

SEX RECOGNITION IN ZEBRA FINCH MALES RESULTS FROM EARLY EXPERIENCE

by

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(With 5 Figures)

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Summary

This study investigated whether sexual imprinting plays a role in the recognition of the sex of conspecifics. Subjects were zebra finch males that had been raised with either normal pairs, white pairs or pairs of both morphs. They were tested for their preferences in six two-stimuli tests covering all combinations of both morphs of either sex. Males of all groups showed a clear preference for females of their mother's morph over males of their father's morph. Moreover, a majority of the males from mixed parentage preferred a male of their mother's morph over a female of their father's morph, indicating that morphological characteristics are more important than behavioural differences for discrimination between the sexes. This was confirmed in a subsequent series of tests in which males raised by parents of the white morph, which are sexually dimorphic only in respect to the intensity of the red colour of the bill, were given a choice between a white male with his bill painted orange and a white female with her bill painted red. All males of this group preferred to court the male in this test. In addition to differential responses in a sexual context, males showed discrimination in an aggressive context; that is, most aggression was directed towards stimulus birds resembling the father. The implications of these results for the evolution of sexual dimorphism and sexual selection are considered.

Introduction

The ability to recognize the sex of conspecifics is likely to affect the reproductive success of individuals in many animal species. In birds, mate preferences often originate from early experience with social companions. This process of 'sexual imprinting' generally results in a sexual preference

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for the rearing species. Such learned preferences can be very precise. For instance, Japanese quail can, on the basis of early experience, distinguish between conspecifics which differ in degree of relatedness (BATESON, 1982). Less is known about the influence of early experience on the ability to distinguish male from female conspecifics. NASH *et al.* (1989) found that adult Japanese quail males can discriminate males from females only after extensive copulatory experience with females and repeated exposure to males (see also: DOMJAN & RAVERT, 1991). They concluded that for Japanese quail not all information necessary for successful reproduction is acquired during early life. Observations on red-winged blackbirds by NOBLE & VOGT (1935) and on red junglefowl by KRUIJT (1964) suggest that also in these species sexual discrimination between the sexes is acquired later in life.

In contrast to these findings, IMMELMANN (1985) reported that adult male zebra finches that were raised by a mixed pair, consisting of a wild-type male and a white female or *vice versa*, had a clear preference for females with the plumage of their mother. Vos *et al.* (1993) confirmed this finding and demonstrated that the differential responding to females with a different plumage, was a result of attraction to females with their mother's plumage, and avoidance of females resembling their father's plumage.

As the zebra finch is a sexually dimorphic species, the latter studies suggest that early social experience enables zebra finch males to discriminate between the sexes on the basis of plumage characteristics. However, as all stimulus birds were females, these experiments did not demonstrate whether the morphological difference is the main factor on which males will base sexual discrimination. It is possible that when a zebra finch male is faced with a male and a female conspecific, behavioural cues provide enough information to overrule any morphological preference.

The present study examines whether morphological characteristics are also important in a choice situation with male and female stimulus birds. Moreover, the study investigates whether males raised by wild-type (normal) or white pairs, in which the dimorphism between the parents is considerably less than in mixed pairs, are able to discriminate between the sexes. Therefore, males raised by pairs consisting of one or two colour morphs received a series of choice tests between all combinations of stimulus birds of both sexes and colour morphs. This procedure made it

possible to tease apart the effects of morphological and non-morphological (e.g. behavioural) features on sexual discrimination in zebra finch males.

Method

Experimental groups and rearing conditions.

The subjects were 57 phenotypically wild-type (normal) zebra finch males (*Taeniopygia guttata*), divided into four groups that were raised under different conditions (Table 1). Except for two males of group N♀ N♂, which had no previous test experience, all males had been used in a previous experiment (Vos *et al.*, 1993). All subjects were raised by their own parents (normal is genetically dominant over white), except for those in group W♀ W♂. These normal males were cross-fostered to a white pair within 3 days after hatching. In order to reduce the possible influence of the (normal) siblings on the later preference, each male was individually transferred to another couple of the same composition at the age of 30 days. The males were visually isolated at about 65 days after hatching. Testing started at 120 days, when they were sexually mature. For details on the first series of tests see Vos *et al.* (1993).

Stimulus tests.

For testing, a male was put in a cage measuring 55 × 30 × 40 cm, on each side of which a smaller side cage (25 × 30 × 40 cm) was placed, separated by wire mesh. During a test each side cage contained a stimulus bird. The duration of a test was 20 minutes and the side cages were exchanged halfway through the test. Stimulus birds were white and normal males and females raised by normal parents. There were two sets of four stimulus birds. Half of the males, distributed evenly over all groups, were tested with one set of stimulus birds, the other half with the other set. All males were tested six times covering all possible combinations of stimulus birds. There was at least one day in between two tests. The number of song strophes, the number of aggressive behaviours (pecking, attack flights) and the time spent in front of each stimulus bird was recorded. Directed song to stimulus birds was used to establish a sexual preference. Preference ratios were calculated by dividing the number of song strophes directed to one stimulus bird by the number of strophes sung to both stimulus birds multiplied with 100%. So, preference ratios could vary between 0 and 100%, with a ratio of 50% indicating no preference. In tests with a male and a female stimulus bird, a preference ratio of 100% implies an absolute preference for the female. In tests in which both stimulus birds are of the same sex, a preference ratio of 100% means an absolute preference for the normal stimulus bird. Differences between mean preference ratios and the 50% level were tested with Wilcoxon matched pairs signed ranks (WMP) tests. Differences in mean preference ratios between groups were examined by means of the

TABLE 1. Experimental groups

groups	N	Colour morph of (foster)parents	
		female	male
N♀ N♂	13	normal	normal
N♀ W♂	14	normal	white
W♀ N♂	15	white	normal
W♀ W♂	15	white	white

Mann-Whitney U tests (MWU). Whether males showed differential amounts of aggressive behaviour to the four stimulus birds was investigated with the Friedman two-way analysis of variance. All tests were two-tailed.

Results

a. Sexual behaviour.

Sexual preferences.

The results of the choice tests between a male of the same morph as the father and a female of the same morph as the mother are presented in Fig. 1. Males in all four groups showed a significant preference for the female (WMP; group N♀ N♂: test N♀ vs N♂ (N=12): $T=8$, $p<0.01$; group N♀ W♂: test N♀ vs W♂ (N=14): $T=0$, $p<0.001$; group W♀ N♂: test W♀ vs N♂ (N=13): $T=8$, $p<0.01$; group W♀ W♂: test W♀ vs W♂ (N=14): $T=4$, $p<0.01$). Thus, it can be concluded that zebra finch males prefer females resembling their mother over a male resembling their father.

Effect of behaviour on sexual discrimination.

If the discrimination in the above “mother” vs “father” test is based on behavioural cues and not on morphological characteristics, then it is expected that males raised by mixed pairs (group N♀ W♂ & group W♀ N♂) will also prefer a female over a male in a stimulus test between a

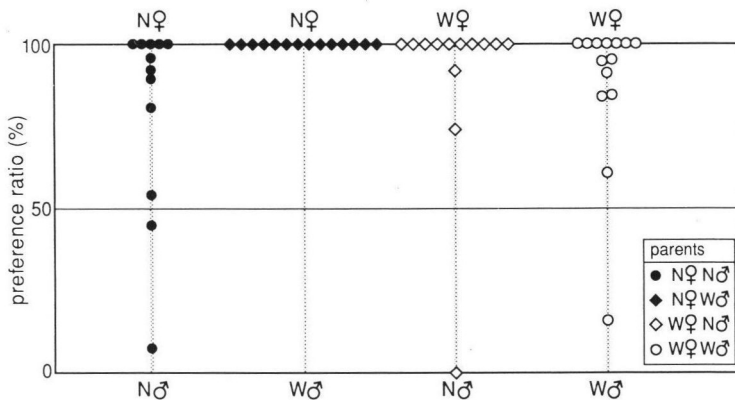


Fig. 1. Preference ratio (%) of males raised by normal(N), white(W) or mixed morph parents in a two-stimulus test with a female of their mother's morph and male of their father's morph.

male resembling the mother and a female resembling the father in morphological characteristics. On the other hand, should morphological characteristics be the main factor for discrimination, then it is expected that the male will be preferred. Figure 2 gives the results of the stimulus tests between a female of the same morph as the father and a male of the same morph as the mother for males of group N♀ W♂ and group W♀ N♂. Most males (14 out of 25) courted the male stimulus bird exclusively, although these stimulus males sang regularly during the test. Only 8 birds showed a preference for the female. Of these, one male (group W♀ N♂) had shown a preference for the N male in “mother” *vs* “father” test (Fig. 1), which indicates that his preference was also consistently based on colour morph and not on behaviour. When this male was left out, the overall preference for the male choice bird was just significant (WMP; N=24, T=82, $p=0.05$). So, morphological characteristics appear to be more important than behavioural cues for sexual discrimination in zebra finch males. Although, not all males prefer the male stimulus birds and the average preference is less strong than in the previous test (WMP; N=11, T=3, $p<0.01$), so an additional effect of behaviour might be present. However, it should be noted that the less strong preference might also be caused by the fact that, due to the clear sexual dimorphism in the normal morph, there was a difference in appearance between the normal parent the males grew up with and the normal stimulus bird used in this test.

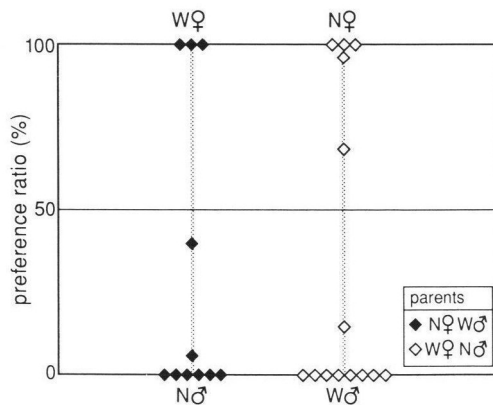


Fig. 2. Preference ratio (%) of males raised by mixed morph parents in a two-stimulus test with a male of their mother's morph and a female of their father's morph.

The effect of early experience with both parents on sexual discrimination.

The above analyses demonstrate that, even in a choice situation with a male and female stimulus bird, most males seem to use morphological characteristics for discrimination between the sexes. In theory such discrimination could be achieved by learning the characteristics of the mother only. So the question remains whether the father has an influence on the sexual preference as well.

If only the mother's characteristics are important, then it should be expected that males, that were raised by a mother of a certain morph (*e.g.* groups N♀ N♂ and N♀ W♂), will prefer a female of this morph over the male of this morph, irrespective of the morph of their father. If, on the other hand the father's characteristics are also important, it is expected that males raised by parents of one morph only, will be better able to discriminate between a female and a male of their mother's morph than males which had no prior experience with a male of that morph. In the latter case generalization from the mother's phenotype is not counteracted by some kind of inhibition to respond sexually to the father's phenotype.

Figure 3 gives the results of the tests in which males raised by mixed pairs had a choice between a female and male of their *mother's* morph. All males raised by a mother of the normal morph (N♀ W♂) showed a preference for the female (WMP, N=14, T=0, $p < 0.001$). This result does

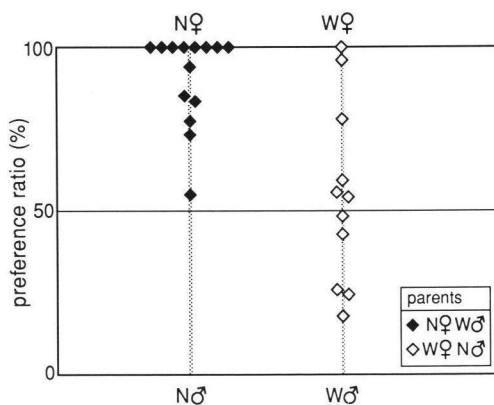


Fig. 3. Preference ratio (%) of males raised by mixed morph parents in a two-stimulus test with a male and a female of their mother's morph.

not differ from that obtained in the same test for males of group $N\text{♀ } N\text{♂}$ ($N\text{♀ } W\text{♂}$ *versus* $N\text{♀ } N\text{♂}$; MWU, $U=69$, $p>0.4$). So the sexual dimorphism in the normal morph appears to be adequate to discriminate the sexes without experience with a father of the normal morph. However, males raised by a white mother and normal father ($W\text{♀ } N\text{♂}$) failed to discriminate between the sexes (WMP, $N=11$, $T=39$, $p>0.5$). This result is in contrast to the results obtained in the same test for males of group $W\text{♀ } W\text{♂}$ ($W\text{♀ } N\text{♂}$ *versus* $W\text{♀ } W\text{♂}$; MWU, $U=27.5$, $p<0.01$), which showed a significant preference for the white female (Fig. 1). In the white morph, sexual dimorphism is reduced to the slight quantitative difference in bill colour, the male's bill being somewhat more red than the female's bill. Apparently, such a small difference in appearance has no influence on the preference of males that had no experience with a white father ($W\text{♀ } N\text{♂}$). However males that were raised by two parents of the white morph, have evidently learned to discriminate between the sexes on bill colour. This difference between the groups implies that sexual discrimination is not only based on learning the morphological characteristics of the mother but also on learning those of the father during early life. So, males do not only learn to respond sexually to a mother-like stimulus but also learn to suppress sexual behaviour towards a father-like stimulus. It should be added that the dimorphism in bill colour was also present in the $W\text{♀ } N\text{♂}$ -pairs, so it has to be assumed that discrimination on this cue was hampered by other more salient cues, such as plumage colour.

A problem with this line of reasoning is that it rests on the assumption that males raised by white parents use the same mechanism for sexual discrimination as males raised by mixed pairs. It is conceivable that males raised by parents that differ only slightly in appearance, use behaviour as an alternative cue.

The effect of bill colour on sexual discrimination.

To investigate whether it was correct to assume that males raised by white parents (group $W\text{♀ } W\text{♂}$) discriminate between the sexes using morphological characteristics (*i.e.* bill colour), another series of stimulus tests was performed. In these tests, the bill colour of the stimulus bird was manipulated with nail polish. In one test the female's bill was changed from orange to red by painting it with two layers of red nail polish (Invite

super rich 17, general cosmetics b.v., Amsterdam). The result was an intense red bill (Munsell Value: 8.75 R 4/14; Munsell Book of Color, Glossy finish Collection, Kolmorgen, Baltimore) that resembled the bill colour of an average non-breeding white male (*cf.* BURLEY & COOPERSMITH, 1987). The male's bill was changed from red to orange by applying two layers of orange nail polish (Gold fish 73, Miners make-up LTD, London). The resulting male had a pale orange bill (Munsell Value: 3.75 YR 6/12), which was somewhat paler than that of an average non-breeding white female (*cf.* BURLEY & COOPERSMITH, 1987). For another test this procedure was reversed (female orange, male red). The series was completed with a test in which the stimulus birds kept their natural bill colour. For each subject the two stimulus birds used were the same in all three tests. These stimulus birds were the same as used in the first test series.

The preference ratios of each individual in each test are given in Fig. 4. In the choice test between a male and a female with their natural bill colour, all males preferred the female. In the test in which the bill colours of the sexes were reversed, this preference was fully reversed, and all males showed a preference for the *male*, with the orange bill. Finally, all males preferred the female in the test between a female with her bill painted orange and a male with his bill painted red. There was no significant additional effect of the sex of the stimulus birds, *i.e.* male and

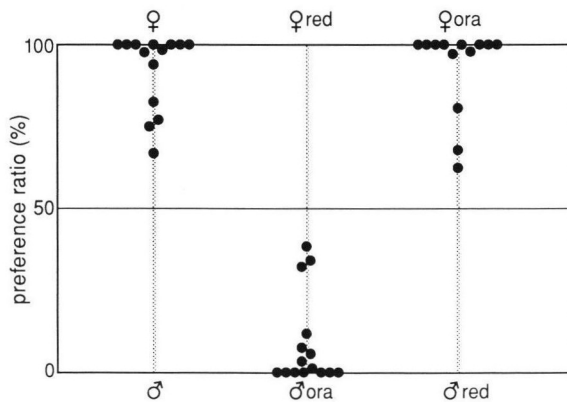


Fig. 4. Preference ratio's (%) of males raised by white parents in 3 two-stimulus tests with white stimulus birds of which the bills were respectively unpainted, male's bill painted orange, female's bill painted red and *vice versa*.

female with orange painted bills were equally preferred (WMP, $T=11$, $p>0.36$). So, in these tests at least, no additional effect of behaviour on the preference was found.

These results show that for males raised by white parents, which show very little sexual dimorphism in appearance, the recognition of the opposite sex is also primarily based on morphological features. These results justify the conclusion reached in the previous paragraph, that sexual discrimination is based on learning the characteristics of both parents.

Since, it was possible for this morph to change the appearance of one sex into that of the opposite sex and *vice versa*, these results suggest that the previous results which indicated an additional effect of behaviour (Fig. 2) might have been due to an imperfect match between the normal parent and the normal stimulus bird.

b. Aggressive behaviour.

So far only sexual behaviour has been considered, but it is likely that the object for aggressive behaviour is also influenced by early experience.

Overt aggression was relatively scarce, and observed in only 25 of the 57 males. The number of instances of aggression against the four different stimulus types (N♀, N♂, W♀, W♂) was calculated for each individual male. For the purpose of the analysis, the data of males from groups N♀ N♂ ($N=7$) and W♀ W♂ ($N=7$) and the data of males from groups N♀ W♂ ($N=5$) and W♀ N♂ ($N=6$) were pooled. Males raised by pure pairs (N♀ N♂, W♀ W♂) responded differentially to the four stimulus birds (Friedman Test, $N=14$, $\chi^2=17.33$, $p<0.001$, Fig. 5a). Multiple comparison tests revealed that males of the father's (familiar) morph received significantly more aggression than females of mother's (same) morph ($p<0.01$). Novel stimulus birds (W♀ and W♂ for group N♀ N♂, N♂ and N♀ for group W♀ W♂) received intermediate amount of aggression. Males raised by mixed pairs (N♀ W♂, W♀ N♂) also responded differentially to the stimulus birds (Friedman Test, $N=11$, $\chi^2=10.9$, $p<0.05$, Figure 5b). Multiple comparison tests showed that males of the father's (same) morph received more aggression than females of mother's (same) morph ($p<0.05$), whereas it should be noted that males raised by mixed pairs directed almost as much aggression to *females* of their father's morph (opposite ♀) as to males of their father's morph (same ♂).

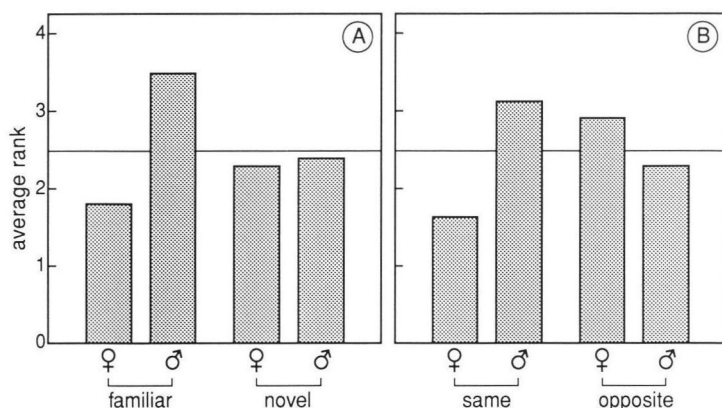


Fig. 5. Aggressive responses of male zebra finches. For each individual male that showed aggression, the total number of aggressive pecks and attack flights directed to each of the four stimulus types was summed. The results were ranked 1-4, where 1 represents the stimulus type at which the least aggressive behaviour was directed at. The average ranks were calculated for a: males raised by white or normal parents for stimulus birds of the parental morph (familiar) and of the novel morph (groups N♀ N♂ and W♀ W♂) and b: males raised by mixed morph parents for stimulus birds in which the morph corresponds with that of the parents (same) and for stimulus birds in which the sex and the morph are reversed as compared to their parents (opposite).

Taking the data of all groups together, only 2 (0.3%) of 701 observed occurrences of aggressive behaviour were directed to a female of the mother's morph, whereas 323 (46.1%) were directed towards a male of the father's morph. These results show that also the choice of an object for aggressive behaviour is influenced by early experience and suggest that it is based also on the appearance of the father rather than on behavioural cues by males.

Discussion

The present study demonstrates that zebra finch males can discriminate between male and female conspecifics. Sexual discrimination in this species is primarily based on learned morphological characteristics. The effect is so strong that the males can be "fooled" into courting a "mother" like male in favour of a "father" like female. Although the results of the first series of tests suggested an additional influence of behaviour on the preference, this might have been caused by the con-

founding effect of an imperfect match between parents and stimulus birds. No effect of behaviour was found in a subsequent series of tests, in which the stimulus birds resembled the opposite sex parent more accurately. The importance of morphological characteristics for discrimination between the sexes has been reported for a number of bird species. The sexes of shell parakeets (*Melopsittacus undulatus*) can be distinguished by the blue cere of the male. CINAT-TOMSON (1926) demonstrated that males of this species are completely deceived by a female with a blue-painted cere, which they attack, and by a male with a brown-painted cere, which they court. Other examples of the importance of morphological cues for sex recognition are reported by NOBLE & VOGT (1935; northern yellow-throat, *Geothlypis trichas*), NOBLE (1936; flicker (*Colaptes auratus*) and SÆTRE & SLAGSVOLD (1992: pied flycatcher, *Ficedula hypoleuca*). In none of these cases it is known whether learning is involved.

Experiments by IMMELMANN (1985) have already demonstrated that zebra finch males develop a preference for females of the same morph as their mother. The results of the present experiment show that sexual discrimination in zebra finch males is a result of early experience with both sexes. They are in concordance with the conclusions from a previous study (Vos *et al.*, 1993), which suggested that sexual discrimination is a result of learning to respond sexually to features of the mother and not to those of the father. Furthermore, these results show that differential responses in an aggressive context follow the opposite direction, *i.e.* most aggression is directed to males possessing features of the father, whereas aggression is almost absent to females with features of the mother.

The finding that sexual discrimination learning of males takes place at the juvenile stage in this species is different from what is found in some other sexually dimorphic bird species. NOBLE & VOGT (1935) found that one-year old male red-winged blackbirds (*Agelaius phoeniceus phoeniceus*) attempted to mate with taxidermic models of various species and sexes, whereas older males mounted the model of an adult female red-winged blackbird almost exclusively. Observations on male red junglefowl (*Gallus gallus*) by KRUIJT (1964) suggest that sexual discrimination in this species is not completed before the age of 120 days. Recent research on male Japanese quail (*Coturnix coturnix japonica*) has shown that males that were raised in groups until the age of 30 days do not discriminate between the sexes. As adults, they learned to discriminate between the sexes only after

extensive copulatory females and non-rewarded experience with males (NASH *et al.*, 1989; DOMJAN & RAVERT, 1991). Since, sexual imprinting in this species takes place in the first few weeks after hatching (GALLAGHER, 1977), NASH *et al.* (1989) concluded that not all information relevant for mate selection is acquired when the birds are immature. It is not clear whether this conclusion can be extended to the natural situation, since in these studies the males were deprived of experience with adult conspecifics. But even if the timing differs between species, the nature of the learning process might share some common features. For instance, the necessity of experience with both sexes to learn sexual discrimination was also reported for red junglefowl (KRUIJT, 1964) and Japanese quail (NASH *et al.*, 1989; DOMJAN & RAVERT, 1992).

The present findings suggest that zebra finch males have connected the internal representation of the morphological characteristics of each sex with a different behavioural system before they are tested as adults. The mechanism bringing about this connection is still unclear. It can be hypothesized that there are differences in the way male and female parents interact with the young male, which then result in the ability to discriminate between the sexes (see also TEN CATE *et al.*, 1993).

Although the findings of this study are quite easily understood in a functional way, since it is obvious that a preference to mate with the wrong sex leads to lower fitness prospects, the way sex recognition is achieved has some other consequences. For instance, as a result of discrimination learning, males will not only avoid other males but also, as a side-effect, females which resemble males in some morphological characteristic. In an evolutionary context this would at least have a stabilizing effect on the appearance of females in monogamous species in which both sexes exert mate choice. Under certain circumstances discrimination learning may lead to a phenomenon called “peak shift” (*e.g.* SPENCE, 1937; HANSON, 1959; HOGAN *et al.*, 1975). When an animal that is trained with a positive and a negative stimulus within the same stimulus dimension, is given a generalization test with a range of stimuli in this dimension, it often responds most to a stimulus that is away from the positive in the direction opposite to the negative stimulus (PURTLE, 1973). Recently, WEARY *et al.* (1993) proposed that “peak shift” might occur in the context of sexual imprinting. They suggested that female preferences for elaborate male secondary sexual characteristics could be a by-product of sexual

discrimination learning. WEISMAN *et al.* (this volume) provide evidence that female zebra finches can also recognize the visual appearance of the opposite sex on the basis of early experience. It should be mentioned that a role for sexual imprinting in the evolution of conspicuous characteristics has been proposed previously by TEN CATE & BATESON (1988) and TEN CATE (1991). However, their hypothesis does not refer to sexual discrimination learning. Whether or not sexual discrimination learning actually results in a "peak shift" needs further investigation.

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