

The Influence of Early Experience Upon the Development of Social Behavior in Estrildine Finches

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INTRODUCTION

Besides the mother-infant-relationships discussed in a previous paper, experience during the first days or weeks of life has also proved to exert an important influence on adult behavior, mainly upon the determination of sexual preferences, but also on several other aspects of social behavior. The establishment of sexual attachments through early experience is generally referred to as sexual imprinting. Its characteristics have first been compiled by Lorenz (1935) although the phenomenon of early sexual fixation had been mentioned long before (cf. Gray 1963). Since 1935, numerous experimental investigations have been carried out about sexual imprinting. Most of them have been concerned with precocial birds (for review, see Moltz 1963, Hess 1964, Schutz 1965, 1968, Sluckin 1965, Bateson 1966, o.a.). For altricial birds, material is still very scanty and consists mainly of numerous occasional observations of hand-raised individuals which became imprinted on humans (for review, see Klinghammer 1967). The only experimental investigations with altricial birds are those by Nicolai (1956, 1959, 1964) with Bullfinches *Pyrrhula pyrrhula* and the parasitic widow birds *Viduinæ*, by Warriner, et al. (1963) with pigeons and by Klinghammer (l.c.) with Ring Doves *Streptopelia risoria* and Mourning Doves *Zenaidura macroura* (Klinghammer l.c.).

Due to the differences in sensory and motor development and due to the lack of any following response of altricial birds during their first days of life connected with the absence of any filial imprinting meaningfully analogous to that found in precocial birds, the context of sexual imprinting may be different in altricial and precocial species. It is to be expected, therefore, that the hitherto neglected study of altricial birds might contribute to the understanding of the various characters of imprinting and its possible differences with other learning processes.

METHODS

For our own investigations about sexual imprinting we have worked with estril-

dine finches (*Estrildidae*). These small, granivorous passerines are easy to be kept and bred even in small cages. They breed all the year round and reach sexual maturity with about 3–4 months of age so that up to 3 generations are available per year. Furthermore, several estrildine finches – especially the Bengalese or Society Finch *Lonchura striata f. domestica* from eastern Asia, and the Australian Zebra Finch *Taeniopygia guttata castanotis* – have been bred by aviculturists for many years and have produced several colour breeds which are now firmly established. Finally, the birds generally will rear youngsters of other estrildines if their eggs or newly hatched young are exchanged against those of another species. This applies mainly to the two domesticated forms, but has also been reported from several other species. Altogether, therefore, estrildine finches have proved to be ideal subjects for large-scale and long-term experimental studies on imprinting.

Most of our work is based on cross-fostering experiments with members of the two abovementioned domesticated estrildines: Eggs or hatchlings of one species or of one colour breed are placed for rearing into the nest with eggs or young of the other species or another colour breed of the same species. After having reached independence the youngsters are separated from their foster parents and – in order to prevent any further inter- or intraspecific experience during adolescence – are isolated on their own.

When sexually mature, the birds are tested in a free-choice situation between the imprinted object and an object of the own species, or breed. As objects, dummies as well as living birds of the opposite sex have been used. In the latter case, several precautions have been observed:

In order to avoid the possible influence

of any individual attachments, the own foster parents or foster siblings of the particular bird have never been used as objects; and to prevent that individual differences in the sexual responses of the presented objects may influence the results every bird was tested in 12 choice experiments of 30 minutes duration, using different objects each time. (A more detailed description of cross-fostering techniques and of the free-choice experiments is given in Immelmann 1969a).

RESULTS

A. Determination of Sexual Preferences in the Male.

For methodical reasons, most of our free-choice experiments have been carried out with male birds which do possess the more elaborate courtship behavior: When presented with a female or a female dummy, they usually will approach it at once with very characteristic pivoting movements in a rather stiff, upright position and with the head and ventral feathers fluffed in a species-specific pattern. During this courtship dance, the brief song phase is uttered continuously. At the end of most courtship sequences, copulation takes place.

Detailed descriptions of courtship behavior in the Zebra Finch are given by Morris (1954, 1958), Kunkel (1959) and Immelmann (1962) and in the Bengalese Finch by Morris (1958) and Eisner (1960).

During the choice experiments, the number of courtship sequences towards one of the other object as well as the number of copulations were recorded. We also measured the time spent in clumping and allopreening, because contact behavior and mutual preening are important parts of pair behavior in both species (cf. Immelmann 1962).

In a first basic series of experiments, 68 Zebra Finches, raised by Bengalese Finches and 17 Bengalese Finches, raised by Zebra Finches have been tested. In the free-choice situation, all males directed their sexual and social activities preferentially or exclusively towards the imprinted object, i.e. towards the female or female dummy of the foster parents' species. They courted those objects, copulated with them and indulged in mutual

¹Gefordert mit Hilfe von Forschungsmitteln des Landes Niedersachsen.

preening and clumping behavior. The conspecific females, on the other hand, were courted only occasionally and usually only at times when the other female was very inactive. At other times, they tended to be ignored or even attacked. Dummies of conspecific females received no measurable reactions at all.

These results were obtained despite the fact that during the free-choice experiments, the conspecific females usually showed strong sexual reactions and sometimes approached the male as soon as it was introduced into the test cage, while the females of the foster parents' species as a rule showed no such reactions but mostly tried to avoid the male's approach.

Similar results have been obtained from males which had been reared by another colour breed of their own species (8 Zebra Finches, 11 Bengalese Finches). They preferred females and dummies of the foster parents' colour as compared with the colour of their own breed (for further details and quantitative data about the experiments reported in this section, see Immelmann 1969a).

In order to study the ontogenetic development of sexual preferences, four males were treated in a slightly different way: They were reared by Bengalese Finches, but instead of being isolated afterwards, they were brought together with a Bengalese Finch female and a Zebra Finch female as soon as they had reached independence. They were kept together with both females, under close and continuous observation, up to an age of 90 days.

In these males, the first courtship displays which occurred between the 61st and 67th day of life were directed towards the Bengalese females, and so were all subsequent courtship patterns. Copulations (first observed between the 70th and 74th day of life) also occurred only with Bengalese female.² This means that the distinct sexual preferences to be found in adult birds are present from the very beginning of orientated courtship activities in the adolescent male.

To sum up, our results clearly indicate that in the two species of estrildine finches under investigation, experience in early juvenile life exerts a crucial influence on the subsequent choice of an object for sexual activities. The same free-choice experiments with 4 foster-raised males of a third species of estrildine finches, the African Silverbill *Euodice cantans*, which have been carried out for comparison, have likewise revealed a distinct sexual preference for the foster parents' species. Finally, it may be mentioned in this con-

nection that it is a common practice among aviculturists to rear the youngsters of various species of estrildines that are difficult to breed with Bengalese Finches as foster parents. In the avicultural literature, however, there is a large amount of observations about those birds constantly refusing to mate with members of their own species at least in the presence of any individuals of the foster parents' species. It may be assumed, therefore, that sexual imprinting through early ex-

periments.

Five males have been kept each in an aviary together with several (2-8) Zebra Finch females but only one Bengalese Finch female. All males paired with the latter, constructed a nest and participated in incubating the clutch(es) which – due to the fairly distant relationship of the two species – always proved to be infertile. The Zebra Finch females were ignored or – in the vicinity of the nest – attacked. There was no change in this

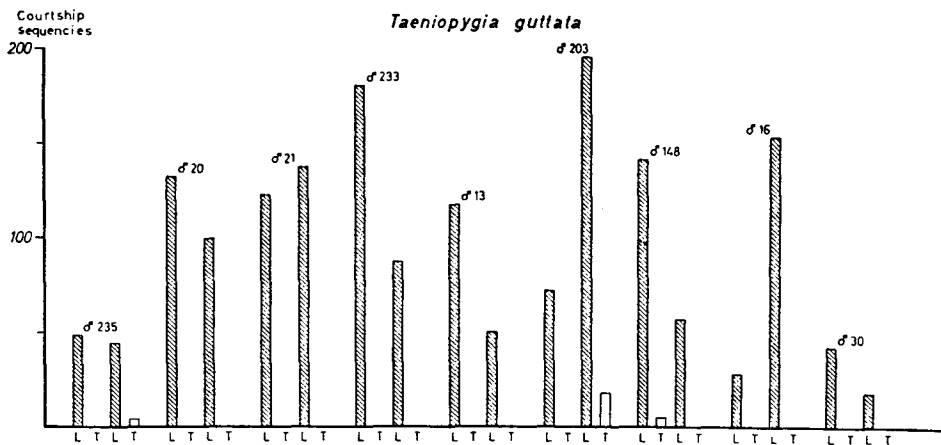


FIGURE 1. Sexual reactions of Zebra Finch males reared by Bengalese Finches before and after long-term intraspecific experience.

The block diagrams give the number of courtship sequences (courtship dances) towards the females of the foster parents' species (L) and the conspecific females (T). For each male, the first L-T-pair represents the results of 12 half-hour free-choice experiments before, the second L-T-pair those of the same number of experiments after intraspecific experience. If there is no block diagram above the symbol T the conspecific female did not receive any sexual reactions at all.

L = Bengalese Finch ♀ (*Lonchura*); T = Zebra Finch ♀ (*Taeniopygia*).

perience is a widespread phenomenon among estrildine finches.

B. Stability of Sexual Preferences.

(1) Stability in adult birds.

One of the most important characteristics of imprinting is its great stability, usually referred to as irreversibility. As a next step, it was tried to find out, therefore, if the sexual preferences established early in life can be changed or reversed through subsequent experience. For this purpose, long-term experiments have been carried out with Zebra Finch males which had been reared by Bengalese Finches and, in the basic series of experiments, had already proved to be sexually imprinted on their foster parents' species. These birds, under strictly controlled conditions, were brought together with Zebra Finch females. The use of conspecific females in this context was chosen deliberately because, as will be shown later, there is also a certain unlearned, preference for the own species. An alteration of sexual preferences, therefore, would be expected if at all to be achieved most easily through intraspecific experience. The main groups of experiments have been as follows:

Series a: Long-term free-choice experi-

behavior even if the experiment was continued for 16 months.

Series b: Long-term intraspecific experience.

In the previous series of experiments, a female of the foster parent species had always been present during the intraspecific experience of the male. The aim of the next group of tests was to find out if sexual preferences remain stable also without such presence. For this purpose, nine males have been kept each in an aviary together with a large number (15-50) of conspecific ♀ or ♂♂ and ♀♀. From the aviaries, no Bengalese Finches could be seen, or heard. After 3-34 months of intraspecific contact, the males were separated again and then tested in the usual series of 12 free-choice experiments with a conspecific female and a Bengalese Finch female. The results revealed as strong a sexual preference for the latter as was found before the long-term experiments. Even after intraspecific experience of almost 3 years without the possibility of any contact with the foster parents' species there was no change in the sexual preferences established during early juvenile life (see Fig. 1). *Contd on next page*

² A detailed description of ontogenetic development of sexual behavior in Zebra Finches is given in Immelmann (1962).

Series c: Long-term intraspecific breeding experience.

In the estrildine finches, in contrast to the majority of passerine birds, both sexes participate almost equally in all stages of parental care (nest-building, incubation, feeding of the young). As a consequence, pair-bond tends to be very strong, and a number of greeting ceremonies have been developed which serve to strengthen this bond (for description see Immelmann 1962).

It has been tested, therefore, if joint breeding activities with a conspecific female which necessarily must create a strong attachment and thus – together with the care for the young – will provide more intense intraspecific experience than the mere presence of conspecifics in an aviary, will be able to influence sexual preference.

14 males have been forced to pair with a conspecific female: They were kept in a breeding cage with one such female in a sound-proof chamber thus depriving them of any opportunity to see or hear members of their foster parents' species. Most of these birds eventually accepted the female as a substitute and the pair finally raised one or several brood(s). At all times, the males participated in the parental duties to the normal extent. Their behavior patterns and their reactions towards the young were not distinguishable from those of males raised by their own parents.

After 3-46 months of intraspecific experience, the males were separated and tested in the usual series of free-choice experiments. The results correspond with those of the previous series: Even after almost four years of intraspecific breeding experience and the joint raising of up to nine broods, the males still preferred females of the foster parents' species if again given the choice (see Fig. 2).

(2) Stability in adolescent birds.

Series d: in the series a-c, the males were sexually mature and – during the basic series of experiments – already had courted females of the foster parents' species. In order to find out if this first sexual experience in the birds' life has a stabilizing effect upon sexual preferences or if persistence is realized already before any such experience a new series of experiments was conducted. 14 Zebra Finch males were reared by Bengalese Finches in the usual manner but instead of being isolated when having reached independence, the birds were separated from their foster parents at different ages between independence and sexual maturity. After separation, they were kept in aviaries with other Zebra Finches as in series b for 7-122 days. Afterwards they were isolated

and finally tested in the usual free-choice experiments.

The results can be summarized as follows:

All males whose intraspecific contact had begun at or after their 40th day of life (7) showed the same sexual preference for Bengalese Finch females as did the males without any intraspecific experience (basic series). Males which had been together with other Zebra Finches before that age, on the other hand, showed no such rigid preference for the foster parents' species. They either restricted their sexual activities to conspecific ♀♀ (2), or they courted ♀♀ of both species with a certain preference for their own (1) or for the foster parents' species (4). Naturally, there is no proof that they also had been imprinted on Bengalese Finches before their intraspecific contact. But from comparison with the basic series of experiments, this seems to be beyond question. It follows, then, that in these birds the original preference must have been reversed or extenuated through intraspecific experience before their 40th day of life.³

bird: Up to an age of about 40 days, preference for the foster parents' species may be changed through intraspecific experience while after that date it has been proved to be impossible to alter sexual preferences in any way either by the mere presence or by joint breeding activities with conspecific females. (For further details about the stability tests, see Immelmann 1970).

C. Sensitive Periods for the Establishment of Sexual Preferences.

Next to its great stability, the existence of critical or sensitive periods, i.e. the fact that preferences can be determined only during specific stages in ontogeny, has always been regarded as the most important characteristic of imprinting.

The previous series of experiments has clearly shown that in sexual imprinting of Zebra Finches, such a period also exists and that it closes around the 40th day of life. From other experiments it appears that at the same age the first intentions of fear towards unknown members of the own species or – in foster-reared birds – of the foster parents' species as well as the

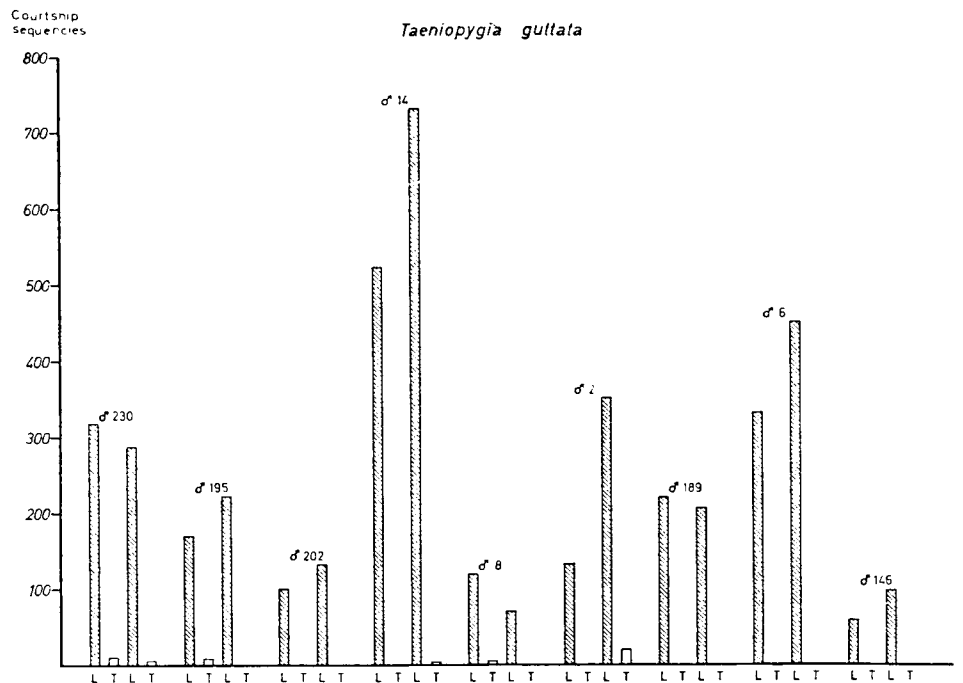


FIGURE 2. Sexual reactions of Zebra Finch males reared by Bengalese Finches before and after long-term intraspecific breeding experience. For explanations, see Figure 1.

To sum up, the stability tests lead to the conclusion that sexual preferences of male Zebra Finches which have been established very early in life, may be reversible or irreversible according to the age of the

³The duration of intraspecific contact, despite of great differences (7-122 days), does not seem to have a pronounced influence on the extent to which preferences have been altered before the 40th day of life. In order to find out how much experience is needed for such alterations new experiments are at present carried out with intraspecific exposure of less than 7 days.

first aggressive motivations occur and that this may have some causal relationship with the end of the sensitive period. This question is at present under investigation (in preparation).

For methodical reasons, the onset of the sensitive period for sexual imprinting is much more difficult to evaluate than its end. In another series of cross-fostering experiments, however, at least some approximate data have been obtained. In this series, the young Zebra Finches were

Woodrails stand up very straight with their head held high to make the noise. When one bird makes the call the other birds in the aviary will invariably come out of their seclusion and join in. It is not clear to me whether this call is aggressive, territorial or a mating call or maybe something else altogether. It seems unlikely that it is a mating call since I heard the call several times while observing the birds and it was not the breeding season.

The fact that the Woodrails are noisy and the bright nature of their coloring makes them an attractive bird for use in the aviary. Generally, the Woodrails adapt well to captivity. Their behavior is little different from that of their wild counterparts - what little is known of them! They settle down quickly, they are hardy and quite active, they breed readily under favorable conditions and are, on the whole, tolerant of the other birds around them. There is still a lot more to Woodrails that is not yet known but by observation of captive birds a lot can be learned about them ■

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reared successively both by their own parents and by Bengalese Finch foster-parents: The young were hatched by the parents and remained in the nest for a certain number of days, then they were transferred into a nest of Bengalese Finches which reared them to independence. Afterwards they were separated and subsequently tested in the usual way.⁴

From these males, the following results have been obtained: All males transferred to the Bengalese foster parents before their 15th day of life oriented their sexual behavior as exclusively to the Bengalese females as did the males reared by Bengalese Finches from the egg and tested in the basic series of experiments. All males, transferred after the 20th day, on the other hand, courted only Zebra Finch females. In the intermediate group, finally, a certain amount of individual variation was to be found with some males imprinted on Bengalese Finches, some imprinted on Zebra Finches and some courting females of both species (see Tables 1 and 2 to be printed in next issue).

⁴ The opposite experiment (young hatched and first reared by Bengalese Finches and then transferred to Zebra Finches for further rearing) has been successful only twice as yet, because the latter usually do not accept large nestlings or fledged young. Therefore, any conclusions about the results are not yet possible.

The results lead to the following conclusions: As the birds did not have any intraspecific contact between their transfer and the beginning of the free-choice experiments, all males which proved to be imprinted on their own species must have been so already at the day of transfer. It follows that sexual preferences may be determined as early as before the 15th to 20th day of life according to the individual. In other words, the sensitive period for sexual imprinting must start before the 15th-20th day of life, i.e. when the birds are still in the nest.⁵ Its exact onset naturally depends on the amount of intraspecific experience required for the establishment of sexual preferences and hence may be earlier than the dates mentioned above. No definite conclusions are possible as yet.

As for the end of the sensitive period, no conclusions can be drawn about the causes for its onset. The very early date of its beginning, however, probably points to a connection with perceptual capacities. Perhaps, the determination of subsequent sexual preferences simply starts as soon as the sensory organs and their neural correlates have reached a developmental stage that allows the nestling to acquire

⁵ In contrast to the majority of small passerine birds, estrildine finches stay in the nest for three weeks.

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