SEXUAL IMPRINTING SUPPORTS THE EVOLUTION OF NOVEL MALE TRAITS BY TRANSFERENCE OF A PREFERENCE FOR THE COLOUR RED

by

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Summary

We investigated if sexual imprinting on birds with a red artificial trait can influence female preference for mates bearing other novel, *i.e.* not-imprinted traits in male Javanese mannikins (*Lonchura leucogastroides*). We tested two groups of females in mate choice tests. One group of females was sexually imprinted on parent birds adorned with a red feather on the forehead. The other group was raised by normal unadorned birds and was assumed to be sexually imprinted on the normal unadorned phenotype. Females could choose between unadorned and adorned males in simultaneous double choice tests. The adorned males were ornamented with three different kinds of artificial ornament, which differed from the learned red feather on the forehead in a specific manner. The novel traits were a blue feather which differed from the familiar red feather in colour only, red stripes at the tail which had the same colour as the red feather but differed in shape and position at the body, and blue stripes at the tail (same colour as the blue forehead feather), which were different from the red feather in all three qualities.

Females which were sexually imprinted on the red feather showed a similar strong preference for the red stripes at the tail as for the learned red feather. These same females showed no preference for males bearing a blue feather on the forehead or for males bearing blue stripes at the tail. This shows that sexual imprinting on a red trait leads to a preference only for another novel red trait due to transference of a preference for the colour red. The control females which were raised by unadorned birds responded on average indifferently to males bearing any of the artificial traits, *i.e.* some females rejected adorned males, some

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females preferred adorned males. To latter females it seems that a novel male ornament is somewhat attractive independent of any previous learning.

Sexual imprinting on the red feather can influence female mate preferences for mates bearing other novel artificial traits due to transference of a preference for the colour red. Transference of colour preference makes it possible to react to a stimulus that differs from the imprinting stimulus in size, shape or position and therefore might play an important role in the evolution of conspicuous male traits.

Introduction

Female mate choice is one of the most powerful driving forces in sexual selection. Females choose males on the basis of secondary sexual ornaments and prefer to mate with those males bearing the most elaborate trait(s) (overview in Andersson, 1994). Thus, female mate choice leads to the exaggeration of conspicuous ornamental traits in males. This has been shown in many studies in which male traits have been artificially enlarged or diminished (Andersson, 1982; Møller, 1994). Female mate choice can not only lead to the exaggeration of already existing male traits but it can also lead to the evolution of novel traits. Jones & Hunter (1998) showed that naturally crestless least auklets (*Aethia pusilla*) preferred conspecifics of the opposite sex adorned with a forehead crest as a novel trait for this species. Witte (1991) and Witte & Curio (1999) found in the Javanese mannikin (*Lonchura leucogastroides*), a monomorphic estrildid finch, that females exhibited a preference for naturally unattractive males and reproduced with them when those males were adorned with a red feather on the forehead as an evolutionarily novel trait. In two other estrildid finches Tyler Burley & Symanski (1998) showed that zebra finch females (*Taeniopygia guttata castanotis*) and both sexes of the monomorphic long-tailed finch (*Poephila acuticauda*) exhibited a preference for mates with a white crest as an evolutionarily novel trait. Additionally, Burley and her co-authors have shown that in zebra finches coloured leg bands have a significant influence on the attractiveness in males and females (Burley, 1986a; Burley *et al.*, 1982), on the sex ratio in offspring (Burley, 1981), on parental investment in the current brood (Burley, 1988), and on reproductive success (Burley, 1986b). Thus in birds, females often show a preference for mates with novel traits.

The sensory exploitation hypothesis (Ryan, 1990) provides an explanation for the initial evolution of novel male traits. This hypothesis holds that females have a hidden preference for male traits before those traits are

expressed in the male phenotype. This hidden preference based on a bias of the females' sensory system might have evolved due to other selection forces. Evidence for the sensory exploitation hypothesis has been provided by several studies in different species (Christy, 1988; Basolo, 1990, 1995a, b; Proctor, 1991, 1992; Ryan & Rand, 1993). Here females have a pre-existing bias for male traits which are not expressed by males of their own species (but see Tobias & Hill, 1998; Wilkinson *et al.*, 1998).

Part of an explanation for the evolution of novel male traits could be sexual imprinting (ten Cate & Bateson, 1988; ten Cate, 1991; Laland, 1994; Vos, 1995; ten Cate & Vos, 1999). During a sensitive period offspring learn characters of their parents, and this early experience can influence mate choice later on in life (Bateson, 1980; Burley, 1985; ten Cate, 1987). Whether sexual imprinting can support the evolution of novel traits is still under debate because different models lead to different results. The mathematical model of Laland (1994) which considered more realistic circumstances than older models showed that sexual imprinting can promote the fixation of novel mutants with heterozygote advantage, or if there are asymmetrical mating preferences. Ten Cate & Bateson (1988) investigated asymmetrical preference in mate choice in the Japanese quail (*Coturnix coturnix japonica*) and observed a shift towards slightly novel partners.

Whenever asymmetrical mate preferences are observed, the preference for a learned character is transferred to a novel or slightly different stimulus. Without this capability of transference an animal can only react to stimuli that are identical to the learned stimulus. Transference is a well known phenomenon in learning processes and supports the learning process or the recognition of novel stimuli by interaction with former learning. It is observed in humans as well as in animals. A response due to transference occurs if new stimuli include characters which are similar or identical with a character of a known stimulus. We refer to these 'simple' forms of transference and not to "more cognitive" forms, which, for example, include the subject's insight in the learning process (*e.g.* human learning by intentional application of formerly successful strategies to unknown contexts). On this view, transference is in some way similar to generalization processes (if generalization is defined more broadly) or both may be explained by similar neuronal mechanisms involved in object recognition.

In mate choice, there are some findings that could be explained by transference of a colour preference: Burley (1986a) reports that zebra finches

(*Taeniopygia guttata*) and double-bar finches (*Stizoptera bichenovii*) prefer mates wearing leg bands, if band colours are present in the species′ natural colouration. In the rock ptarmigan (*Lagopus mutus*), males banded with comb-coloured bands were more successful in obtaining mates (Brodsky, 1988). Unfortunately, in both cases it is not possible to decide, if a learned or a genetical preference is transferred to the new trait of the same colour. Our study could give an answer by focusing on imprinting as a learning process.

In this study we investigate if and how sexual imprinting on a red feather on the forehead can influence female mate preferences for mates bearing other novel traits due to transference from a learned trait to a novel trait. How specific, or how general, are mate preferences formed by sexual imprinting? Do offspring transfer preferences from the learned character to other novel traits?

We introduced four novel traits in Javanese mannikin (*Lonchura leuco-gastroides*) males (one used for the imprinting process and three used for the transference experiments) and investigated female responses to males adorned with such traits. These novel traits were the red feather on the fore-head (the 'imprinting trait′), red stripes at the tail, a blue feather on the fore-head, and blue stripes at the tail (the 'novel traits′). The novel traits differed from the red feather in colour only (blue feather), in shape and position at the body, but not in colour (red stripes at the tail), or in colour, position at the body and shape (blue stripes at the tail). The Javanese mannikin is a monomorphic estrildid finch that bears a drab plumage with only black, brown, and white feathers. Genera closely related to the Javanese mannikin are similarly coloured and lack the colours red and blue. The entire extant family of estrildid finches lacks crests (Wolters, 1979-1982; Goodwin, 1982). The Ploceidae, the sister family of Estrildidae, lacks crests as well with one exception. The males of the crested malimbe (*Malimbus malimbi-cus*) have short feathers on the head which protrude a little bit from the neck (Serle *et al.*, 1977). It is therefore likely that the red feather and the other novel traits qualify as evolutionarily novel in the Javanese mannikin.

We performed female mate choice tests with two groups of females. One female group was sexually imprinted on the red feather on the forehead (Witte *et al.*, 2000). The other female group had no previous experience with males bearing the red feather, and were assumed to be sexually imprinted on the normal unadorned type. By testing these females we will establish a baseline for female preferences for mates adorned with a novel

trait. By comparing responses of both female groups to males which were adorned with unfamiliar traits, we want to test if and how females transfer a preference from the known red feather to unfamiliar traits. By testing these three different novel traits we will examine, which quality of the red feather is salient in being transferred and causing a preference for novel male traits.

Methods

Housing condition

We kept birds in large aviaries (3.0 × 1.6 × 2.5 m) in mixed-sex groups on a constant 14:10 h light:dark photo period at 28°C with food, water and sand available *ad libitum*. Each aviary was visually isolated by cloth from other aviaries. Each bird had a unique combination of no more than three 1.5 mm broad black and white leg bands. Because leg bands have a strong effect on mate choice in zebra finches (Burley, 1981, 1986a; Burley *et al.*, 1982) we used only colours which occur in the plumage and used 1.5 mm broad rings to minimise any effect of banding on mate choice. To determine sex we observed birds repeatedly. In the Javanese mannikin only males sing courtship and undirected song and birds were identified accordingly. Birds were identified as females when three different males directed courtship display to the same bird and moreover we had never seen this bird singing.

Test birds

We tested two groups of females. One group was raised by parents which were both adorned with a red feather ($N = 8$ females) or of which the father only was adorned with the red feather ($N = 5$ females). The red feather was 2.5 cm long, elliptically shaped and a maximum of 0.5 cm wide. The base of the feather was attached to the parent's forehead with a small piece of double-side tape so that the feather stood upright like a crest. The red feather showed no reflection under UV-light (Witte, 1995). The source for all red feathers was a red feather boa.

At the age of 60 days females were separated from their parents and kept together in an aviary with two adult birds which resembled the type of parents and other female and male offspring raised by the same type of parents. One group consisted of 8 female offspring and 9 male offspring from 10 different pairs of parents. Each pair produced two or only one offspring. The offspring were housed together with one adorned adult male and one adorned adult female. The other group consisted of 5 females and 2 males from 5 different pairs of parents. They were housed together with one adorned adult male and one unadorned adult female. This arrangement was chosen, since experiences later on in development can influence mate preferences as well (ten Cate *et al.*, 1984; Bischof & Clayton, 1991; Domjan, 1992; Bischof, 1994; Oetting & Bischof, 1996). There is evidence that siblings can influence the development of sexual preferences but parents have a dominating influence on the development of the later sexual preferences in zebra finch males (Kruijt *et al.*, 1983). Both Javanese mannikin females raised by two adorned parents (Witte *et al.*, 2000) and those raised by an adorned father and an unadorned mother (Witte, 1995) became sexually imprinted on the red feather. We therefore combined all those females in one group 'adorned parents'. To

make sure that these test birds were indeed sexually imprinted on the red feather we tested the preference of this group of females for males adorned with the red feather first. If this group of females showed a significantly stronger preference for adorned males than females imprinted on the normal type, we assumed that test females were sexually imprinted on birds with the red feather.

The other group of females ($N = 12$) was raised by unadorned parents in an aviary together with other unadorned birds (= 'unadorned parents'). Unfortunately, we do not know which of our test females were siblings and which were not. In a previous study, however, Witte *et al.* (2000) found no significant difference between the intra-clutch variation and inter-clutch variation in female response to adorned males. Thus, we think that the response of siblings in tests can be treated as largely independent. In contrast to females of the group "adorned parents" these females had no experience with adorned conspecifics before testing. We assumed that these females were sexually imprinted on the normal unadorned type. This group of females was raised under different conditions than females of the group 'adorned parents'. There is evidence from a previous study in Javanese Mannikins (Witte, 1995) which shows that differences in rearing conditions (cage *vs* aviary) have no detectable influence on mate preferences.

Ornamentation

We adorned males with three other kinds of novel trait which differed from the red feather in colour only, in position at the body and shape but not in colour, or in colour, position, and shape. We adorned males with a blue feather on the forehead (different colour, same shape and position at the body as the red feather). The blue feather had the same size and shape as the red one and was glued on the males' forehead with a small piece of double-side tape so that the feather stood upright like a crest. In another experiment we adorned males with red paper stripes upon and under the tail (same colour, but different position and shape). The paper stripes were coloured with ink which showed the same absorption spectrum as the red feather. The stripes were shaped like tail feathers. Two paper stripes (27×7 mm) were glued with 'Marabo Fixogum' on top of the two longest feathers in the middle and two red stripes (17×4 mm) of the same colour were glued on the outermost tail feathers under the tail. The stripes were visible from every watching position even when the tail was not fanned out. Paper stripes could be removed from the tail without damaging the feathers. In another experiment we adorned males with blue paper stripes (different position, shape, and colour). The blue paper stripes had the same shape as the red stripes and were fixed at the same positions as were the red ones. The blue colour had a similar absorption spectrum as the blue feather. None of the artificial traits showed UV reflection.

Female mate choice tests

We performed female mate choice tests in cages (Fig. 1). Two male cages stood side by side, a female cage was centrally placed in front of both male cages. Each cage ($50 \times 49 \times 43$ cm) 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 in the female cage) and one high perch near and parallel to the back offering the bird another perching position. A wooden partition between the males' cages excluded visual male-male interaction and other screens beside and behind
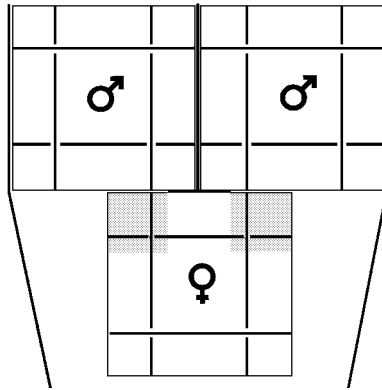
Fig. 1.   Top view on the choice apparatus. Grey area shows the preference zones.

the cages excluded any other visual stimuli. A baffle of 12 cm width attached to the front of the female′s cage prevented the female from seeing the right male when perching adjacent to the left male and vice versa.

For familiarisation, all birds were kept in test cages at least three hours before testing in visual but not acoustic isolation. Before the test started, the female′s cage was hidden behind another screen in front of the male cages for 10 min. Immediately after removing this screen, tests began and lasted 40 min, with a 30 min break in addition and switching position of males′ cages to control for side preference in females after 20 min. During tests, singing and courtship rates in males and all positions of the three birds were continuously recorded during test with a PC. The female′s mate preference was measured as the time [s] she spent perching in a very restricted area: on the first third of the perches of choice adjacent to the males when facing them or when clinging to the mesh above these perches in front of them. Other positions were scored as no-choice positions, even when the female was near the male′s cages but below the perches, because it was not clear if she was interested in the male or in food. A male was scored as being chosen when a female spent more time with that male and when the difference between the time spent with each male was larger than 10% of total time spent with both males. Time spent in front of a male is an indication of sexual preference for that male in the Javanese mannikin. Witte (1990) could show under the same choice situation as in this study that Javanese mannikin females showed tail quivering significantly more often in front of attractive males (= males with which females spent most time) than in front of unattractive males (= males with which females spent least time). In the present study we could observe tail quivering, but it was very rare, so we could not use it as a measure of sexual preference.

Tests were performed daily between 10.00-12.00 and 14.00-16.00 between 27 January and 30 April 1997. Tests in which females showed side biases were excluded from the analysis. Males and females used in a test were from different aviaries, so test females had not seen males used in the test before testing. Two days before testing males bearing the novel traits were shown to females for 15 min to avoid fear reaction by females during tests. To test female response to a novel male trait, a randomly chosen male of a male test pair was adorned with one of the artificial traits, *i.e.* with a red feather, a blue feather, red tail stripes, or blue tail stripes. Both males of a test pair were adorned with the same trait once in different

experiments to avoid unwanted random effects due to males′ natural attractiveness. Males were adorned at least two hours before testing. Adorned males showed normal behaviour already one hour after manipulation and did not preen the plumage more often than unadorned males.

Each female of both imprinting groups was used in each experiment with the four different male traits. The order of all tests was randomised and we used different male pairs with the same female in different tests.

We performed five different experiments. First we tested if females of the group 'adorned parents′ showed a significantly stronger preference for males adorned with the red feather than females of the group 'unadorned parents′. If so, we concluded that females of the group 'adorned parents′ were sexually imprinted on the red feather and that our requirement for the following tests was fulfilled. In the following three experiments we tested female response of both imprinting groups when one of two males was adorned with one of the unfamiliar traits. The response of females of the group 'unadorned parents′ gave us the baseline for female response to a novel trait without any experience with that trait. In a fifth experiment females of the group 'adorned parents′ could simultaneously choose between a male adorned with the red feather and a male adorned with red stripes. This experiment allowed a direct comparison between these two traits.

For all five experiments we tested whether females ($N = 8$) raised by two adorned parents differ in preference for adorned males from females ($N = 5$) raised by an adorned father and an unadorned mother. We found no significant difference between these females (Mann-Whitney-U-test: red feather: $p = 0.24$, blue feather: $p = 0.87$, blue stripes: $p = 0.13$, red stripes: $p = 0.17$, red feather *vs* red stripes: $p = 0.5$). Thus, we combined these females in one group 'adorned parents′.

Analysis

We analysed the absolute and relative time a female spent in front of the adorned and the unadorned male in a test. We compared the motivation of females for choosing a male among all tests by measuring the total time spent in front of both males in a test with the Kruskal Wallis H-test. We used the Wilcoxon matched pairs test to compare female response within each experiment and imprinting group and the Kruskal-Wallis H-test and the Mann Whitney-U-test to compare female response between different experiments and imprinting groups. We did not use parametric tests because of the bounded test intervals: Under these conditions and due to a small sample size normal distribution of data is unlikely. The H-test is only one-dimensional, which is a problem when comparing sets of data differing in more than one dimension. We used the H-test to clarify whether there were any differences between the test groups. If so, we grouped the data by different dimensions (colour/shape and position) and performed U-tests for all dimensions separately to clarify which dimension caused significant differences in responses. All p-values are two-tailed. For multiple comparisons p-values were corrected after Bonferroni.

Results

The total time spent with both males in a test did not differ between the four experiments with an adorned and an unadorned male within and between

both test groups. (Kruskal Wallis H-test, $\chi^2 = 10.97$, $p = 0.203$). Thus, the motivation of females to choose a mate was independent of the kind of novel trait used for ornamentation and of the imprinting group.

Red feather

Females of the group 'adorned parents' preferred adorned males significantly more often than unadorned males (Wilcoxon matched pairs test, $N = 13$, $z = -2.62$, $p = 0.009$, Fig. 2). Females spent on average ($\bar{x} \pm$ SD) 988 ± 293.7 s in front of adorned males and 552 ± 337.3 s in front of unadorned males (Fig. 2). Thus, females of the group 'adorned parents' preferred adorned males over unadorned males.

Females of the group 'unadorned parents' showed no preference for any of both male types. They spent on average ($\bar{x} \pm$ SD) a similar amount of time with adorned males (648 ± 281.4 s) and with unadorned males (642.7 ± 429.3 s) (Wilcoxon matched pairs test, $N = 11$, $z = -0.56$, $p = 0.59$, Fig. 2).

The relative time spent by females in front of an adorned male was significantly higher in the group 'adorned parents' than in the group 'unadorned parents' (Mann Whitney U-test, $N = 13$, $M = 11$, $z = -2.0$, $p = 0.046$). Females of the group 'adorned parents' preferred adorned males significantly more than females of the group 'unadorned parents'. Thus, we conclude that females of the group 'adorned parents' were sexually imprinted on birds with a red feather. Our requirement for the females of the group 'adorned parents' was therefore fulfilled.
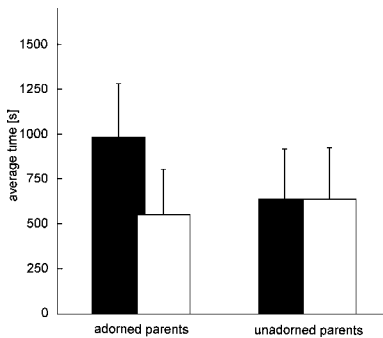

Fig. 2.   The red feather: Time spent of females of the group 'adorned parents' and females of the group 'unadorned parents' in front of males adorned with the red feather (black columns) and unadorned males (white columns). Females of the group 'adorned parents' preferred adorned males significantly more often than females of the group 'unadorned parents'.
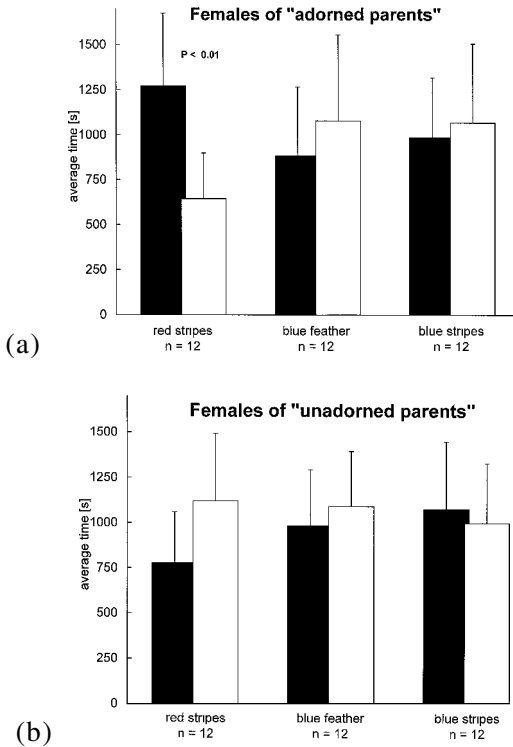
Fig. 3. (a) The novel, *i.e.* non-imprinted traits: Time spent of females of the group 'adorned parents' in front of adorned males (black columns) and unadorned males (white columns) in different experiments. (b) The novel, *i.e.* non-imprinted traits: Time spent of females of the group 'unadorned parents' in front of adorned males (black columns) and unadorned males (white columns) in different experiments.

Blue feather

Females of the group 'adorned parents' did not prefer males with a blue feather more often than unadorned males (Wilcoxon matched pairs test, $N = 12, z = -0.94, p = 0.35$, Fig. 3a). Females spent on average ($\bar{x} \pm$ SD) a similar amount of time in front of males with the blue feather on the forehead (885.4 ± 380.8 s) and in front of unadorned males (1079.7 ± 477.4 s). In the group 'unadorned parents' we found a similar response of females. These females showed no preference for one of the two types of males (Wilcoxon matched pairs test, $N = 12, z = -0.78, p = 0.43$, Fig. 3b) and spent on average ($\bar{x} \pm$ SD) a similar amount of time with both types of males (adorned males: 984.7 ± 310.9 s, unadorned males: 1093.2 ± 304.4 s). Thus, females

of both imprinting groups did not differ in their responses to males adorned with a blue feather.

Blue stripes

Females of the group 'adorned parents' showed no preference for males with blue stripes (Wilcoxon matched pairs test, $N = 12$, $z = -0.24$, $p = 0.81$, Fig. 3a). They spent on average ($\bar{x} \pm$ SD) a similar amount of time with adorned males (986.9 ± 331.7 s) and with unadorned males (1069.5 ± 437.8 s). We found a similar result in tests with females of the group 'unadorned parents' (Wilcoxon matched pairs test, $N = 12$, $z = -0.39$, $p = 0.69$, Fig. 3b). They spent on average ($\bar{x} \pm$ SD) a similar amount of time in front of both types of males (adorned males: 1078.6 ± 373.4 s, unadorned males: 1003 ± 328.9 s).

Females of both groups did not differ in the relative time spent in front of adorned males with blue stripes (Mann Whitney U-test, $N = M = 12$, $z = -0.17$, $p = 0.86$, Fig. 4).

Red stripes

Females of the imprinting group 'adorned parents' preferred males with red stripes at the tail significantly more often than males without red stripes (Wilcoxon matched pairs test, $N = 12$, $z = -2.59$, $p < 0.01$, Fig. 3a). Females spent on average ($\bar{x} \pm$ SD) 1272.7 ± 401.6 s in front of males with
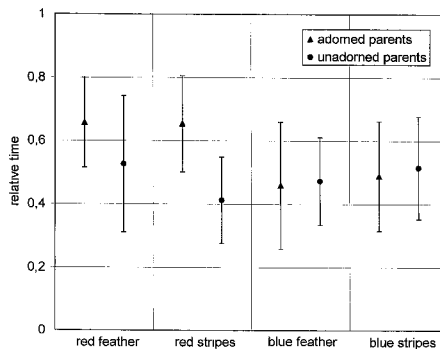

Fig. 4.   Relative time spent (measured as the proportion of total time spent with both males in a test for each male) of females of the group 'adorned parents' and females of the group 'unadorned parents' in front of adorned males bearing a red feather, red stripes, blue stripes, or a blue feather.

red stripes and 645.5 ± 254.2 s in front of males without red stripes. Females of the group 'unadorned parents' showed no preference for one of the two male types (Wilcoxon matched pairs test, $N = 12$, $z = -1.8$, $p > 0.05$, Fig. 3b) and spent on average ($\bar{x} \pm$ SD) a similar amount of time in front of adorned (777.2 ± 282.8 s) and unadorned males (1121.7 ± 372.3 s).

When comparing the relative time females spent in front of males with red stripes, we found that females of the group 'adorned parents' spent significantly more time in front of adorned males than females of the other group (Mann Whitney U-test, $N = 12$, $M = 12$, $z = -3.23$, $p = 0.001$, Fig. 4) and females of the group 'adorned parents' preferred adorned males significantly more often than females of the other group (Fisher's exact test, $N = 9$, $M = 5$, $p = 0.003$). Thus, females of the group 'adorned parents' showed a significantly stronger preference for males with red stripes than did females of the group 'unadorned parents'.

Red feather vs red stripes

In this experiment females of the group 'adorned parents' could choose simultaneously between a male adorned with the red feather and another male adorned with red stripes. Females spent on average ($\bar{x} \pm$ SD) a similar amount of time with both types of males (Wilcoxon matched pairs test, $N = 12$, $z = -0.79$, $p = 0.43$; red stripes: 1209.7 ± 433.3 s, red feather: 984.6 ± 441.8 s). Thus females of the group 'adorned parents' exhibited a similar response to males with two different kinds of red ornaments.

Comparison between the red feather and the other traits

We compared the relative time spent by females of the group 'adorned parents' in front of males adorned with the red feather with the relative time spent in front of males adorned with one of the other three traits. The H-test yields a significant difference between the four groups (Kruskal Wallis H-test, $N_1 = 13$, $N_2 = N_3 = N_4 = 12$, $\chi^2 = 10.72$, $p = 0.01$, Fig. 4) and, after regrouping the data, a significant difference in the dimension 'colour' (data sets of traits of the same colour grouped together: Mann Whitney U-test, $N = 25$, $M = 24$, $z = -3.28$, $p = 0.001$), but not in the dimension 'shape and position' (Data sets of traits with same shape and position grouped together: Mann Whitney U-test, $N = 25$, $M = 24$,

$z = -0.12$, $p = 0.90$). So the dimension 'colour' alone is responsible for the observed differences, shape and position of the trait have no effect.

In contrast, females of the group 'unadorned parents' showed no difference in response to adorned males between the experiments with an adorned and an unadorned male (Kruskal Wallis H-test, $N_1 = 11$, $N_2 = N_3 = N_4 = 12$, $\chi^2 = 3.05$, $p = 0.38$, Fig. 4). There were neither any differences in the dimensions 'colour' (data sets of traits of the same colour grouped together: Mann Whitney U-test, $N = 23$, $M = 24$, $z = -0.48$, $p = 0.62$) nor 'shape and position' (data sets of traits of the same shape and position grouped together: Mann Whitney U-test, $N = 23$, $M = 24$, $z = -0.72$, $p = 0.47$). All comparisons between the original four ungrouped data sets by Mann Whitney U-tests confirm this result by not showing any significant differences. Thus, the colour effect observed in the group 'adorned parents' can only be attributed to the imprinting process.

Discussion

The major result of the study is a demonstration of what feature of a learned trait females transfer from the imprinted stimulus to other, unfamiliar traits. Our results show that sexual imprinting on the red feather had a strong influence on female mate preferences for males bearing a novel red trait. Females which were sexually imprinted on the red feather showed a similarly strong preference for males adorned with red tail stripes as for males bearing the red feather on the forehead, although the stimulus red differed in both shape and position. Thus, females transferred their preference for the colour red to the red stripes.

Imprinting on the red feather, however, had no influence on the preference for males bearing a blue feather. Females of the group 'adorned parents' (ornament red feather) showed no preference for males adorned with the blue feather, although shape and position were the same as in the red feather. This indicates that the colour of a familiar trait had a stronger influence than had its position or shape: The colour of a learned trait was transferred to a novel trait, both position and shape were not.

Imprinting on the red feather had no influence on mate preferences for males bearing blue stripes at the tail, either. This trait was new to females in all three qualities (colour, shape and position). Hence, the transference of a familiar quality to the novel trait was impossible.

Sexual imprinting on the red feather leads to a preference for a novel trait of the same colour. Although the red feather had two conspicuous qualities, the colour and the position at the body, the colour had a stronger influence on mate preference. Thus, females transferred a specific quality of a learned character to a novel trait. It could be, however, that the colour red is just a specific case. Further experiments in which females are imprinted on a blue feather and tested with males adorned with a red feather, red stripes and blue stripes can show if females transfer from another colour of a trait to other novel traits as well.

The transference of a colour preference might open a bias for other novel traits of the same colour. Transference of colour can lead to an 'asymmetrical' preference for a novel trait of the same colour: An asymmetrical preference denotes a non-random variation in preference for a specific stimulus. The variation in preference is shifted to a stimulus which differs from the original stimulus, *e.g.* the parent's type in a specific direction. The dimension and the direction of the new preference can be determined by different factors. In our study, transference of colour explains a preference for another red trait. Ten Cate & Bateson (1988) proposed that an asymmetrical preference for slightly novel partners exists due to a combination of sexual imprinting on the parents' traits and a sensitivity for 'contrasting elements'. With these two factors alone, however, it is difficult to predict the direction of the asymmetry in mate preference. Our results suggest that the combination of sexual imprinting on a parent's trait and transference of a preference for the colour of that trait to novel traits can determine the qualities of a stimulus, in which asymmetrical deviations of preference are possible. This finding can not explain, why deviations from a learned stimulus should be asymmetrical in direction of more exaggerated traits, but it answers the question, in which qualities or dimensions this deviation is allowed to occur.

Transference of a preference for a colour to novel stimuli can also explain the hidden female preferences for males bearing a novel trait which are predicted by the sensory exploitation hypothesis (Ryan, 1997). If transference of a colour preference is not restricted to sexual imprinting, a colour of *e.g.* a preferred fruit could be transferred to a novel male ornament of the same colour which may be expressed in males by mutation.

If females transfer from the learned red trait to other novel red male traits all males bearing a novel red trait would be preferred as mates. Within a population males with novel red traits are considerably more likely to drift

above a threshold frequency at which males are favoured by sexual selection. Transference of a colour preference would be another viable hypothesis to account for the evolution of conspicuous secondary sexual male characters in imprinting species.

In our experiments females of the group 'unadorned parents' showed on average no preference for adorned males over unadorned males, independent of what trait was used. These females exhibited no preference for males bearing a red feather or bearing red tail stripes and displayed a significantly weaker response to males adorned with red stripes at the tail than females of the group 'adorned parents'. Females of the group 'unadorned parents' showed no preference for males adorned with the blue feather nor males adorned with blue stripes, neither. It might be that females showed no preference for any kind of male type because they did not become sexually imprinted on the unadorned type, or because they became imprinted on the unadorned type and, therefore, did not give any attention to any of the novel traits. Because these females were raised by unadorned parents it is very likely that they became imprinted on the unadorned type. Thus the latter explanation may explain the lack of a preference best.

On the other hand these females did not significantly reject the adorned males. This shows that the ornaments are moderately attractive; although being unfamiliar they match in strength the attractiveness of the known natural phenotype. In a previous study Witte & Curio (1999) showed that females raised by unadorned parents exhibit a specific response to adorned males. Their preference for adorned males depended on the natural attractiveness of males when unadorned. Naturally attractive males lost in attractiveness when adorned with the red feather on the forehead, and naturally unattractive males gained in attractiveness when adorned with a red feather. This specific response might explain the lack of a preference for unadorned or adorned males in this study, because some adorned males were more attractive, some were less attractive than unadorned males to test females.

A female preference for males bearing a novel trait may lead to the establishment of new morphs within a population, if the effect of this preference is stronger than the effect of other females rejecting this morph or preferring males with the familiar trait. Our study shows that transference of an imprinted preference for the colour red to novel traits plays an

important role in female mate choice and may drive the evolution of male ornamentation.

References

Andersson, M. (1982). Female choice selects for extreme tail length in a widow bird. — Nature 299, p. 818-820.

— — (1994). Sexual selection. — Princeton University Press, Princeton.

Basolo, A. (1990). Female preference predates the evolution of the sword in swordtails. — Science 250, p. 808-810.

— — (1995a). A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. — Anim. Behav. 50, p. 365-375.

— — (1995b). Phylogenetic evidence for the role of a pre-existing bias in sexual selection. — Proc. R. Soc. Lond. B 259, p. 307-311.

Bateson, P.P.G. (1980). Optimal outbreeding and the development of sexual preferences in Japanese quail. — Z. Tierpsychol. 53, p. 231-244.

Bischof, H.-J. (1994). Sexual imprinting as a two-stage process. — In: Causal mechanisms of behavioural development (J.A. Hogan & J.J. Bolhuis, eds). Cambridge University Press, Cambridge, p. 82-97.

— — & Clayton, N. (1991). Stabilization of sexual preferences by sexual experience in male zebra finches *Taeniopygia guttata castanotis*. — Behaviour 118, p. 144-155.

Brodsky, L.M. (1988). Ornament size influences mating success in male rock ptarmigan. — Anim. Behav. 36, p. 662-667.

Burley, N. (1981). Sex-ratio manipulation and selection for attractiveness. — Science 211, p. 721-722.

— — (1985). The organization of behavior and the evolution of sexually selected traits. — In: Avian monogamy (P.A. Gowaty & D.W. Mock, eds). American Ornithologists' Union, Washington D.C.

— — (1986a). Comparison of band-colour preferences of two species of estrildid finches. — Anim. Behav. 34, p. 1732-1741.

— — (1986b). Sexual selection for aesthetic traits in species with biparental care. — Am. Nat. 127, p. 415-445.

— — (1988). The differential allocation hypothesis: An experimental test. — Am. Nat. 132, p. 611-628.

— — , Krantzberg, G. & Radman P. (1982). Influence of colour banding on conspecific preferences of zebra finches. — Anim. Behav. 30, p. 444-455.

ten Cate, C. (1987). Sexual preferences in zebra finch males raised by two species: II. The internal representation resulting from double imprinting. — Anim. Behav. 35, p. 321-330.

— — (1991). Sexual imprinting, mate preferences and plumage evolution. — Acta XX Congr. Intern. Ornithol., Wellington, New Zealand, p. 1081-1088.

— — & Bateson, P. (1988). Sexual selection: The evolution of conspicuous characteristics in birds by means of imprinting. — Evolution 42, p. 1355-1358.

— — & Vos, D.R. (1999). Sexual imprinting and evolutionary processes in birds: a reassessment. — Adv. Study Behav. Vol. 28, p. 1-31.

— — , Los, L. & Schilperoord, L. (1984). The influence of differences in social experience on the development of species recognition in zebra finch males. — Anim. Behav. 32, p. 852-860.

Christy, J.H. (1988). Pillar function in the fiddler crab *Uca beebei*. II. Competitive courtship signalling. — Ethology 78, p. 113-128.

Domjan, J. (1992). Adult learning and mate choice: Possibilities and experimental evidence. — Amer. Zool. 32, p. 48-61.

Goodwin, D. (1982). Estrildid finches of the world. — British Museum (Natural History), Oxford University Press, Oxford.

Jones, I.L. & Hunter, F.M. (1998). Heterospecific mating preferences for a feather ornament in least auklets. — Behav. Ecol. 9, p. 187-192.

Kruijt, J.P., ten Cate, C.J. & Meeuwissen, G.B. (1983). The influence of siblings on the development of sexual preferences of male zebra finches. — Dev. Psychobiol. 16, p. 233-239.

Laland, K.N. (1994). On the evolutionary consequences of sexual imprinting. — Evolution 48, p. 477-489.

Møller, A.P. (1994). Sexual selection and the barn swallow. — Oxford University Press, Oxford.

Oetting, S. & Bischof, H.J. (1996). Sexual imprinting in female zebra finches: Changes in preference as an effect of adult experience. — Behaviour 133, p. 387-397.

Proctor, H.C. (1991). Courtship in the water mite *Neumannia papillator*: males capitalize on female adaptations for predation. — Anim. Behav. 42, p. 589-598.

— — (1992). Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona). — Anim. Behav. 44, p. 745-752.

Ryan, M.J. (1990). Sexual selection, sensory systems and sensory exploitation. — Oxford Surv. Evol. Biol. 7, p. 157-195.

— — (1997). Sexual selection and mate choice. — In: Behavioural ecology: an evolutionary approach, 4th edn (J.R. Krebs. & N.B. Davies, eds). Blackwell, Oxford, p. 179-202.

— — & Rand, S. (1993). Sexual selection and signal evolution: the ghost of bias past. — Phil. Trans. R. Soc. Lond. B 340, p. 187-195.

Serle, W., Morel, G.J. & Hartwig, W. (1977). A field guide to the birds of West Africa. — Collins, London.

Tobias, M.C. & Hill, G.E. (1998). A test of sensory bias for long tails in the house finch. — Anim. Behav. 56, p. 71-78.

Tyler Burley, N. & Symanski, R. (1998). "A taste for the beautiful": Latent aesthetic mate preferences for white crests in two species of Australian grassfinches. — Am. Nat. 152, p. 792-802.

Vos, D.R. (1995). The development of sex recognition in the zebra finch: Sexual imprinting from an evolutionary perspective. — PhD thesis, Rijksuniversiteit Groningen.

Wilkinson, G.S., Kahler, H. & Baker, R.H. (1998). Evolution of female mating preferences in stalk-eyed flies. — Behav. Ecol. 9, p. 525-533.

Witte, K. (1990). Versuche zur intersexuellen Selektion beim Java-Bronzemännchen (*Lonchura leucogastroides*), einer monomorphen Prachtfinkenart. — Diploma thesis, Bochum.

— — (1991). Natürliche Attraktivität und künstlicher Schmuck beim Java-Bronzemännchen *Lonchura leucogastroides*. — Verh. Dtsch. Zool. Ges. 84, p. 336.

— — (1995). Zur Evolution männlicher Schmuckmerkmale durch intersexuelle Selektion beim Java-Bronzemännchen *Lonchura leucogastroides*. — Dr. Kovac, Hamburg.

— — & Curio, E. (1999). Sexes of a monomorphic species differ in preference for mates with a novel trait. — Behav. Ecol. 10, p. 15-21.

— — , Hirschler, U. & Curio, E. (2000). Sexual imprinting on a novel adornment influences mate preferences in the Javanese mannikin *Lonchura leucogastroides*. — Ethology 106, p. 349-363.

Wolters H.E. (1979-1982). Die Vogelarten der Erde. — Verlag Paul Parey, Hamburg.