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Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ

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We investigated the effect of a novel trait, a red feather on the forehead, on sexual imprinting in the dimorphic zebra finch, *Taeniopygia guttata*. Parents reared young in one of four imprinting groups: (1) both parents adorned with the red feather; (2) the father only adorned; (3) the mother only adorned; (4) both parents unadorned. After the young matured, we tested their preference for adorned and unadorned conspecifics of the opposite sex in simultaneous double-choice tests. Females but not males sexually imprinted on the red feather when their parents or father were adorned. In further tests, females that had sexually imprinted on the red feather did not generalize from the learned preference for a red feather to a preference for an orange or blue feather. Neither males nor females reared by unadorned parents showed a latent preference for potential mates adorned with a red, orange, or blue feather. Our results show that in the dimorphic zebra finch, only females sexually imprint on a novel trait. Sexual imprinting can support the evolution of novel male traits and would enhance the dimorphism in this species.

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The evolution of mate preferences is a complex process in which genetic and nongenetic factors are involved (Andersson 1994). Although genetic factors in mate choice are well studied and modelled (Kirkpatrick & Ryan 1991; Bakker 1993, 1999; Iwasa & Pominakowski 1999), the contribution of nongenetic factors such as social factors is still not clear. Social factors can influence the mate preference of individuals (Freeberg et al. 1999) and, through sexual imprinting, even lead to novel mate preferences within a generation (Payne et al. 2000).

Sexual imprinting has been investigated extensively in birds (Bolhuis 1991; ten Cate & Vos 1999) and mammals (Kendrick et al. 1998; Penn & Potts 1998; Owens et al. 1999). During an early phase in development, young individuals learn specific traits of their parents, and this learning process influences mate preferences later in life. In zebra finches, *Taeniopygia guttata*, the process of sexual imprinting is considered a two-step process (Bischof 1994). During the early acquisition phase, young learn stimuli in their environment and characters of their parents and form representations of the environment and social partners. During the consolidation phase, young birds learn by interaction with conspecifics which of the representations are possible mates, and the early acquired

Correspondence: K. Witte, Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, 55301 Bielefeld, Germany (email: Klaudia.Witte@biologie.uni-bielefeld.de). preference is linked to sexual behaviour and stabilized (Oetting et al. 1995; Oetting & Bischof 1996).

Sexual imprinting can have several functions. Immelmann (1972) assumed that it is necessary for species recognition and Bateson (1978) proposed that birds learn characters of their close relatives by sexual imprinting to allow optimal outbreeding during mate choice. In addition, in some bird species, males learn sex recognition during sexual imprinting. This has been shown in the zebra finch (Immelmann 1975; Vos et al. 1993; Vos 1994), great tit, *Parus major* (Slagsvold 1993) and pied flycatcher, *Ficedula hypoleuca* (Sætre & Slagsvold 1992).

There have been some studies on the role of sexual imprinting in hybridization, speciation and sexual selection (Irwin & Price 1993; Todd & Miller 1993). Payne et al. (2000) showed that the young of the brood-parasitic indigobird, *Vidua chalybeata*, sexually imprinted on a new host species within a generation and preferred that species as their new host. Thus, within a generation, these indigobirds can form a new branch within the species, which is the first step for reproductive isolation and therefore speciation.

Whether sexual imprinting can support the evolution of novel traits within a species is still under debate, because different theoretical models lead to different results. Older models assume that sexual imprinting is a conservative process that will not support the evolution of novel traits (O'Donald 1960; Kalmus & Maynard Smith 1966; Seiger 1967). ten Cate & Bateson (1989), however, showed in the Japanese quail, Coturnix coturnix japonica, that offspring preferred mates that had slightly different plumage characters to their parents. The authors assumed an asymmetrical preference in combination with a preference for contrasting elements, which can lead to a preference for mates with slightly novel traits (ten Cate & Bateson 1988). Laland (1994) designed a model that is more realistic than previous models (O'Donald 1960; Kalmus & Maynard Smith 1966) showing that when there is an asymmetrical mate preference, sexual imprinting can support the evolution of novel traits. Besides these theoretical studies, only one experimental study has shown that sexual imprinting can occur on an artificial novel trait: Witte et al. (2000) demonstrated that in a monomorphic estrildid finch, the Javanese mannikin, Lonchura leucogastroides, males and females sexually imprinted on a red feather on the forehead standing upright like a crest as an evolutionary novelty and preferred potential mates adorned with such a feather. In another study, those females that had imprinted on the red feather showed a similar strong preference for another novel red trait, red stripes on the tail, as they did for males adorned with a red feather (Plenge et al. 2000). Thus, females transferred the learned preference for a red feather to the other novel red trait. In a third study, Hörster et al. (2000) showed that Javanese mannikin males and females did not sexually imprint on a red bill in parents. Thus, it seems that not all kinds of novel traits can be sexually imprinted on.

In the present study, we investigated the role of sexual imprinting for the evolution of a novel trait in a dimorphic species, the Australian zebra finch, T. g. castanotis. We tested whether males and females can sexually imprint on a red feather on the forehead as a novel trait, as Witte et al. (2000) reported in the monomorphic species. In contrast to the monomorphic Javanese mannikin, which has only black, white and brown in the plumage, the colour red is not a novel character in zebra finches, since males have red bills. However, zebra finches lack an exaggerated crest, as do other estrildid finches (Goodwin 1982; Wolters 1982). Species in the Ploceidae, the sister family of the Estrildidae, also lack crests with one exception: the males of the crested malimbe, Malimbus malimbicus, have short feathers on the head that protrude from the neck (Serle et al. 1977). Therefore, we considered the red feather to be a novel adornment in the zebra finch. We investigated two questions. First, we tested whether male and female zebra finches can sexually imprint on the red feather. Second, we tested whether birds that had sexually imprinted on the red feather also preferred mates with an orange feather or a blue feather on the forehead, that is whether birds generalized from the learned preference for mates with a red feather to a preference for mates with an orange or blue feather of the same shape on the forehead. The colours red and orange have similar reflection patterns and differ only in that orange is shifted to lower wavelengths. The colour blue has a different reflectance pattern from red.

METHODS

Imprinting Groups

We randomly selected males and females of the F₃ generation of our main stock of zebra finches that were experienced in breeding and put them together as single pairs in 18 aviaries in two rooms at 21 °C and on a 13:11 h light:dark photoperiod with fluorescent lighting on at 0700 hours. Twelve aviaries $(0.95 \times 0.64 \text{ m} \text{ and } 2 \text{ m})$ high) stood side by side in two rows but visually isolated in one room; six aviaries $(0.89 \times 1.85 \text{ m and } 1.86 \text{ m high})$, also visually separated, were in another room. Each aviary contained several perches, coconut fibres for nest building, four nestboxes and food, water and sand ad libitum. We fed the birds with an ad libitum mixture of seeds containing Senegal, red, yellow and Canary millets. During the laying and breeding periods, we offered daily an additional egg-biscuit mixture, containing pieces of boiled egg and a commercial standard mixture (CeDe birdfood Eivoer) with wheat flour, sugar, honey, hemp seed, niger seed, broken hulled oats, poppy seed, vitamins, minerals, lysine, methionine and yeast.

We removed coloured rings from parents to prevent any sexual imprinting on the rings by the offspring. We formed four imprinting groups and assigned pairs randomly to one of them: (1) parents adorned: both parents were adorned with a red feather on the forehead; (2) father adorned: the father only was adorned with the red feather; (3) mother adorned: the mother only was adorned; and (4) parents unadorned: none of the parents was adorned. The parents unadorned group served as a control for latent preferences for a red feather on the forehead. These birds had had no experience with an adorned bird before they were tested. The source of all red feathers was a red feather boa made of natural feathers. We cut feathers from this boa 2.5 cm long, elliptical in shape and with a maximum width of 0.5 cm. All feathers used in the imprinting groups were identical in length and shape. The base of the feather was glued with a small piece of double-sided tape on to natural forehead feathers of the birds, so that the red feather stood upright like a crest. The red feather showed no reflection under UV light (Witte 1995). We adorned parents in three imprinting groups when chicks were 8 ± 1 days old, or 1–2 days before the chicks opened their eyes. The sensitive phase for visual stimuli begins when the young open their eyes (Immelmann 1972). We had to reglue a feather on to the parents' forehead on average every fifth day. We observed no adverse effect of glueing the feather on to the natural forehead feathers in birds. When we removed the feather, we cut only the tips of the natural forehead feathers. Thus, there was no damage after removing the feather. On day 20, we marked the young with orange-coloured rings with numbers for identification; orange rings are assumed to be neutral in mate choice in zebra finches (Burley et al. 1982).

When the young were 60 days old, we separated them from their parents. We kept all young from the same imprinting group together in a separate aviary. These four aviaries were visually isolated and contained food, water



Figure 1. Top view of the simultaneous double-choice situation in female and male mate choice tests. Two cages for stimulus birds stood side by side. The cage for the test bird stood in front of both stimulus birds' cages. Grey area shows preference zones in the test bird's cage.

and sand ad libitum as well as perches. To each group, we introduced an adult male and an adult female which were ornamented in the same manner as the parents of the young. We presented these adult birds to the young because experiences later in development can also influence mate preferences (ten Cate et al. 1984; Bischof & Clayton 1991; Domjan 1992; Bischof 1994; Oetting & Bischof 1996). Although males and females still saw two adult birds adorned like their parents, most of the birds in each aviary were unadorned. So it was more likely that the young males and females directed their first courtship displays and had their first experiences in mate choice with unadorned conspecifics. This experimental condition simulated a situation in the field where zebra finches live in groups and when a mutation is still rare in a population. When the birds were 100 days old or older, we tested their sexual preference for adorned versus unadorned conspecifics of the opposite sex.

Mate Choice Tests

We performed all mate choice tests in cages $(49 \times 43 \text{ cm} \text{ and } 50 \text{ cm} \text{ high})$ in a room at 23 °C and under light with ultraviolet (UV). We performed tests daily between 1000 and 1700 hours between May and December 2000.

Two cages with one stimulus bird each stood side by side in front of a test bird's cage (Fig. 1). Each cage contained water, seeds and sand ad libitum and four perches: one low perch near and parallel to the front to make the food more accessible, two perches of intermediate height parallel to the sides of the cage (perches of choice) and one high perch near and parallel to the back. A wooden partition between the stimulus birds' cages excluded visual contact between stimulus birds, and other screens beside and behind the cages excluded other visual stimuli. All birds were kept in test cages at least 1 day to acclimate before being tested in visual but not acoustic isolation. Before the test started, the test bird's cage was hidden behind another screen in front of the stimulus birds' cages. Immediately after removing this screen, we began the tests which lasted 40 min, with a break at 20 min to switch the position of the stimulus birds' cages to control for side preferences. A 15-cm-wide baffle, vertically attached to the front of the test bird's cage, prevented the test bird from seeing the right stimulus bird when perching adjacent to the left stimulus bird and vice versa.

We measured the attractiveness of stimulus birds as the time (s) that the test bird spent perching on the outer one-third of the perches of choice adjacent to the stimulus bird when facing them or when clinging to the mesh above these perches in front of them (grey area in Fig. 1). Other positions were scored as no-choice positions, even when the test bird was near a stimulus bird's cage but below the perches, because it was not clear whether the test bird was interested in the stimulus bird or in the food. We recorded the position of the test bird every 5 s. Perch time was scored as 2.5 s when the test bird changed perches within a 5-s interval; otherwise it was scored as 5 s. This measure is a good estimate of the real time that females or males perch in front of stimulus birds (B. Caspers, unpublished data).

In female mate choice tests, we also measured the number of nondirected song bouts of stimulus males to test whether the feather manipulation on males influences their behaviour. In male mate choice tests, we measured the time that a test male spent in front of females and the number of courtship displays to each stimulus female as a measure of the female's attractiveness to males.

Test males and females that showed side preferences, that is, spent more than 80% of their time in both preference zones on the same perch, even though we switched the position of the stimulus cages, were excluded from the analysis.

We did three experiments. In experiment 1, females and males could choose between two stimulus birds, one with and one without a red feather on the forehead. Here, we tested whether females and males had sexually imprinted on the red feather. In experiment 2, females and males could choose between stimulus birds either with an orange feather on the forehead or unadorned. This tested whether those birds that sexually imprinted on the red feather would generalize this preference to the orange feather. In experiment 3, females and males could choose between birds either with a blue feather on the forehead or unadorned. This tested whether birds would generalize the new preference to the blue feather.

We measured the relative reflectance of the red, orange and blue feathers through a quartz lens (focal length: 100–200 mm) which does not filter UV light (Fig. 2).



Figure 2. Reflectance curves of white, orange, red and blue feathers.

Feathers were illuminated at 45° to the surface by a 200-W halogen lamp. The reflectance was measured with a McPherson monochromator. As a white standard, we measured the reflectance of a white feather.

In total, 45 males and 48 females were reared in the four conditions (parents adorned: 12 males, 12 females; father adorned: 12 males and 13 females; mother adorned: 11 males and 10 females; parents unadorned: 10 males, 13 females). Each bird was tested in all three experiments. The sequence of the experiments was randomized across subjects. Each bird was tested in front of different stimulus birds in the three experiments.

Analysis

We analysed the time that the male and female test bird spent within the preference zones. With a binomial test, we compared the number of tests in which the test bird chose the adorned or unadorned stimulus bird by spending more time in front of that stimulus bird. For time spent we used a Wilcoxon signed-ranks test. Where necessary, we applied a Bonferroni correction for multiple comparisons. For a repeated measures ANOVA, with ornamentation as a within-groups factor and imprinting group as a between-groups factor, we applied a In transformation, so that the data were not significantly different from a normal distribution (Shapiro Wilk's test: 0.09 < P < 0.73). We used an LSD test for multiple comparisons as a post hoc test. All *P* values are two tailed.

RESULTS

Female Mate Choice Tests

The red feather

We excluded four females from the analysis because of side biases: two females from the parents unadorned group, one female from the mother adorned group, and one female from the father adorned group. Females of the father adorned group showed a significant preference for stimulus males adorned with a red feather (binomial test: N=12, P=0.04): they spent significantly more time in front of adorned males than in front of unadorned males (Wilcoxon signed-ranks test: T=10, N=12, P=0.02; Fig. 3a). Females of the parents adorned group showed a significant preference for adorned males (binomial test:



Figure 3. Results of the mate choice tests. Box plots and whiskers show median with first and third interquartiles and minimum and maximum values for the time (a) females and (b) males spent in front of the stimulus birds and (c) the number of courtship displays by males to the stimulus birds. The stimulus birds were of the opposite sex to the test birds and were either adorned with a red feather (\blacksquare) or unadorned (\Box).

N=12, P=0.006) and spent significantly more time in front of adorned males than in front of unadorned males (T=9, N=12, P=0.02; Fig. 3a). Females of the mother adorned group did not show a preference for a male type (binomial test: N=9, P=0.5) and spent a similar time in front of adorned and unadorned males (T=18.0, N=9, P=0.6; Fig. 3a). Finally, females of unadorned parents which had had no experience with adorned birds, also showed no preference for adorned or unadorned males (binomial test: N=11, P=0.2) and spent a similar time in front of adorned and unadorned males (T=29.0, N=11, P=0.77; Fig. 3a). We then compared the responses of females from all four imprinting groups to males adorned with the red feather and to unadorned males. Ornamentation had an effect on female mate choice (repeated measures ANOVA: $F_{1,42}$ =6.12, P=0.02). A post hoc test for multiple comparisons showed that the significant differences were due to differences between the parents unadorned and father adorned groups (LSD pairwise test: P=0.03), and between the parents unadorned groups (LSD pairwise test: P=0.03), and between the parents unadorned groups (LSD pairwise test: P=0.02). Thus, we conclude that females that had been reared either by an adorned father or by adorned parents sexually imprinted on the red feather in males.

The orange feather

We excluded four females from the analysis because of side biases: three females from the parents unadorned group and one female from the father adorned group. When they could choose between a male adorned with an orange feather and an unadorned male, females from all four imprinting groups failed to show a preference for adorned birds (binomial test; father adorned: N=12, P=0.77; parents adorned: N=12, P=0.77; mother adorned: *N*=10, *P*=0.75; parents unadorned: *N*=10, *P*=0.75). For all the imprinting groups, there were no significant differences between the times that females spent in front of adorned and unadorned males (Wilcoxon signed-ranks test; father adorned: T=23.0, N=12, P=0.21; parents adorned: *T*=34.0, *N*=12, *P*=0.7; mother adorned: *T*=26.0, N=10, P=0.87; parents unadorned: T=17.0, N=10, P= 0.3). Ornamentation had an effect on female mate choice (repeated measures ANOVA: $F_{1,42}$ =4.74, P=0.035), but none of the single comparisons was significant in the LSD pairwise post hoc test. The imprinting group had no effect on female mate choice (repeated measures ANOVA: $F_{3,40}=0.3$, P=0.82). Thus, females of the father adorned and parents adorned groups did not generalize from the learned preference for the red feather to the orange feather.

The blue feather

We excluded four females from the analysis because of side biases: two females from the parents unadorned group, one female from the parents adorned group, and one female of the father adorned group. In all four imprinting groups, females showed no significant preference for males with a blue feather or unadorned males (binomial test; father adorned: N=12, P=0.1; parents adorned: N=11, P=0.6; mother adorned: N=10, P=1.0; parents unadorned: N=11, P=1.0), and differences between the time spent in front of adorned and unadorned males were also nonsignificant (Wilcoxon signed-ranks test; parents adorned: T=25.5, N=11, P=0.5; mother adorned: T=25.0, N=10, P=0.8; parents unadorned: T=26.0, N=11, P=0.53). Females of the father adorned group showed a nonsignificant trend for a preference for unadorned males (T=15.0, N=12, P=0.06).

Repeated-measures ANOVA revealed no significant effect of ornamentation ($F_{1,42}$ =0.13, P=0.72) and no

effect of imprinting groups ($F_{3,40}$ =0.074, P=0.97). Thus, females that had sexually imprinted on the red feather did not generalize to a preference for mates with a blue feather.

In all three experiments, females from the parents unadorned group showed no preference for adorned males or unadorned males. Thus, females whose parents were unadorned had no latent preference for males with a red, orange or blue feather on his forehead.

To test whether the feather manipulation influenced the song activity of males adorned with the ornament, we compared the number of nondirected song bouts of males that were used twice as stimulus birds, once as an unadorned male (with the piece of glue only) and once as an adorned male (with a crest feather). These males did not differ in the number of their nondirected song bouts (Wilcoxon signed-ranks test: Z = -0.13, N = 53, P = 0.89).

Male Mate Choice Tests

The red feather

We excluded three males from the analysis because of side biases: two males from the father adorned group and one male from the mother adorned group. In terms of the time spent in front of females, no males from any imprinting groups showed a preference for one of the two female types (binomial test: father adorned: N=10, P=1.0; parents adorned: N=12, P=0.4; mother adorned: N=10, P=1.0; parents unadorned: N=10, P=1.0). Males spent a similar time in front of adorned and unadorned females (Wilcoxon signed-ranks test: father adorned: T=23.0, N=10, P=0.64; parents adorned: T=22.5, N=12, P= 0.95; mother adorned: T=25.0, N=10, P=0.79; parents unadorned: T=27.0, N=10, P=0.96; Fig. 3b). Repeated measures ANOVA revealed no significant effect of ornamentation ($F_{1,40}$ =0.2, P=0.66) and no effect of imprinting groups ($F_{3.38}$ =0.28, P=0.83).

Males of the parents unadorned group courted unadorned and adorned females equally often (Wilcoxon signed-ranks test: T=0, N=10, P=0.07), as did males of the father adorned group (T=1.0, N=10, P=0.08; Fig. 3c). Males that had been reared by an adorned mother showed no difference in courtship display towards adorned and unadorned females (T=15.0, N=10, P=0.37), as did males of the parents adorned group (T=6.0, N=12, P=0.09; Fig. 3c). Thus, we conclude that, regardless of their imprinting group, no male sexually imprinted on the red feather. Males of the parents unadorned group had no latent preference for females bearing a red feather.

The orange feather

We excluded from the analysis one male from the mother adorned group and one male from the father adorned group because of side biases. We found no preference by males for females with an orange feather in any of the four imprinting groups (binomial test: father adorned: N=11, P=1.0; parents adorned: N=12, P=0.77; mother adorned: N=10, P=0.75; parents unadorned:

N=10, P=0.75). We found no significant difference between the time males spent in front of adorned and unadorned females (Wilcoxon signed-ranks test: father adorned: T=31.0, N=11, P=0.85; parents adorned: T=37.0, N=12, P=0.87; mother adorned: T=24.0, N=10, P=0.72; parents unadorned: T=25.0, N=10, P=0.8), or between the number of courtship displays towards adorned and unadorned females (father adorned: T=4.0, N=11, P=0.17; parents adorned: T=18.5, N=12, P=0.63; mother adorned: T=21.5, N=10, P=0.9; parents unadorned: T=4.5, N=10, P=0.85). Males, therefore, had no latent preference for females with an orange feather on the forehead, and experience with at least one adorned parent did not influence the mate choice of males for females adorned with an orange feather.

The blue feather

We excluded from analysis one male from the mother adorned group and one male from the father adorned group because of side biases. Males did not discriminate between females with and without a blue feather (binomial test: father adorned: N=11, P=0.22; parents adorned: N=12, P=1.0; mother adorned: N=10, P=1.0; parents unadorned: N=10, P=0.11). Males spent a similar time in front of both female types (Wilcoxon signed-ranks test: parents adorned: T=34.0, N=12, P=0.7; mother adorned: T=25.0, N=10, P=0.79; parents unadorned: T=10.0, N=10, P=0.07; father adorned: T=19.0, N=11, P=0.21).

In all four imprinting groups, males showed no significant differences in their preference to court in front of females with and without a blue feather (Wilcoxon signed-ranks test: parents adorned: T=10.5, N=12, P=0.5; mother adorned: T=12.0, N=10, P=0.4; parents unadorned: T=3.0, N=10, P=1.0; father adorned: T=14.0, N=11, P=0.3). Thus, experience with the red feather early in life did not influence the males' mate choice for females with a blue feather.

DISCUSSION

Our results showed that, in the dimorphic zebra finch, only females sexually imprinted on a novel trait, the red feather on the forehead of their parents. When the father or both parents were adorned with the red feather, females preferred males adorned with a red feather over unadorned males. Females reared by an adorned mother and an unadorned father showed no such preference later on. This result shows that the father was a more important stimulus to females than the mother.

Weary et al. (1993) proposed a model in which the father serves as a positive stimulus and the mother as a negative stimulus to females. In our case, it seems that the father was indeed a positive stimulus, since females reared by an adorned father preferred males with the paternal ornament. It is, however, unlikely that the mother served as a negative stimulus. If that had been the case, we would have found a strong preference for unadorned males in females of the mother adorned group. We conclude instead that, in these zebra finch females, the father served as a positive stimulus and the mother as a neutral rather than a negative stimulus.

Why did females of the mother adorned and parents unadorned groups, both of which had been reared by unadorned fathers, not prefer unadorned males over adorned ones in the binary choice situation? Why did they not sexually imprint on the naturally red bill? Although zebra finch females show a strong preference for redder bills in males (Burley & Coopersmith 1987) male bill colour seems unimportant during sexual imprinting in females (Vos 1995c, but see Weisman et al. 1994). Vos (1995c) performed an imprinting experiment in which young white zebra finches were reared by white parents. The white morph lacks all sexually dimorphic characters except that females have a more orange bill and males a red bill. Vos (1995c) manipulated the bill colour of parents so that some zebra finches were reared by parents with the normal bill coloration, and some were reared by females with a red bill and males with an orange bill. Test males sexually imprinted on the bill colour. Females, however, did not sexually imprint on the bill colour. Thus, bill colour might not be a trait that female zebra finches learn during sexual imprinting. Another imprinting study with Javanese mannikins showed that, although they could sexually imprint on the red feather on the forehead (Witte et al. 2000), they did not sexually imprint on a red bill in parents (Hörster et al. 2000).

No males in any of the four imprinting groups showed a preference for females with a red feather over unadorned females. Thus, in contrast to females, males did not sexually imprint on the red feather. In a parallel study, K. Witte & B. Caspers (unpublished data) investigated whether male and female zebra finches could sexually imprint on a blue feather on the forehead. Male and female test birds were reared in the same four imprinting groups as in the present study and tested in binary choice tests after they had reached maturation. Females that had been raised by adorned fathers preferred males adorned with a blue feather over unadorned males, and females reared by adorned parents showed a tendency to prefer adorned males. Females reared by adorned mothers or unadorned parents showed no preference, and none of the males showed a preference for females adorned with a blue feather. Thus, this study supports our findings that only females but not males sexually imprint on a red feather.

Why do the sexes differ in sexual imprinting on a novel trait? In other experiments with zebra finches, males learn to discriminate between the sexes on morphological features during sexual imprinting, but females seem to learn sex differences based on different behaviours (Vos et al. 1993; Vos 1994, 1995a). Vos (1995b) proposed that sex differences in sexual imprinting might reflect the different roles of the sexes in pair formation. Males generally initiate courtship. When only morphological cues can provide information about the sex of another individual, it is important to learn sex recognition on the basis of these cues. In addition, males will save time and energy and avoid injuries from male–male interactions if they

can identify females on the basis of morphological cues. Females, however, choose males on the basis of courtship display and song (Collins et al. 1994; ten Cate & Mug 1984), so it is not necessary to learn sex-specific morphological traits. Our results, however, showed that females from the parents adorned and father adorned groups learned a morphological trait in males, the red feather. Our results are consistent with those of Weisman et al. (1994), which showed that female zebra finches sexually imprint on the beak colour of males, but contradicts findings that zebra finch females do not learn morphological cues (Vos et al. 1993; Vos 1994, 1995a).

Why did males not sexually imprint on the red feather? Red is a male-specific trait in zebra finches, and males have red bills. Perhaps females with a red feather on the forehead look more like males and are therefore a negative stimulus for discriminative learning for males (Weary et al. 1993).

Unlike previous studies investigating sexual imprinting in zebra finches, in our study males and females were not isolated from conspecifics. We kept them together with other young birds from the age of 60 days. This situation is more natural because in nature young birds live together in flocks (Zann 1996). During the consolidation phase of the imprinting process, young birds lived together with mostly unadorned birds, although we placed two adult birds adorned like the parents of the young into the aviary. It was therefore likely that males performed their first courtship displays to unadorned females. Perhaps the consolidation phase for sexual preference is more important in males than in females, which might explain the lack of sexual preference for adorned females in males reared by an adorned mother or adorned parents.

Did females generalize from the learned preference for the red feather to a preference for the orange and blue feather? Generalization is an important component in learning processes and a prerequisite for recognition. Through generalization, novel variants that differ from a known stimulus in only one or a few components can be recognized as similar stimuli (Enquist & Arak 1993) and elicit a similar response to a known stimulus. Females of the parents adorned and father adorned groups did not show a similar preference for males with an orange feather as for males with the red feather. Thus, females did not generalize their preference for males with the red feather to those with the orange feather. Similarly, females did not generalize from the learned preference for the red feather to a preference for males with a blue feather. To test whether females primarily learned the specific colour of the novel trait and not its shape and position on the body, one should present males with another red trait, for example red leg bands, to females and see whether those males were similarly attractive to females. In the monomorphic Javanese mannikin, Plenge et al. (2000) showed that females that had sexually imprinted on a red feather transferred this learned preference to males with another novel red trait, red stripes on the tail. The same females, however, did not prefer males adorned with a blue feather on the forehead or males adorned with blue stripes on the tail. In the Javanese mannikin, sexual imprinting on a red trait leads to a preference for males with other red traits independent of the shape and position on the body and can therefore support the evolution of other traits of the same colour as the learned trait.

Did male and female zebra finches show a latent preference for a crest feather on the forehead? The sensory exploitation hypothesis predicts that males and females have evolved certain traits through sexual selection owing to a preexisting bias in the oppposite sex for those traits. A bias may be due to random factors, other forms of mate choice (e.g. species recognition), physiological constraints and the action of natural selection (Ryan 1990; Ryan & Keddy-Hector 1992). If a novel trait matches one of these preexisting biases, it will be favoured by sexual selection through female and/or male mate choice. In our study, the response of males and females reared in the parents unadorned group to potential mates adorned with a feather tested whether they had a latent preference for adorned birds. Neither males nor females from this group preferred any of the adorned birds presented in the choice tests.

Tyler Burley & Symanski (1998) tested whether male and female domesticated, wild-type zebra finches and males and females of the monomorphic long-tailed finch, Poephilia acuticauda, had latent preferences for crested conspecifics of the opposite sex. Birds were tested in a four-arm choice chamber and could choose between conspecifics of the opposite sex, three adorned and one unadorned. Male zebra finches that could choose between females with a white, black or light blue crest and an unadorned female preferred unadorned females and did not discriminate between the crested females. Female zebra finches preferred males with a white crest over males with a red, green or no crest. Both sexes of the monomorphic long-tailed finch preferred potential mates with a white crest over those with a light blue, red or no crest. Thus, Tyler Burley & Symanski showed that female zebra finches and both sexes of the long-tailed finch had a latent preference for mates adorned with a white crest. In our study, we used feathers of different colours, so it might be that the latent preference is limited to a specific colour, white. Another difference between these studies is that we tested Australian and not domesticated zebra finches. Both studies showed, however, that zebra finch males had no latent preference for adorned females.

Do dimorphic species differ from monomorphic species in sexual imprinting on novel traits? We found one major difference between this study and one on sexual imprinting on a red feather in the monomorphic Javanese mannikin under similar conditions (Witte et al. 2000). In the monomorphic species, both sexes sexually imprinted on the novel trait. Thus, sexual imprinting would support the establishment of a novel trait in both sexes. This species would evolve to a more adorned species, but remain monomorphic. In the dimorphic zebra finch, only females sexually imprinted on the red feather. Thus, sexual imprinting in only females would lead to a species with more dimorphism. This comparison shows that the status quo of a species, dimorphic or monomorphic, is an important factor for the evolution of novel traits through sexual imprinting.

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