Z♂Z♀)	0	0	0	10	10
F (B♂B♀)	3	7	0	0	10
G (Z♂B♀)	0	0	3	7	10
H (B♂Z♀)	0	0	1	7	8
I (B♂B♀)	10	0	0	0	10
J (Z♂Z♀)	0	0	10	0	10
K (Z♂B♀)	6	2	0	0	9'
L (B♂Z♀)	6	2	0	0	8

TABLE 11.V: The relationship between sexual preference and song learning.

(a). Zebra finch males.

Group	No males with an exclusive preference for:-				Total No.
	Z♀ & SONG.	Z♀.	Z SONG.	NEITHER.	
A (Z-Z-Z)	8	0	0	0	8
B (B-B-B)	0	0	0	6	6
C (Z-B-Z)	2	4	0	4	10
D (B-Z-B)	0	0	9	1	10
E (Z♂Z♀)	10	0	0	0	10
F (B♂B♀)	0	0	1	9	10
G (Z♂B♀)	5	2	2	1	10
H (B♂Z♀)	1	6	1	0	8
M (Z♂Z♀)	6	1	0	0	8*
N (Z♀)	7	2	0	0	10*
O (B♂B♀)	0	0	7	3	10

(b). Bengalese finch males.

Group	No. males with an exclusive preference for:-				Total No.
	B♀ & SONG.	B♀.	B SONG.	NEITHER.	
I (B♂B♀)	10	0	0	0	10
J (Z♂Z♀)	0	0	4	6	10
K (Z♂B♀)	3	4	1	0	9'
L (B♂Z♀)	5	1	2	0	8
P (B♂B♀)	5	3	0	0	8
Q (B♀)	6	4	0	0	10
R (Z♂Z♀)	0	0	4	4	8

Key:-

' One male in group K failed to court either zebra finch or Bengalese finch females.

* Two males (group M and N) did not learn song from either tutor or the father.

Figure 11.1:

Histograms of the mean sexual preference per group for the four groups of zebra finches (A - D) which were successively exposed to zebra finch and Bengalese finch pairs in experiment I.

NR = Normally-raised males.

XF = Cross-fostered to the other species.

Z-B-Z = Raised in successive five week periods by a pair of zebra finches, a pair of Bengalese finches and then a second pair of zebra finches.

B-Z-B = Raised in the reverse situation.

FIG 1·1

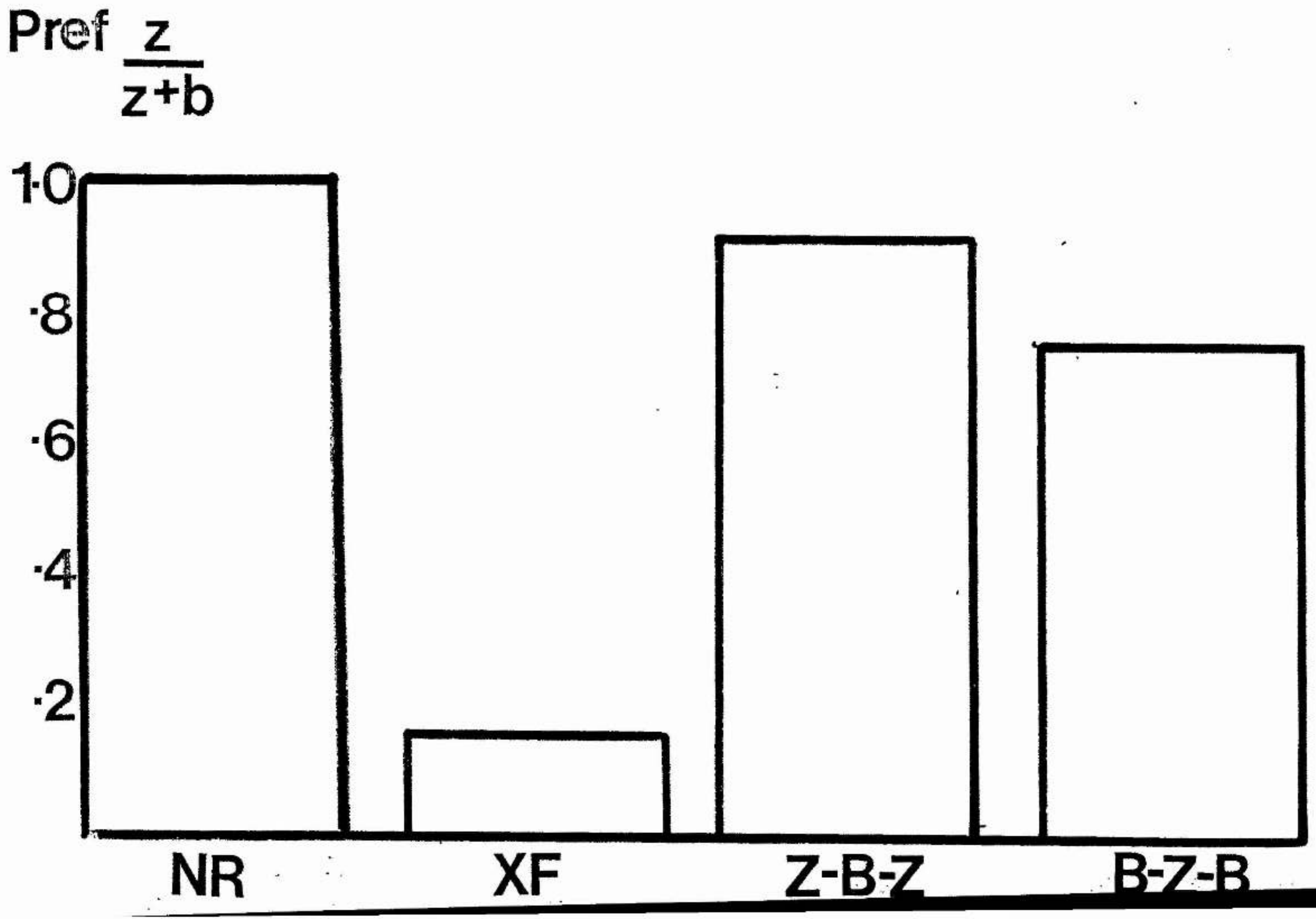


Figure 11.2:

Histograms of the mean sexual preference per group for four groups of zebra finches (E - H) and four groups of Bengalese finches (I - L) in experiment II.

ZB = Raised by a zebra finch "father" and a Bengalese finch "mother".

BZ = Raised by a Bengalese finch "father" and a zebra finch "mother".

☐ Zebra finch males.

■ Bengalese finch males.

FIG 11·2

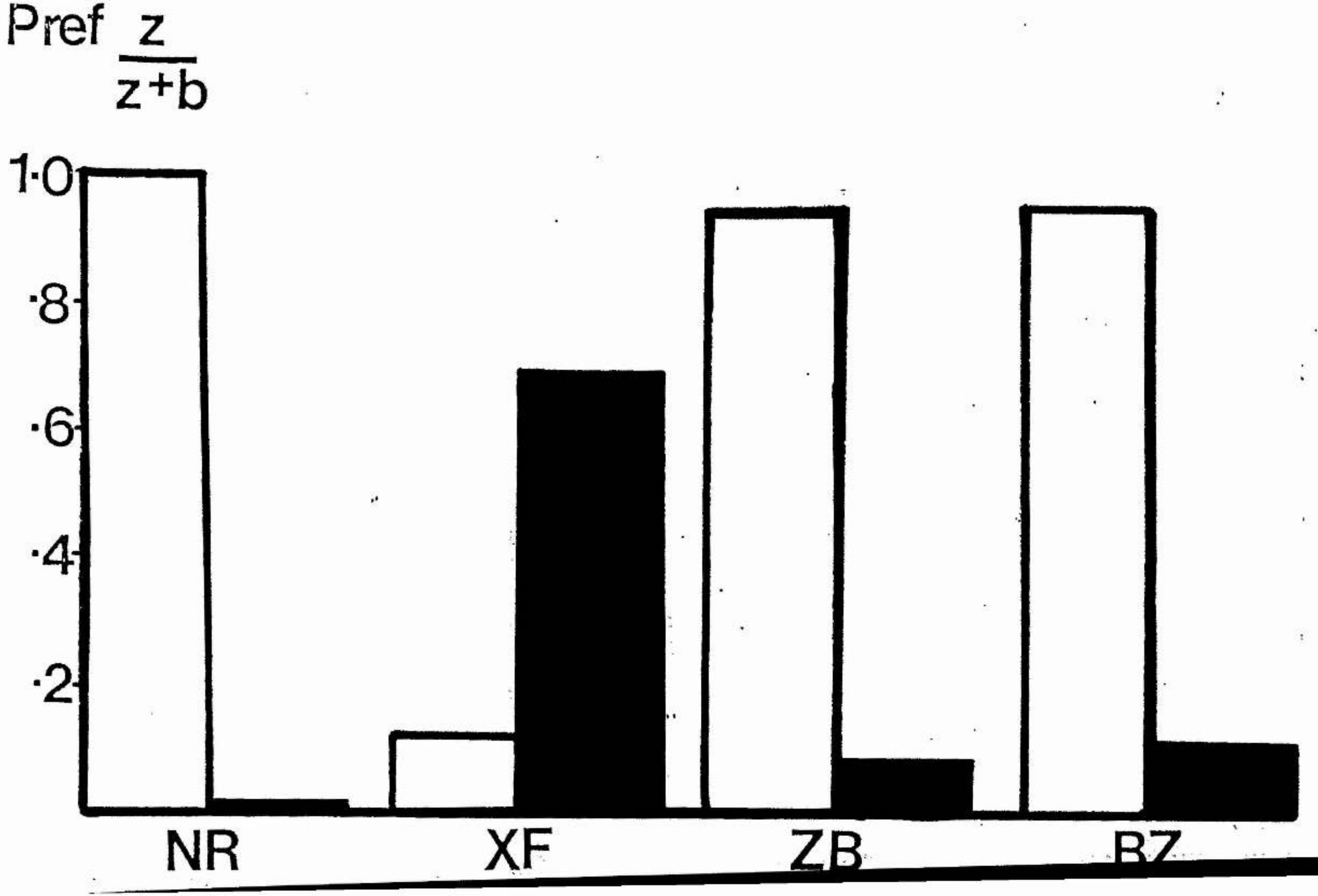


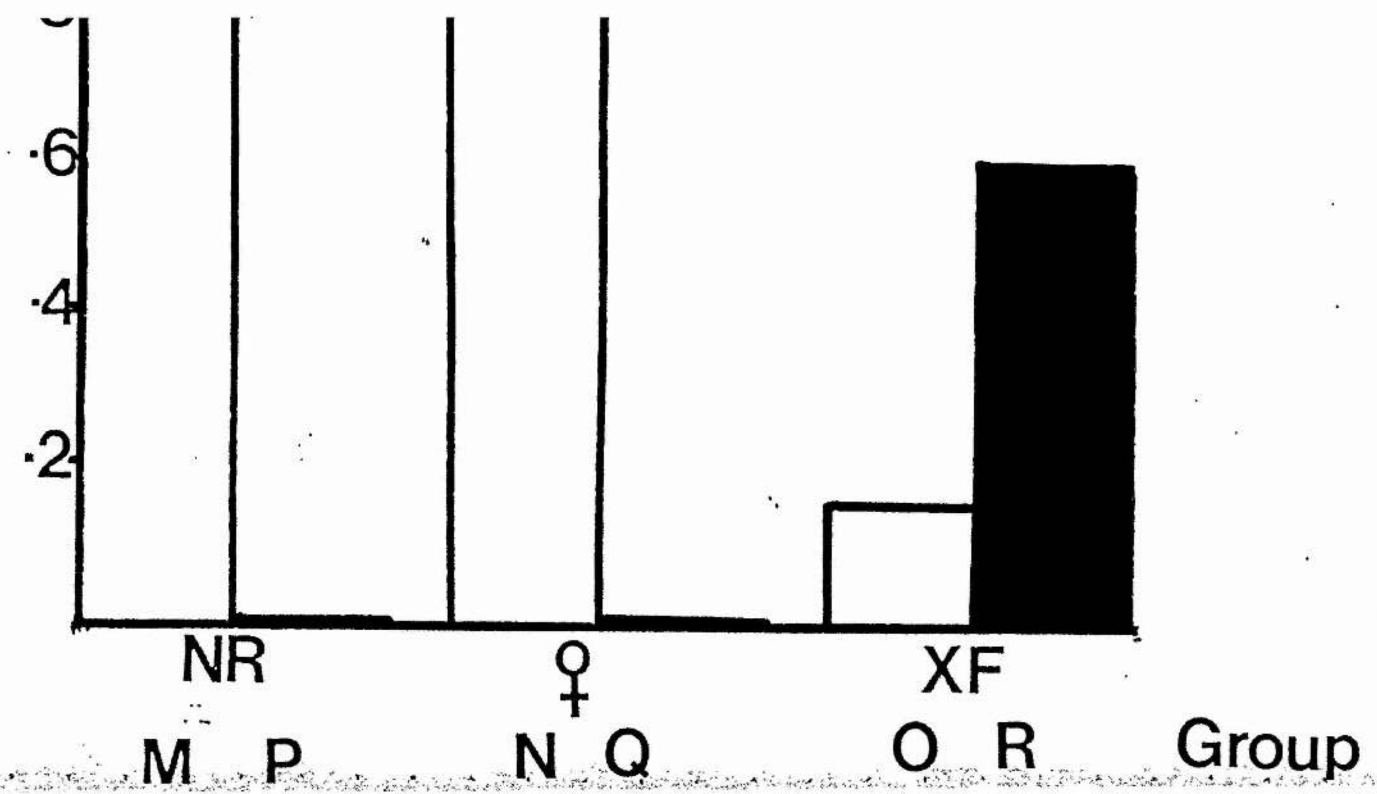
Figure 11.3:

Histograms of the mean sexual preference per group for the three groups of zebra finches (M - O) and three groups of Bengalese finches (P - R) in experiment III.

♀ = Raised by the conspecific "mother" alone.

☐ Zebra finch males.

■ Bengalese finch males.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Chapter 12.

CONCLUSIONS.

Since the pioneering chapter by Immelmann (1969) our knowledge of song learning in zebra finches has progressed considerably and it is now clear that social experiences early in life are extremely influential in governing what a bird learns, when and from whom.

From his original studies, in which zebra finches were raised by Bengalese foster-parents and then moved into isolation at different ages, Immelmann (1969) concluded that young zebra finches show a preference for both song of the right tonal quality (own species bias) and for that of the male which reared them. These results might be taken to suggest that zebra finches would normally learn their father's song. However, in the wild young zebra finches become independent of their parents at about 35 days of age (Immelmann 1962), before the normal sensitive phase for song production learning (Eales 1985b). By this time most parents have begun a fresh clutch and become increasingly aggressive to the fledglings, chasing and driving them away from the nest. These behaviours are also seen in captive birds (Chapter 2). After 35 days the father is therefore unlikely to be available for the young birds to learn from except where they are housed together experimentally. In the wild zebra finches form small flocks (Immelmann 1965) where young birds will experience a variety of songs after separation from the father and experience during this period immediately after independence is likely to be the most important factor influencing which songs they sing as adults. This does not mean that experience before 35 days is irrelevant to song learning. Indeed, Chapter 3 shows that experience before independence can lead to a preference for a song tutor who sings like the father in subsequent tutor choice.

If a young male is to base his song on that of a tutor whose song is similar to the father's then he must learn some features of his father's song by the time he gains independence. discrimination learning need not involve the memorization of details, such as those required in song production learning. Nonetheless, both males and females are capable of learning to discriminate between a whole variety of songs (Chapter 4) and this discrimination learning may help them to distinguish between individuals, neighbours and strangers, and perhaps to recognise relatives. The latter depends on the extent to which male performance learning involves the transmission of kinship cues. If closely related males have similar songs as a result of choosing to learn song from a tutor whose song is similar to their fathers' then song could be used as a cue for mate choice and, if it is advantageous for a female to choose a mate who is neither too distantly nor too closely related to herself, then she might choose a male whose song differed from that of her father by a particular amount. The results in Chapter 4 show that female zebra finches can discriminate between their fathers' songs and those of other males: this might provide the basis for such a mechanism.

In the wild zebra finches associate in mixed-species flocks (Immelmann 1962) and it is therefore crucial that young males choose a conspecific song tutor to learn their song from. This thesis shows that physical contact, visual cues and vocal interactions are important in ensuring species-specificity. Although physical contact is not essential, in the sense that zebra finch song development will proceed normally provided the bird can interact visually and vocally with a tutor throughout the sensitive phase for song learning (Eales 1985a), aggressive interactions between the tutors and the young males appear to influence song tutor choice (Chapter 3). In the tutor choice studies in Chapters 7, 8 and 10 involving zebra finches which had been cross-fostered to Bengalese finches and vice-versa, behavioural interactions between young males and their tutors were minimised by separating the two tutors from each other and from the young males by wire mesh screens because zebra finches are known to be more aggressive than Bengalese finches (Chapter 2). Nonetheless, previous interactions with the parents before 35 days might be important. Cross-fostered zebra finches receive less parental care from their Bengalese finch foster-parents (ten Cate 1982, ten Cate et al 1984) and Bengalese parents are less aggressive towards their young (Chapter 2). As well as basic differences between the two species adults may also differ in their reactions to chicks of their own species and those of the other. This is most obvious in mixed-species pairs where the conspecific parent feeds the chicks more and directs more contact behaviour and aggression towards them (ten Cate 1982). In mate choice tests young males subsequently prefer a female of their own species (ten Cate 1985). The preference for a conspecific song tutor might also be established in this way (Chapter 10).

Another factor which may bias learning stems from the species-specific differences in vocalizations. Zebra finches are capable of copying song from a Bengalese finch tutor but they tend to sing these Bengalese elements in phrases which are more nearly zebra finch in length (Chapter 6). Bengalese finches also learn from the other species: they tend to sing zebra finch elements in longer phrases with elements being repeated in typical Bengalese finch fashion. These elements tend to be copied inaccurately and are more widely spaced so that the song is sung at a slower tempo. An additional feature is that species-specific call notes are often incorporated into the song by zebra finches but not by Bengalese finches. This could serve as a label indicating the suitability of a song tutor. However, the results in Chapter 8 showed no tendency to learn from the male with a normal song and distance call in choice tests with two zebra finch tutors, one with a normal song and one which sang Bengalese finch song elements.

If zebra finches and Bengalese finches are given the choice of two tutors, a zebra finch singing Bengalese finch elements and a Bengalese finch singing zebra finch elements, they tend to learn from the conspecific irrespective of which species raised them (Chapter 7). This suggests that visual cues are very important for song tutor choice. Comparing the results in Chapter 7 with those in Chapter 10, where cross-fostered males which were exposed to a zebra finch and a Bengalese finch song tutor from 35 to 70 days tended to sing a hybrid song containing elements copied from both tutors, suggest that vocal cues from the foster-father may bias learning in favour of the tutor who has a similar song to that of the male which raised them.

Siblings might also bias song tutor choice, a factor which has often been overlooked in the past, but one which is known to be crucial in the development of sexual preference (Kruijt et al 1983). The number per clutch and the number of each sex might both be important. A subtle point is that, because of the difficulties in raising birds by the other species, particularly for Bengalese finches cross-fostered to zebra finches, there tend to be fewer siblings per clutch.

Physical factors, visual cues and vocal differences are all likely to contribute to the own species bias. As well as affecting what and from whom a bird learns, cross-fostering can also affect the timing of song learning (Chapters 9 and 10). If males are denied visual interaction with the tutor during the normal sensitive phase (Eales 1985a), or if they have been exposed successively (Chapter 9) or simultaneously (Chapter 10) to both species, then there is a tendency to produce song heard from their father or foster-father before 35 days of age. In all three studies, vocal and or visual stimulation during the sensitive phase did not match in quality that received earlier. Such a mismatch seems to cause the bird to recall and reproduce song learnt before 35 days and to block further learning after the normal sensitive phase.

What all three studies show is that experience, in addition to age, is important in governing the timing of song learning. The results of Chapter 11 show the same flexibility in the timing of sexual imprinting. Further evidence of this flexibility in the timing of the sensitive phase is reflected in the finding that birds raised in similar situations sometimes learn at quite different times. Some of the cross-fostered males in Chapters 9 and 10, for example, learnt before 35 days whereas none of the cross-fostered males in Chapters 7 and 8 did so. Clutch mates often differ in their choice of song tutor as well as in how accurately they copy a song. The crucial point is that the timing of the sensitive phase is flexible: what and when a bird learns will depend on the experiences he gains. This applies to the development of both sexual preference and song. Individuals vary considerably and this should serve as a caveat in rigid interpretations of the results.

An element of caution should be employed when relating the results of this thesis to song learning in the wild. The studies in Chapters 3 and 4 have been designed to mimic as nearly as possible the experience which young zebra finches would receive in the wild. I have assumed that raising young zebra finches by their parents until independence and then separating them into small groups is a reasonably close fit to the natural situation. Nonetheless, questions concerning the function of song and of song learning can only be answered in relation to the environment in which that song evolved. Obviously the controlled laboratory conditions are essential for carrying out experiments on song acquisition but the extent to which these results can explain what happens in the wild depends on how accurately the laboratory situation mirrors the natural one. Although some studies of wild zebra finches have been done (Immelmann 1962, Zann 1984) the species is not an easy one for detailed behavioural observations in the bush. More information is required, particularly on population structure and dispersal and on precise details of their development, if these results for captive birds are to be put in a natural context. Crucial to the whole story is a knowledge of how and when zebra finches choose their song tutors in the wild. At present there is no information on this, yet such details are vital if the functional significance of laboratory results are to be fully appreciated.

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APPENDIX 5a: Results of song learning in Bengalese finches aged six months

Group	Bird	No elements in bird's song phrase	No improvised elements	No elements learnt from			No elements in tutor's song		
				F	T_1	T_2	F	T_1	T_2
A	B70	7	5	–	–	2	–	–	9
	B71	6	3	–	–	3	–	–	9
	B72	6	3	–	–	3	–	–	9
	B74	10	7	–	–	3	–	–	9
	B75	6	3	–	–	3	–	–	9
	GBk	6	2	–	–	4	–	–	9
	B76	6	1	–	–	5	–	–	8
	B77	6	2	–	–	4	–	–	8
	B78	8	1	–	–	8	–	–	8
	B79	9	1	–	–	8	–	–	8
	B80	8	2	–	–	6	–	–	8
B	O 1	9	6	–	–	3	–	–	9
	O 4	10	6	–	–	4	–	–	9
	Y 9	11	6	–	–	5	–	–	10
	Y10	8	4	–	–	4	–	–	10
	B 4	8	5	–	–	3	–	–	7
	B 5	10	7	–	–	3	–	–	7
	B 9	6	2	–	–	4	–	–	7
	B11	6	3	–	–	3	–	–	7
	B13	7	3	–	–	4	–	–	7
C	O 5	12	5	–	7	–	–	10	–
	B 1	9	1	–	8	–	–	10	–
	B 3	9	1	–	8	–	–	10	–
	Y 7	9	4	–	5	–	–	8	–
	Y 9	7	2	–	5	–	–	8	–
	Y10	7	2	–	5	–	–	8	–
	P 6	8	3	–	5	–	–	8	–
	P 7	7	2	–	5	–	–	8	–
	PR	6	0	–	6	–	–	8	–
	PW	8	2	–	5	–	–	8	–
D	W 7	10	4	6		–	9		–
	W 8	12	7	5		–	9		–
	D	7	1	6		–	10		–
	B	7	1	6		–	10		–
	R	9	1	8		–	10		–
	P10	8	2	6		–	9		–
	P11	7	0	7		–	9		–
	P12	7	0	7		–	9		–
	P 8	7	2	5		–	9		–
	DP1	9	3	6		–	9		–

APPENDIX 7a: Results of song leaning.

(I). Zebra finches.

Group.	Bird.	Song tutor choice.
A (Z♂Z♀)	B142	Z calls.
	B144	ZBS
	B146	ZBS
	B150	ZBS
	B153	ZBS
	B154	ZBS + BZS
	B157	ZBS
	B158	ZBS
B (Z♀)	B19	ZBS
	B20	ZBS
	B10	Z calls
	G10	ZBS
	Pk8	ZBS
	B18	ZBS
	P8	ZBS + BZS
	G1	ZBS
	P9	ZBS + BZS
	Pk9	ZBS
C (B♂B♀)	B61	BZS
	B63	ZBS + BZS
	B64	ZBS
	B65	ZBS
	B66	ZBS + BZS
	B67	ZBS
	B68	ZBS
	B70	ZBS
	B71	ZBS
	PB12	ZBS

(II). Bengalese finches.

Group.	Bird.	Song tutor choice.
D (B♂B♀)	B135	BZS + ZBS
	B137	BZS + ZBS
	B139	BZS + ZBS
	B140	BZS
	B142	BZS
	B148	BZS
	B149	BZS
	B155	BZS
	B156	BZS
E (B♀)	B12	BZS
	B21	BZS
	B23	BZS + ZBS
	B41	BZS + ZBS
	B42	BZS
	B43	BZS + ZBS
	WG	BZS
	H	BZS
	B55	BZS
	B58	BZS + ZBS
F (Z♂Z♀)	B56	BZS
	B57	ZBS
	G	BZS + ZBS
	WN	BZS
	B51	BZS
	B52	BZS
	B53	ZBS
	B19	BZS + ZBS

APPENDIX 8a: Song learning in zebra finches.

Group.	Bird.	Prop. song learnt from:		Tutor(s) chosen.
		Z	ZBS	
A (Z♂Z♀)	B35	0.86	0	Z
	B36	0.78	0.22	Hybrid
	B96	0.67	0	Z
	B110	0.625	0.25	Hybrid
	B111	0.875	0	Z
	B113	0	0.67	ZBS
	B103	0	0.40	ZBS
	B104	0	0.80	ZBS
	B105	0	0.58	ZBS
	W12	0.70	0	Z
	B14	0.78	0	Z
B (Z♀)	B10	0	0.5	ZBS
	B12	0.33	0.33	Hybrid
	B13	0	0.57	ZBS
	B15	0	0.375	ZBS
	P73	0	1	ZBS
	P74	0	1	ZBS
	P75	0	0.83	ZBS
	B3	0	0.5	ZBS
	B7	1	0	Z
	P71	0.80	0	Z
C (B♂B♀)	B31	0	0.9	ZBS
	B33	1	0	Z
	B34	0	0.83	ZBS
	B39	0	1	ZBS
	B43	0	0.57	ZBS
	B44	0.375	0.25	Hybrid
	B47	0	1	ZBS
	GBk	0	1	ZBS
	BPk	0.33	0.5	Hybrid

APPENDIX 9a: Results of song learning at six months.

Group	Bird	No. elements in phrase	No. improvised elements	No. elements learnt from			No. elements in tutor's song		
				T_1	T_2	T_3	T_1	T_2	T_3
A (Z-Z-Z)	R1	5	0	0	5	0	12	5	9
	B3	3	0	0	3	0	12	5	9
	Y5	5	0	0	5	0	12	5	9
	P76	6	1	0	5	0	8	10	7
	P77	6	0	0	6	0	8	10	9
	P78	6	1	0	5	0	8	10	9
	W2	8	1	0	7	0	8	9	11
	W4	6	2	0	4	0	8	9	11
B (B-B-B)	YB4	8	3	0	5	0	9	9	7
	YB5	5	2	0	3	0	9	9	7
	Y408	6	2	0	4	0	11	10	9
	P55	11	3	0	8	0	10	11	10
	P57	10	4	0	6	0	10	11	11
	P59	9	3	0	6	0	10	11	11
C (Z-B-Z)	P20	12	8	3	1	0	12	11	4
	P21	12	7	5	0	0	12	11	4
	P23	12	9	3	0	0	12	11	4
	B1	7	2	1	4	0	8	12	10
	B2	7	3	2	2	0	8	12	10
	P31	4	4	0	0	0	8	11	10
	P33	4	4	0	0	0	6	10	7
	P35	4	4	0	0	0	6	10	7
	DP2	10	4	3	3	0	8	10	8
	P2	7	4	0	3	0	8	10	8
D (B-Z-B)	P29	6	3	0	3	0	10	7	11
	YB8	5	0	3	2	0	9	7	7
	P40	9	2	0	7	0	10	8	9
	P41	12	6	0	6	0	10	8	9
	P43	7	2	0	5	0	11	9	11
	P45	9	4	0	5	0	11	9	11
	DP1	6	0	2	4	0	11	8	9
	DP2	7	3	0	4	0	11	8	9
	G6	9	3	0	6	0	10	9	12
	G7	9	4	0	5	0	10	9	12

APPENDIX 10a: Results of song learning and sexual preference.

(I). Zebra finches.

Group.	Bird.	Song learning.
A (Z♂B♀)	B27	F, Z+B
	B29	F, Z
	Y9B6	F, Z
	B52	Z+B
	B53	F, Z
	B54	Z
	B55	F
	B57	Z+B
	B59	Z
	B60	Z
B (B♂Z♀)	G9	F, Z
	B72	Z
	B75	Z
	DG2	Z
	DG3	Z
	B79	F, Z
	B80	F, Z+B
	B82	F, Z+B
C (Z♂Z♀)	R1	Z
	R3	Z
	R5	Z
	Y2	Z
	Y5	Z
	B1	Z
	B2	Z
	G4	Z
	G5	Z
	G8	Z
D (B♂B♀)	B116	Z+B
	B117	Z+B
	B119	Z+B
	B120	Z+B
	B131	Z+B
	B133	Z+B
	B135	Z calls
	B136	Z+B
	B137	Z+B
	B140	B

APPENDIX 10a: Results of song learning and sexual preference.

(II). Bengalese finches.

Group.	Bird.	Song learning.
E	B46	B
(Z♂B♀)	B48	B
	B50	B
	B58	F,B
	B59	F,B+Z
	B60	F,B+Z
	B61	F,B+Z
	B90	B
	B91	None
F	B92	B
(B♂Z♀)	B94	B
	B96	B
	B97	F,B
	B99	B
	B100	F,B
	GBst	F,B+Z
	PBst	F,B
G	W1	B
(B♂B♀)	W4	B
	W5	B
	P1	B
	P2	B
	P4	B
	P7	B
	P9	B
	P10	B
	G,Bst	B
H	B121	B
(Z♂Z♀)	B126	B
	B128	B+Z
	B130	B+Z
	B132	F, Z
	B133	F, Z
	B134	Z
	PBst	B+Z
	P11	B
	W13	B+Z

APPENDIX 11a: Results of song learning and sexual preference

(I). Zebra finches.

Group.	Bird.	Sexual pref. (z/z+b).	Song learning.
A (Z-Z-Z)	R1	1.00	Z
	B3	1.00	Z
	Y5	1.00	Z
	P76	1.00	Z
	P77	1.00	Z
	P78	1.00	Z
	W2	1.00	Z
	W4	1.00	Z
B (B-B-B)	YB4	0.00	B
	YB5	0.00	B
	Y408	.39	B
	P55	.15	B
	P57	.20	B
	P59	0.00	B
C (Z-B-Z)	P20	.83	Z+B
	P21	1.00	Z
	P23	1.00	Z
	B1	1.00	Z+B
	B2	.90	Z+B
	P31	1.00	Z calls
	P33	1.00	Z calls
	P35	1.00	Z calls
	DP2	.78	Z+B
	P2	.88	B
D (B-Z-B)	P29	.72	Z
	YB8	.82	Z+B
	P40	.85	Z
	P41	.71	Z
	P43	.86	Z
	P45	.69	Z
	DP1	.64	Z+B
	DP3	.87	Z
	G6	.75	Z
	G7	.72	Z

E (Z♂Z♀)	R1	1.00	Z
	R3	1.00	Z
	R5	1.00	Z
	Y2	1.00	Z
	Y5	1.00	Z
	B1	1.00	Z
	B2	1.00	Z
	G4	1.00	Z
	G5	1.00	Z
	G8	1.00	Z
F (B♂B♀)	B116	0.00	Z+B
	B117	0.00	Z+B
	B119	.12	Z+B
	B120	.20	Z+B
	B131	0.00	Z+B
	B133	.12	Z+B
	B135	.18	Z calls
	B136	.20	Z+B
	B137	.15	Z+B
	B140	.10	B
G (Z♂B♀)	B27	.82	F,Z+B
	B29	.68	F,Z
	Y9B6	1.00	F,Z
	B52	1.00	Z+B
	B53	1.00	F,Z
	B54	1.00	Z
	B55	1.00	F
	B57	1.00	Z+B
	B59	.83	Z
	B60	1.00	Z
H (B♂Z♀)	G9	1.00	F,Z
	B72	.78	Z
	B75	1.00	Z
	DG2	1.00	Z
	DG3	1.00	Z
	B79	1.00	F,Z
	B80	1.00	F,Z+B
	B82	1.00	F,Z+B

M	B142	1.00	Z calls
(Z♂Z♀)	B144	1.00	Z
	B146	1.00	Z
	B150	1.00	Z
	B153	1.00	Z
	B154	1.00	Z+B
	B157	1.00	Z
	B158	1.00	Z
N	B19	1.00	Z
(Z♀)	B20	1.00	Z
	B10	1.00	Z calls
	G10	1.00	Z
	Pk8	1.00	Z
	B18	1.00	Z
	P8	1.00	Z+B
	G1	1.00	Z
	P9	1.00	Z+B
	Pk9	1.00	Z
O	B61	.125	B
(B♂B♀)	B63	0.00	Z+B
	B64	0.00	Z
	B65	.39	Z
	B66	.27	Z+B
	B67	.20	Z
	B68	.18	Z
	B70	.15	Z
	B71	.10	Z
	PB12	.20	Z

APPENDIX 11a: Results of song learning and sexual preference.

(II). Bengalese finches.

Group.	Bird.	Sexual pref. (z/z+b).	Song learning.
I	B46	0.00	B
(Z♂B♀)	B48	0.00	B
	B50	0.00	B
	B58	0.00	F, B
	B59	0.00	F, B+Z
	B60	0.00	F, B+Z
	B61	0.00	F, B+Z
	B90	.23	B
	B91	.34	None
J	B92	0.00	B
(B♂Z♀)	B94	0.00	B
	B96	0.00	B
	B97	0.00	F, B
	B99	.30	B
	B100	0.00	F, B
	GBst	0.00	F, B+Z
	PBst	.37	F, B
K	W1	0.00	B
(B♂B♀)	W4	0.00	B
	W5	0.00	B
	P1	0.00	B
	P2	0.00	B
	P4	0.00	B
	P7	0.00	B
	P9	0.00	B
	P10	0.00	B
	G, Bst	0.00	B
L	B121	.78	B
(Z♂Z♀)	B126	.72	B
	B128	.50	B+Z
	B130	.60	B+Z
	B132	.70	F, Z
	B133	.58	F, Z
	B134	.67	Z
	PBst	.70	B+Z
	P11	.82	B
	W13	.60	B+Z

P (B♂B♀)	B135	0.00	B+Z
	B137	0.00	B+Z
	B139	0.00	B+Z
	B140	0.00	B
	B142	0.00	B
	B148	0.00	B
	B149	0.00	B
	B155	0.00	B
	B156	0.00	B
Q (B☿)	B12	0.00	B
	B21	0.00	B
	B23	0.00	B+Z
	B41	0.00	B+Z
	B42	0.00	B
	B43	0.00	B+Z
	WG	0.00	B
	H	0.00	B
	B55	0.00	B
	B58	0.00	B+Z
R (Z♂Z♀)	B56	.50	B
	B57	.58	Z
	G	.47	B+Z
	WN	.60	B
	B51	.62	B
	B52	.48	B
	B53	.70	Z
	B19	.76	B+Z