

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

CONTINUED FROM
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Theoretically, there are two possibilities how sexual imprinting on the own species could be guaranteed:

(1) an unlearned preference for the own species, i.e. a preference for some species-specific stimuli at the outset or

(2) the requirement for strong social attachment as a condition for the establishment of preferences.

In this connection, the following experiments have been carried out:

(a) Influence of neighbors.

To evaluate the influence of neighbors upon the determination of sexual preferences we repeated the basic series of experiments (section A) with only one slight alteration: The wire cages in which Zebra Finches were reared by Bengalese foster parents were not isolated completely (in sound-proof chambers) or visually (by cardboard blinds), but were set up on large tables where they were surrounded by other breeding cages with pairs of Zebra Finches. When leaving the nest, therefore, the young were able to see females and males of their own species in the neighbouring cages.

When tested in the usual free-choice experiments, these birds (34) proved to be as rigidly imprinted on Bengalese Finches as those reared in isolated breeding cages (section A). This means in the presence of their own species they must have developed a preference for another species. As they were fed only by the Bengalese foster parents, however, while their experience with the conspecifics was merely optical, it can be concluded that it is mainly the personal relationship between parents — or in this case, foster parents — and youngsters established through parental feeding that is responsible for the determination of preferences. The effect of this attachment is so strong that it prevails over possible unlearned preferences for the own species (see below).

(b) Influence of siblings.

In order to study the possible influence on the establishment of sexual preferences, the Zebra Finches tested in the basic series (section A) and in the previous series (section D, a) were raised by their Bengalese foster parents

- individually,
- together with conspecific siblings,
- together with Bengalese siblings,

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— together with siblings of a third species (African Silverbill).

In the free-choice experiments, no differences in the sexual preference for Bengalese Finches could be found between the

four groups. This means that the influence of siblings as compared with that of the parents is negligible (for details, see Immelmann 1969a).

This result seems to be remarkable in view of the fact that between siblings, there seems to be a certain amount of personal attachment, too. These relationships, however, are the same as those that occur between any flock mates (joint roosting, contact behavior, mutual preening). It appears, therefore, that for the

TABLE I

SEXUAL REACTIONS OF ZEBRA FINCH MALES RAISED SUCCESSIVELY BY ZEBRA FINCHES AND BENGALESE FINCHES

Animal	Transfer	Duration	Courtship sequences	
			L	T
♂ 189	6	46	220	—
♂ 238	7	45	63	—
♂ 234	8	35	160	3
♂ 265	10	31	70	—
♂ 202	10	35	101	—
♂ 269	11	25	148	4
♂ 225	11	35	46	—
♂ 203	11	42	72	—
♂ 209	11	47	237	17
♂ 228	12	35	186	17
♂ 121	13	29	555	130
♂ 251	14	31	114	15
♂ 230	14	35	318	—
♂ 233	14	54	180	—
♂ 190	14	84	226	63
♂ 122	15	43	9	125
♂ 123	15	43	118	207
♂ 262	15	55	81	1
♂ 140	16	35	158	100
♂ 146	16	55	46	44
♂ 157	17	19	20	617
♂ 248	17	45	193	83
♂ 249	17	45	—	93
♂ 268	18	20	—	37
♂ 279	18	25	—	73
♂ 216	18	35	1	168
♂ 215	19	25	12	274
♂ 218	19	36	—	129
♂ 232	19	45	80	111
♂ 106	20	16	49	1
♂ 108	22	16	—	30
♂ 266	22	45	—	133
♂ 143	24	16	3	154
♂ 144	24	16	13	162
♂ 264	25	45	—	34

TRANSFER: Age in days when transferred from Zebra Finch nest to Bengalese Finch nest.
DURATION: Number of days spent with Bengalese Finch foster parents before separation.
COURTSHIP SEQUENCES: Number of male courtship dances towards the females of the foster parents' species (L) and the conspecific females (T) during 12 half-hour free-choice experiments.
L AND T: as in Figure 1.

determination of sexual preferences an emotional attachment of exceptional strength is required, as it exists only between (foster) parents and young by means of parental care.

(c) Unlearned preferences.

Despite the great importance of personal attachments for sexual imprinting, there are several indications, however, that there is also a certain preference for the own species which is independent of intraspecific experience. These indications are:

(1) Reversal of sexual preferences mentioned to occur, under certain conditions, before the 40th day of life (section B, d), has been proved to be possible only from Bengalese to Zebra Finches i.e. from a strange to the own species. No such alteration has been possible in the opposite direction: birds raised by their own species always retained their sexual preference for conspecific females even if they had been given the opportunity for extensive contact with other species before their 40th day of life. This is shown most distinctly by experiments reported in section C: In Zebra Finches reared by their own parents a definite preference for the own species may be established as early as between the 15th and 20th day of life; it is retained even after subsequent parental care by another species which, in other individuals, has proved to be very effective for the determination of preferences (see above). It follows that a high degree of stability is reached earlier when the imprinted object belongs to the own species.

(2) In a next series of experiments, Zebra Finches were reared by mixed pairs of foster parents, i.e. a foster mother of their own species and a foster father of the other species, and vice versa. In the usual series of free-choice experiments, 13 out of 21 males directed their courtship activities exclusively or almost exclusively¹ to the conspecific objects, i.e. proved to be imprinted on the own species. Only one male (♂ 195) was imprinted on Bengalese Finches, while 7 males courted both species with a preference for the own species (♂ 50, ♂ 97, ♂ 111, ♂ 220), or for the other species (♂ 63, ♂ 191), or no preference at all (♂ 87) (Tables 3 and 4). Altogether, out of 21 males, 17 preferred their own species, 1 showed no preference, while only 3 males preferred the other species. These preferences were independent of the sex of the conspecific parent. This means, if there is a personal bond to two birds of which only one belongs to the own species, the latter is more effective for establishing sexual preferences.

TABLE 2

SEXUAL PREFERENCES OF MALE ZEBRA FINCHES RAISED SUCCESSIVELY BY ZEBRA FINCHES AND BENGALESE FINCHES

Transfer	L	bL	bT	T
6	1	—	—	—
7	1	—	—	—
8	1	—	—	—
10	2	—	—	—
11	4	—	—	—
12	1	—	—	—
13	—	1	—	—
14	3	1	—	—
15	1	—	1	1
16	—	2	—	—
17	—	1	—	2
18	—	—	—	2
19	—	—	1	2
20	1	—	—	—
22	—	—	—	2
24	—	—	—	2
25	—	—	—	1

TRANSFER: as in Table 1.

L: number of males courting exclusively or almost exclusively¹ Bengalese Finch ♀♀.

T: do., courting Zebra Finch ♀♀.

bL: number of males courting ♀♀ of both species, but preferring Bengalese Finch ♀♀.

bT: do., preferring Zebra Finch ♀♀.

Up to this time, no definite conclusions about the nature of unlearned preferences are possible. Preliminary observations seem to indicate that the birds react to some of the species-specific calls, i.e. certain frequencies or tonal qualities, without intraspecific experience. It seems to be possible, therefore, that these unlearned preferences, due to which conspecific parents or foster parents send more effective stimuli, will facilitate sexual imprinting on the own species. Similar observations have been made in other species of birds (Guiton 1962, Gottlieb 1965, Schutz 1965, Bateson 1966, Hess & Hess 1969).

Summing up the section about conditions for the establishment of sexual preferences, it can be concluded that in the Zebra Finch, a twofold security seems to guarantee that despite of being closely surrounded by other species the young birds are always imprinted on their own species; an unlearned preference for some species-specific characters (probably the calls) and the requirement for a very strong social attachment to the imprinting object. If, however, under experimental circumstances, both conditions (possession of species-specific characters, existence of strong attachment) are realized in different imprinting objects the personal bond has proved to be more effective. The great importance of intense social bonds for the determination of long-lasting preferences has likewise been stressed for other species of birds (Bullfinch, Nicolai 1959; Raven, Gwinner 1964; Mallard, Schutz 1965; Grey Lag Goose, Schutz 1970).

E. Determination of Sexual Preferences in the Female.

Courtship behavior of female estrildine finches is much less elaborate than that of the males. During the early phases of courtship display, the female stays still on the branch, engaged only in calling or in some rather undirected bowing and pivoting movements. These movements, however, may also occur spontaneously whenever a male and a female come together and have hence been called "greeting ceremonies" (Immelmann 1962). As a rule, they are accompanied by frequent beak-wiping and a rapid opening and closing of the beak (mandibulation) which may have evolved from the carrying of nesting material (Morris 1958). Only towards the end of the male's courtship dance, a responsive female will show a definite reaction: it assumes a forward position and quivers the tail in a vertical plane (solicitation), thus giving the signal for the male to copulate (cf. Morris 1954, Eisner 1960).

It seems to be clear, therefore, that quantitative data about sexual preferences in the female are difficult to obtain. For this reason only very preliminary results are available as yet. They are based on 5 Zebra Finch ♀♀ raised by Bengalese Finches and 3 Bengalese ♀♀ raised by Zebra Finches. These birds were separated from their foster parents between their 42nd and 66th day of life and after having

¹The term "almost exclusively" is used if in the series of 12 free-choice experiments, one of the objects is courted only very occasionally (up to about 10 times) as this, as indicated by numerous observations, might be accidental.

reached sexual maturity, were tested in the usual free-choice experiments with a male of their own species and a male of the foster parents' species.¹ During the experiments, the number of invitation displays (solicitation), greeting ceremonies, and mandibulations were taken. We also measured, through automatic registration, the time spent with either of the males which during preliminary observations had proved to be a good indication of the respective preferences. Each female was tested, in a special testing cage, in 5 free-choice experiments of 2 hours' duration with different males each time. The testing cage was divided, through wire netting, into three parts. During the experiments, the female was placed in the central part and of the males in the lateral parts of the cage (for detailed description of the test situation, see Immelmann 1969a).

The first reactions of the females were comparable to those of foster-reared males: When introduced into the test cage the females at once approached the male of the foster parents' species with frequent spontaneous greeting ceremonies and usually stayed in its vicinity. As soon as the conspecific male started to call or court, however, the female turned to the latter. From now on, it reacted to both males alternately always preferring the male which at that time was courting² the female or at least showed greater overall activity. During the further course of the free-choice experiments, most females eventually developed a preference for one of the males and more and more stayed with that particular male even if the other male was courting.

These differences between the beginning and the further course of the experiments become apparent when Tables 5 and 6 are compared with Figures 3 and 4: During the first minutes of each experiment the sexual behavior patterns are oriented preferentially towards the imprinted object. The spontaneous greeting displays are even restricted almost exclusively to the latter. If the full duration of the experiments is considered, on the other hand, the total amount of time spent with either of the males indicates that only 5 out of 8 females, showed an overall preference for the foster parents' species. One female (♀ 33) showed no clear preference at all, while 2 females (♀ 220, ♀ 229) preferred the conspecific

¹The same precautions as in the experiments with male birds have been observed

²For the experiments, only those males of the foster parents' species have been used which in turn had been raised by the female's species, and, on the average, courted the female as frequently as did the conspecific males.

males. In the later case, the preference was developed despite the fact that prior to the free-choice experiments, the females never in their life had seen a conspecific male before.

It can be concluded, therefore, that in female Zebra Finches, as in the males, two separate mechanisms for mate selection occur: an unlearned preference for the own species and an imprinted preference established early in juvenile life. In contrast to the males, however, the unlearned preference seems to be fairly strong and in some cases, has proved to prevail over sexual imprinting and to lead to a final selection of the conspecific male. The biological significance of these sexual differences will be discussed below.

Due to the methodical difficulties mentioned above, no data about the stability of preferences and the occurrence of a sensitive period for sexual imprinting are available for female birds as yet.

An obvious case of sexual imprinting

in female estrildine finches has been mentioned by Goodwin (1971): Two female Blue-headed Waxbills *Uraeginthus cyanocephalus* reared by Red-checked Waxbills *U. bengalus*, but kept from the moment they fledged in a room with adults of both species, showed sexual reactions only to males of *bengalus* and this is in spite of indifference or hostility from these males and their frequently being courted by males of their own species.

DISCUSSION

The characteristics of sexual imprinting:

In his original paper (l.c.), Lorenz claimed that imprinting can be distinguished from other learning processes by four characters (of which the first and second follow logically from each other): (1) It is confined to a sensitive period. (2) It is irreversible. (3) It involves learning of supra-individual characters. (4) It may be completed at a time when the appropriate

TABLE 3

SEXUAL REACTIONS OF ZEBRA FINCH MALES RAISED BY ZEBRA FINCH ♂ AND BENGALIAN FINCH ♀

Animal	Date of isolation	Courtship sequences	
		T	L
♂ 51	32	133	5
♂ 101	32	204	1
♂ 49	38	179	—
♂ 87	52	287	304
♂ 100	57	120	—
♂ 29	58	53	—
♂ 92	59	65	—
♂ 50	67	115	34
♂ 97	69	138	53
♂ 111	71	124	38
♂ 112	71	36	—
♂ 57	84	102	—
♂ 63	127	66	110
♂ 220	130	124	47

DATE OF ISOLATION: Age in days when separated from foster parents.

COURTSHIP SEQUENCES: as in Table 1.

TABLE 4

SEXUAL REACTIONS OF ZEBRA FINCH MALES RAISED BY BENGALIAN FINCH ♂ AND ZEBRA FINCH ♀

Animal	Date of isolation	Courtship sequences	
		T	L
♂ 156	38	211	—
♂ 191	38	56	133
♂ 187	43	84	—
♂ 195	47	8	173
♂ 267	47	154	—
♂ 158	48	131	—
♂ 170	57	71	—

Legend as in Table 3.

TABLE 5

SEXUAL REACTIONS OF FEMALE ZEBRA FINCHES RAISED BY BENGALESE FINCHES

Animal	Date of isolation	GS		GR		Solicitation		Mandibulation	
		L	T	L	T	L	T	L	T
♀ 214	63	21	1	2	1	—	—	—	—
♀ 215	63	16	—	3	6	1	—	11	6
♀ 220	66	12	1	8	17	21	9	16	—
♀ 221	53	22	6	5	6	—	—	—	—
♀ 229	52	2	—	12	4	1	—	—	—

DATE OF ISOLATION: as in Table 3.

GS: Spontaneous greeting ceremony.

GR: Greeting ceremony as a response to male courtship.

T: Zebra Finch.

L: Bengalese Finch.

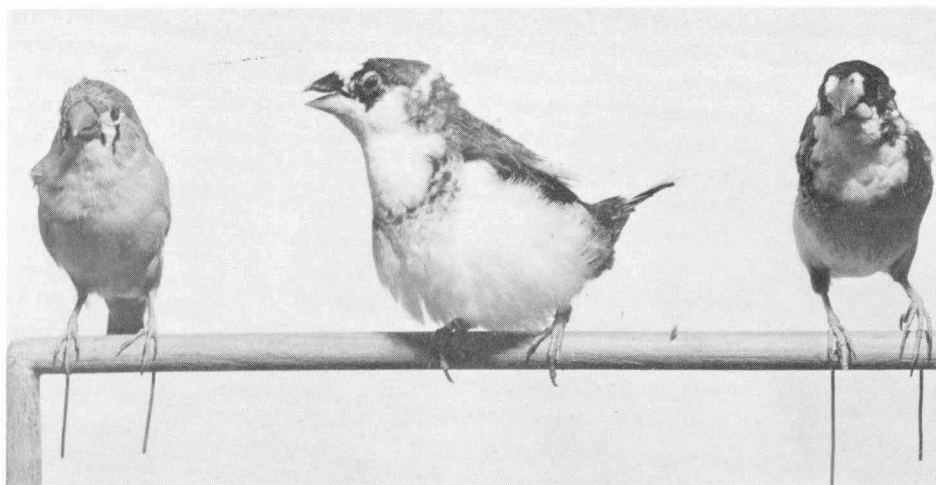
In Tables 5 and 6 the total sum is given of all sexual reactions which have been observed during the first 10 minutes of each of the five free-choice experiments.

TABLE 6

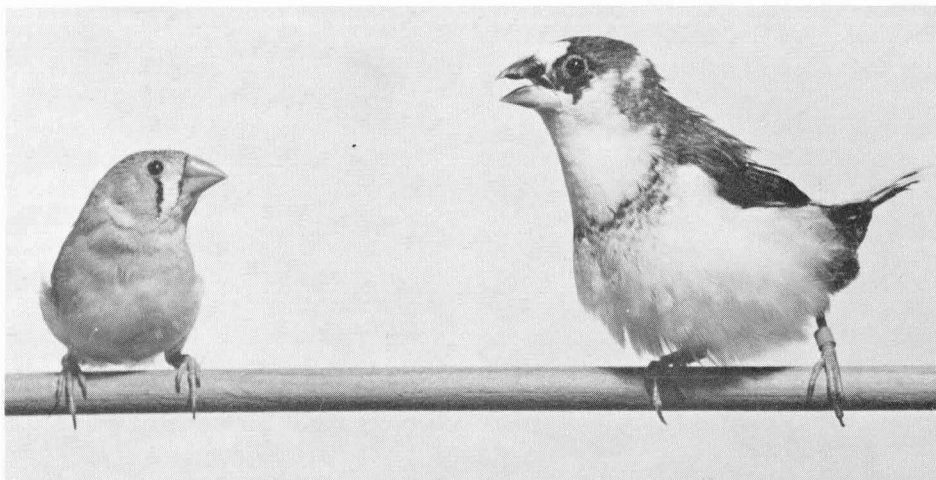
SEXUAL REACTIONS OF FEMALE BENGALESE FINCHES RAISED BY ZEBRA FINCHES

Animal	Date of isolation	T		Solicitation		Mandibulation		L	
		T	L	L	T	L	T		
♀ 1	41	13	—	6	7	—	—	1	—
♀ 31	60	20	2	2	3	13	—	11	1
♀ 33	55	9	1	1	2	—	—	2	—

Legend as in Table 5.



Bengalese Finch male courting Zebra Finch female dummy in a double choice test.



Bengalese Finch male courting Zebra Finch female.

reaction itself is not yet performed. These claims have repeatedly been criticized as it has been found that not all criteria apply to all groups of birds in which sexual imprinting occurs (cf. Fabricius 1962, Hinde 1962, Bateson 1966).

In the present case, however, the four characters are fully realized:

(1) In the two species of estrildine finches sexual imprinting is confined to a definite sensitive period which in the Zebra Finch lasts from briefly before the 15th to about the 40th day of life. Social experience outside this period has proved to be without any influence for the determination of sexual preferences. The sensitive period, however, is not a uniform one, but may consist of different phases (see below).

(2) After the end of the sensitive period, imprinting is absolutely irreversible and the imprinted preference has proved to be maintained for years even in the face of very intense and long-lasting experience with other objects. To the best of my knowledge, this seems to be the first case where, under very strictly controlled conditions, definite irreversibility has been proved for a period of time which markedly exceeds the life expectancy of the birds under natural conditions (cf. Immelmann 1970).

The onset of irreversibility, however, and hence the duration of the sensitive period, has been found not to be strictly species-specific but to vary considerably according to the previous experience of the individual bird: If it was raised by its own species irreversibility has been found as early as between the 15th and 20th day of life. This means, the original determination of preferences must take place early and—as the eyes of the nestling are not fully open before the 10th day of life—very quickly. In accordance with the period of maximum imprintability in the following response of ducklings (for discussion see Fabricius 1964) this first and short part of the sensitive period may perhaps be called “critical period”.

If, on the other hand, the bird is raised by another species, sexual preferences can still be altered through subsequent intra-specific experience after the 15th to 20th day. It can be concluded that, under these conditions, a second, longer sub-period of the sensitive period occurs in which sexual preferences have been established already but are still reversible and may be redirected onto the own species. This period closes at an age of 40 days when absolute irreversibility is reached even in cross-fostered birds. A similar subdivision of the sensitive period has been described in Jackdaws by Lorenz (1935).

For the definite end of reversibility

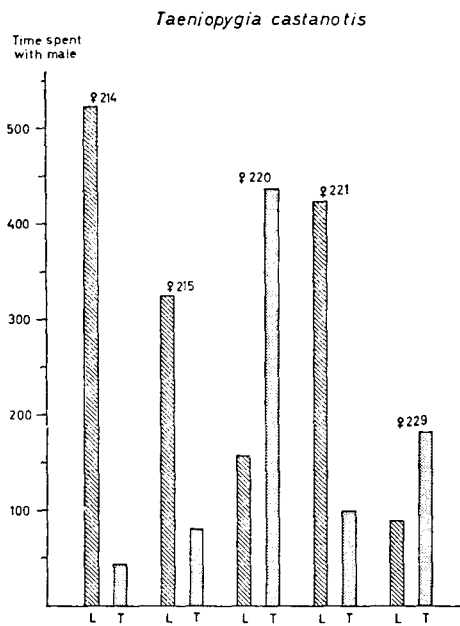


FIGURE 3. Preferences of Zebra Finch females reared by Bengalese Finches.

The block diagrams give the total amount of time (in minutes) spent on the perch close to the male of the foster parents' species (L) and close to the conspecific male (T) during 5 two hours' free-choice experiments. (The rest of the time was spent on other perches or on the ground.)

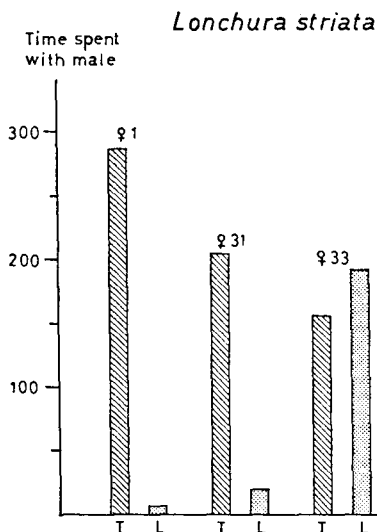


FIGURE 4. Preferences of Bengalese Finch females reared by Zebra Finches. For explanations, see Figure 3.

after which alterations of preferences are no longer possible I propose the term "critical point" which has been introduced by Klinghammer (1967) in a similar context. Altogether, the sensitive period has been found to last for a considerably longer time than needed for the primary establishment of preferences. The reasons for the different onset of irreversibility are due to different degrees of accordance between imprinted and unlearned preferences and have been discussed in section D.

(3) The third character mentioned by Lorenz, the selection of supra-individual, species-specific cues from the picture of

the parents can be followed, in the present case, from the free-choice experiments: In spite of considerable individual variation in the pigmentation of Bengalese Finches, which is a consequence of domestication, the foster-reared Zebra-Finches preferred all females of the foster parents' species to all conspecific females.

This does not exclude, however, that an adult male after pair-formation may develop a definite individual preference for its own female, as it has been observed under experimental conditions as well as in Zebra Finch colonies in the wild (Immelmann 1962). But in this case, as Hess (1959) has assumed, the knowledge gain-

ed through early imprinting is completed subsequently, according to the requirements of the individual, by "normal conditioning". In contrast to the more generalized preferences established early in life, however, such preference for a particular female has proved to disappear very quickly after the birds have been separated again (in preparation).

(4) The occurrence of imprinting at a time when the appropriate reaction itself is not performed becomes apparent from the comparison of sensitive period and sexual development: The choice of the sexual partner is determined before the 20th day of life and can be reversed, at the maximum, until around the 40th day whereas the first complete courtship patterns do not occur before the 60th day and full sexual maturity (occurrence of copulatory behavior, appearance of free spermatozoa in the testis tubules) is attained at an age of 70-90 days (for details, see Immelmann 1970).

In other words, between the establishment of sexual preferences and their first application there is a space of at least 20-40 days.

This statement, of course, is relevant only to the biological significance of imprinting (see below). It does not permit any conclusions about the frequently discussed question whether there are any correlations between sexual imprinting and sexual development. Some preliminary observations point to the existence of such correlations, which have also been suggested in other groups of birds (cf. Guiton 1962). This problem is at present under investigation through artificial hormone treatment (in preparation).

The fact that in some groups of birds, like estrildine finches, all criteria of imprinting originally mentioned by Lorenz have proved to apply, whereas in other groups, they do not seem to occur to the full extent, certainly needs discussion. In part, these differences may be due to methodical reasons and hence may not be quite as large as has been concluded from the results. This applies mainly to research of irreversibility as some of the investigations which claim to have disproved its existence suffer from serious methodical omissions (e.g. lack of free-choice experiments) and thus do not allow any relevant conclusions.

Despite these reservations, however, the real existence of certain differences in the characteristics of imprinting is beyond question. This points to the fact that sexual imprinting in birds is not a uniform process but may vary in nature between species, or groups of species. This has already been emphasized by Lorenz and has been discussed by Klinghammer (1967).

The differences apply to virtually all characteristics of imprinting: The sensitive period, for example, has been found to vary considerably with regard to its onset and duration (see Klinghammer 1967, for review, and Schutz 1970, for new data on geese and ducks). Irreversibility has been proved, for considerable amounts of time, for a number of species (Budgerigars, 2 years, Lorenz 1954; Turkeys, 5 years, Schein 1963; Mallards, 9 years, Schutz 1969; Grey Lag Geese, 6 years, Schutz 1970), while in other species, sexual preferences seem to be less stable as despite of being foster-reared many birds have been found to finally select a mate of their own species (Ravens: Gwinner 1964; Ring Doves: Klinghammer 1967; see also Bateson 1966, for further discussion). In the first group of species, the onset of irreversibility again may be different. In the Zebra Finch, it occurs as early as at the 15th day of life, while in the Bullfinch, the birds are susceptible to lasting influences for more than one year, including the first breeding season (Nicolai 1956).

The object for sexual imprinting may likewise be different. In domestic pigeons (Warriner *et al.* 1963) and estrildine finches, both parents have proved to be of equal importance.¹ In Mallards, on the other hand, sexual preferences are established, except for the siblings, only through the mother (Schutz 1965). Presence or absence of siblings has no effect on sexual imprinting in domestic pigeons (Warriner l.c.) and estrildine finches, whereas in Mallards (Schutz 1965) and mourning doves, such influence exists, and in Bullfinches, subsequent preferences may even be determined mainly through the presence of siblings (Nicolai 1956).

The reasons for the stated differences in nature of sexual imprinting may be divided into two entirely different groups:

(1) Due to species-specific differences in breeding biology the conditions for establishing long-lasting preferences certainly are not identical in all groups of birds. This applies to differences in participation of the sexes in parental duties, in the intensity of attachment between siblings or in the duration of parental care.

(2) Due to species-specific differences in pair-formation and nature of pair-bond, on the other hand, the biological demands on imprinting are also different.

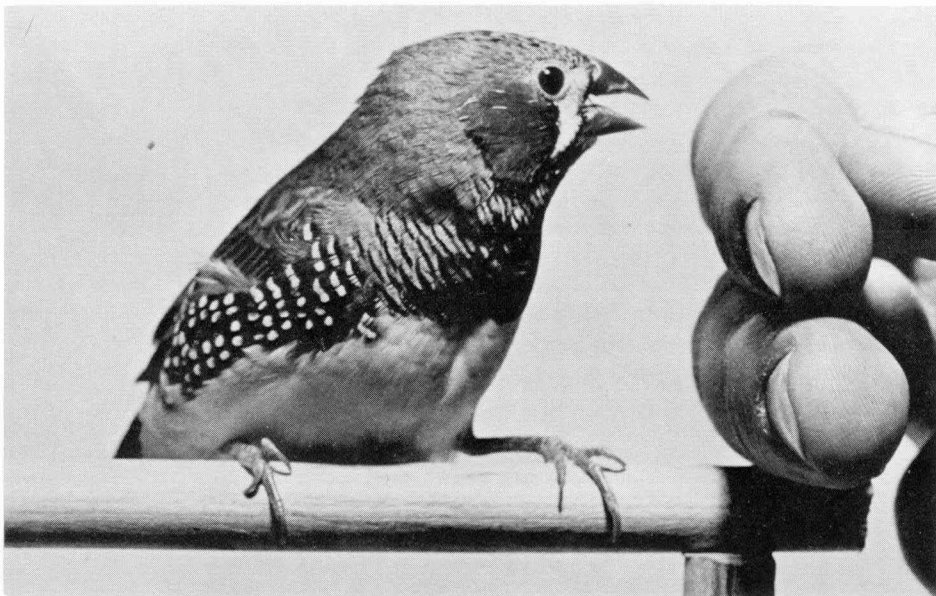
The first group of reasons may have an influence, for example, on the length of the sensitive period which has been found to be closely correlated with the duration

¹Preliminary observations suggest that in the Zebra Finch, the mother might be slightly more important for imprinting than the father but the data do not permit any definite conclusions as yet.

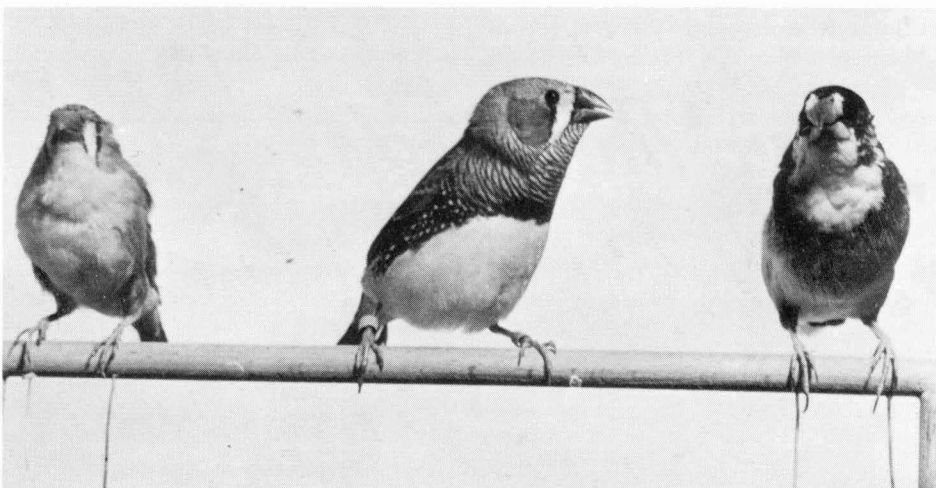
of parental care (Schutz 1970). It may also influence the relative importance of father and mother which follows logically from their participation in parental care, as well as the importance of siblings which becomes clear from the results in Bullfinches: In this species, there is a very close attachment between siblings which after weaning become "engaged" to each other. As a consequence, siblings have

been found to be of greater importance for the subsequent choice of mate than in any other species of birds (Nicolai 1956).

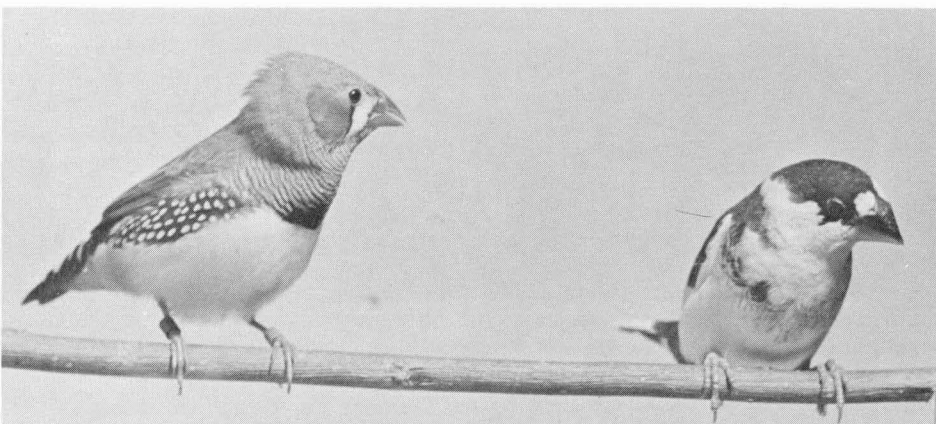
The second group of reasons may exert an influence, for example, on the stability of preferences: For the Zebra Finch, early and rigid irreversibility is highly adaptive with regard to the breeding of several closely related species in mixed colonies and to very early and prompt pair-formation.




Hand raised Zebra Finch male courting human hand.



Zebra Finch male courting Bengalese Finch dummy in a double choice test.



Zebra Finch male courting Bengalese Finch female.



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tion (which in turn is an adaptation to the irregular breeding season, Immelmann 1962). In a species of bird, on the other hand, where pair-formation is a long-lasting process, offering many opportunities for comparison with unlearned preferences, absolute irreversibility may perhaps not be necessary.

It is suggested, therefore, that in future investigations on imprinting, the biology of the relevant species should be taken into close consideration. Furthermore, any generalizations from the results in only one group of birds should be treated with great care because many misunderstandings as to the general context of imprinting, which have occurred in the literature, clearly enough originated from inadmissible generalizations.

Biological Significance of Imprinting:

The most important function of sexual imprinting is to enable the birds to recognize members of their own species and thus to ensure that, under natural conditions, sexual behavior and pair-formation displays are restricted to conspecific mates (Lorenz 1935). For this purpose, imprinting offers the combination of two distinct advantages which otherwise are distributed to different mechanisms of recognition: Due to its early sensitive period and subsequent stability, it ensures the availability of relevant information well before its first application and thus corresponds with any unlearned preferences. On the other hand, it leads to a very precise recognition of the subsequent partner and is quickly adaptable to any change in the species-specific characteristics and in this respect, corresponds with other learning processes.

It can be concluded that imprinting may be of special advantage in any rapidly evolving group as well as wherever several closely related and similar species occur in the same region. Interestingly enough, both statements seem to apply to all groups of birds in which imprinting has been found to be a wide-spread phenomenon (ducks, gallinaceous birds, pigeons and doves, estrildine finches; for detailed discussion see Immelmann 1969b, 1970).

The second suggestion is, among other things, indicated by the sexual differences which have been found in imprintability:

In most species of estrildine finches, the male possesses the more elaborate sexual behavior with a courtship dance and a song phrase, and in several species, as in the Zebra Finch, it carries some additional bright plumage markings. As a consequence, the male offers more distinct signals for species recognition. The female, therefore, may rely to a certain extent on its unlearned preferences, whereas due to the few and less conspicuous distinguishing characters of the females,

For The Birds

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the male needs a much more precise knowledge of the opposite sex. As a consequence, its unlearned preferences are completed, to a greater extent, through early experience. The same situation is found in ducks where sexual differences in the extent to which mating is influenced by early experience are even greater (Schutz 1964). In contrast to ducks, however (if the small number of females tested so far permits any conclusions), no obvious differences in female imprintability have been found between the sexually monomorphic Bengalese Finch and the dimorphic Zebra Finch. This seems to be due to the fact that even in monomorphic estrildines, the remaining characters of the male (behavior, song) are still more distinct than those of the female. The same applies to monomorphic pigeons where according to Warriner *et al.* (1963), mate-selection in the female is apparently unaffected by early experience.

Phylogenetic Applications:

Due to its very precise determination of subsequent mating preferences, imprinting may certainly contribute to maintaining sexual isolation in the case of sympatric species of birds. Under certain circumstances, it may also lead to a reduction of intra-specific gene-flow. If, for example, a mutation in some of the species-specific characteristics occurs within a population, the offspring of parents carrying this particular mutation will become imprinted on the new signs and will subsequently tend to pair preferentially with individuals that likewise possess these characters. As a consequence, a certain isolation between the new form and the rest of the population may be developed eventually. In this context, sexual imprinting may also be an important factor in the speciation of birds. This question has been discussed elsewhere (Immelmann 1969b, 1970).

SUMMARY

In Zebra Finches and Bengalese Finches early experience has been found to exert influence on the establishment of sexual preferences. When tested in free-choice experiments, all males reared by foster parents of the other species orientated their sexual behavior preferentially or exclusively towards females of the foster parents' species. The same preference was found if individuals of different colour breeds of their species were reared by another colour of their own species.

The sensitive period for the determination of preferences lasts from briefly before the 15th to about the 40th day of life. After its end, absolute irreversibility is reached and it has been proved not to be possible any more, to alter the sexual preferences of the birds in any way,

neither by the mere presence, nor by (forced) joint breeding activities with conspecific females.

For the establishment of preferences early in life, a strong social attachment to the imprinting object is essential. For this reason, only the (foster) parents but not the siblings have an effect on subsequent choice of mate.—Besides for the great importance of early experience, unlearned preferences for some of the species-specific characters, probably the calls, have also been found which facilitate imprinting on the own species. As the females have proved to be slightly less imprintable than males, there seem to be sexual differences in the extent of unlearned preferences.

As indicated by our results, all criteria mentioned by Lorenz for characterization of sexual imprinting, are realized in the two species of estrildine finches. The possible reasons for contradictory results in other groups of birds are discussed.

The biological function of sexual imprinting is to enable the birds to recognize members of their own species and thus to restrict sexual behavior to conspecific mates. In this context, it may contribute to maintaining sexual isolation between species. Through reduction of gene-flow within any one species, imprinted preferences may also be important factors in the speciation of birds.

(References for this article will be furnished upon request.)



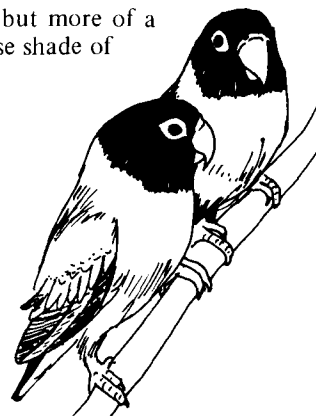
FINALLY, after months of delay this column called "Agapornis Acres" will talk about my favorite bird, the Agapornis (the African Love Bird).

The Agapornis is certainly a popular family of birds, with eight species in this genus. It offers the aviculturists perhaps one of the widest ranges of conditions and variety including price as well as care. Some of the Love Birds are very expensive, others are moderately priced, some are very easily bred such as the Peach Face, masked and Fischer's, others are very difficult or even near to impossible such as the red faced. This diversity, therefore, offers both the experienced aviculturist, as well as the amateur a challenge.

The birds are small in size, six to seven inches, this length includes a very short tail which makes the love bird look like a miniature parrot. Most of the Agapornis are easily cared for. Here in Southern California the genus has always been seen

in Aviculturists aviaries since the 1930's. Mr. Harold Rudkin Sr. of Fillmore, California had large colonies of Black Masked in the 1940's and the 1950's. The blue mutation of this bird first appeared in his aviaries. At that time he also had very large colonies of Fischer's.

The PeachFace love bird has perhaps gone through the greatest change. As a normal green it has been established for years, however, it's mutations have had the greatest impact. The pied form appeared somewhere between 1945 and 1950 in a California breeders pen (if I recall his name was Hebert). Upon his death the collection was sold and part of it went to Mrs. T.M. Towne of Sunland, California and through her efforts the mutation was established. Recently the striking Lutino mutation occurred in a San Diego aviary. Mr. David West of Montebello, California has been striving to establish this mutation for the past few years. The blue mutation of Peach Face, which occurred in Germany, has been established here through the combined efforts of Mr. Bob Barry of Texas, Mr. David West, and myself. They are now quite plentiful, and many aviculturists enjoy them in their aviaries. Mr. David West also made the first cross between the Blue and the Pied. I was the fortunate one who obtained a pair of their young from which I raised the first Blue Pied Peach Face, a truly most beautiful bird. Another cross has been made recently by my friend David West between the Blue and the Lutino. Hopefully the first Albino young will be raised from this cross. Although the "ino" form of the Blue peach face will not be pure white but probably a pale lemon color due to the fact that the Blue Peach Face is not pure Blue like the Blue form of Black Masked but more of a turquoise shade of blue.



Many other mutations have occurred, the lutino form of Fischer and Nyassaland, the pied form of Blue Masked and Fischer's and many others. However, these are still not established. I, for example, have been working for six years with the yellow form of Black Masked (a dilute) and I still have not been able to establish it.

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