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Sexual Imprinting on a Novel Adornment Influences Mate Preferences in the Javanese Mannikin *Lonchura leucogastroides*

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Witte, K., Hirschler, U. & Curio, E. 2000: Sexual imprinting on a novel adornment influences mate preferences in the Javanese Mannikin *Lonchura leucogastroides*. *Ethology* **106**, 349–363.

Abstract

We investigated whether sexual imprinting on an artificial novel adornment in the Javanese Mannikin *Lonchura leucogastroides*, a monomorphic estrildid finch, can occur and might provide a mechanism for the evolution of novel traits. We introduced a red feather on the forehead as a novel adornment. Young were raised by parents which were both adorned, which were both unadorned, or only one of which was adorned with the red feather. We tested the female and male offspring of those parents in mate choice tests with an adorned and unadorned conspecific of the opposite sex. Males raised by an adorned mother or adorned parents preferred adorned females significantly more often than males raised by unadorned parents. We conclude that males were sexually imprinted on the red feather. Females raised by an adorned mother or raised by adorned parents significantly preferred adorned males, whereas females raised by unadorned parents showed no preference for adorned males. Thus, females also became imprinted on the red feather. Males might learn the novel adornment in combination with the parent's sex or learn just the most conspicuous sex, whereas females showed a preference for the adornment independent of which sex bore the feather. Our study shows that sexual imprinting might be an effective mechanism for the evolution of a novel trait and that males and females might become imprinted on a novel trait in different ways.

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Introduction

Theories of sexual selection propose that secondary sexual traits have evolved through mate choice (Darwin 1871; Andersson 1994). Many studies have shown

that females prefer to mate with males expressing the most elaborate secondary sexual trait and that females prefer males with artificially enlarged traits (Andersson 1982; Evans & Hatchwell 1992; Møller 1994). Thus, females may drive the evolution of secondary sexual traits in males. Several studies in biparental species have shown that males discriminate between females as well, and base their mate choice on display traits in females (e.g. Johnson 1988; Hill 1993; Wynn & Price 1993). Therefore, male mate choice can also lead to conspicuous traits in females. Sexual selection can even act on the same trait in both sexes. In the crested auklet *Aethia cristatella*, for example, both males and females prefer mates with larger crests (Jones & Hunter 1993).

A few studies have shown that mate choice can also drive the evolution of novel traits in birds. Jones & Hunter (1998) found that the naturally crestless least auklet *Aethia pusilla* has a preference for conspecifics with crests. Burley and her co-workers have shown, in the dimorphic zebra finch *Taeniopygia guttata*, that coloured leg bands have a strong influence on mate choice (Burley et al. 1982; Burley 1986a) and reproductive success (Burley 1981, 1986b,c). In the monomorphic Javanese Mannikin *Lonchura leucogastroides*, a red feather placed on the forehead as an evolutionary novel adornment influences female mate choice (Witte & Curio 1999). These studies show that artificial novel adornments can become meaningful in mate choice.

Once a novel trait arises in a population, how can this trait spread through the population and be maintained? One possible mechanism might be sexual imprinting, through which mate preference can be influenced by experience at an early stage of development. During a sensitive period, offspring learn the characters of their parents, and this experience could influence mate choice later on in life. Sexual imprinting has been investigated extensively in birds. Immelmann (1972) assumed that sexual imprinting is necessary for species recognition. Bateson (1978) proposed that animals learn the characters of close relatives by sexual imprinting to allow optimal outbreeding by mate choice. Recently, the role of sexual imprinting in the evolution of novel traits has been discussed (ten Cate & Bateson 1988; ten Cate 1991). Ten Cate and Bateson observed a shift towards slightly novel partners in the Japanese quail *Coturnix coturnix japonica*. This is an asymmetrical preference because only a mate which differed in traits in a specific direction from the parental type was preferred (e.g. higher contrast in plumage colours). An asymmetrical preference for novel partners might provide a mechanism for changes in traits meaningful in mate choice. According to a model by Laland (1994), sexual imprinting can support the spread of a novel trait within a population when there is heterozygote advantage and/or asymmetrical mating preferences.

We investigated whether sexual imprinting on an evolutionarily novel adornment is possible in the Javanese Mannikin *Lonchura leucogastroides* and how imprinting influences subsequent mate choice in both sexes. The Javanese Mannikin is a monomorphic estrildid finch with biparental care and has drab plumage with only black, brown and white feathers. We introduced a red feather standing upright like a crest as an evolutionarily novel and highly conspicuous adornment in this species. The entire extant family of estrildid finches lacks crests, and genera closely

related to the Javanese Mannikin are similarly coloured (Goodwin 1982; Wolters 1982). 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 which protrude from the neck (Serle et al. 1977). Therefore, a red feather can be considered as a novel adornment in the Javanese Mannikin.

We tested whether males and females raised by at least one adorned parent showed a stronger preference for mates adorned with the red feather than birds raised by unadorned parents which had no experience with adorned conspecifics.

Methods

Housing Conditions

We kept birds of our stock population in large aviaries (3.0 m × 1.6 m × 2.5 m) in bisexual groups at a constant 14/10 h light/dark photoperiod at 28°C with food, water and sand available ad libitum. Each aviary was visually isolated by cloth from other aviaries. For individual identification, each bird had a unique combination of thin black and white leg bands. We used only colours which occur in the plumage and used thin rings to minimize any effect of banding on mate choice, because leg bands have a strong effect on mate choice in zebra finches (Burley et al. 1982). We observed birds repeatedly to determine their sex. In the Javanese Mannikin only males sing courtship and undirected songs. Birds were identified as males when we observed them singing. Birds were identified as females when three different males showed courtship display to the same bird and we had never seen this bird singing.

Imprinting Groups

We randomly selected males and females from different aviaries and put them together as pairs in nine wooden cages (45 cm × 90 cm × 85 cm) for breeding. The cages contained perches, a nestbox, and coconut fibres, food, water and sand ad libitum. Each cage was visually isolated by cloth and illuminated by 300-W halogen lights from above. We exchanged one of the partners if a pair did not breed successfully within 4 wk. Each pair of parents was used for reproduction only once. Both parents built the nest, incubated the eggs, and fed the chicks, both in the nest and during the 2 wk after the fledglings left the nest.

We formed four imprinting groups. In 10 pairs both parents were adorned with a red feather (= 'parents adorned'). Each pair produced two or three offspring which were used in tests. In a second group of eight pairs of parents, with two or three offspring each, only the mother was adorned with a red feather (= 'mother adorned'). In a third group only the father was adorned with the red feather (= 'father adorned'). In the imprinting group 'father adorned' we had only four pairs of parents which produced one, one, two and three offspring per brood, respectively.

The source of all red feathers used was a red feather boa made of natural feathers. We cut feathers 2.5 cm in length, elliptical in shape and with a maximum width of 0.5 cm out of this boa. All feathers used in a test had the same length and

shape. We did not paint the feathers. The base of the feather was attached to the bird's forehead with a small piece of double-side tape so that the feather stood upright like a crest. The feather showed no reflection under UV light (Witte 1995). We adorned parents with the red feather in the three groups when chicks were 11-d-old, 1 d before they opened their eyes. This manipulation had to be repeated every 5–7 d because the feather became unstuck from the bird's head.

The fourth group was raised by unadorned parents in an aviary (= 'parents unadorned'). In the group 'parents unadorned' we had nine pairs of parents which produced two or three offspring per nest. As in the other imprinting groups, the young lived together with birds of same age and with male and female adult birds. In contrast to the other groups, however, they had no contact with an adorned bird until they were tested in the mate choice tests. We assumed that these birds were sexually imprinted on the normal type of parent and could therefore serve as a baseline for a preference for novel adornments without any experience with the red feather.

At the age of 60 d we separated the chicks from their parents and kept the chicks of the same experimental group together in a separate aviary. The aviaries were visually isolated from each other and were illuminated with halogen lights and contained food, water and sand *ad libitum* as well as perches and nestboxes. To each group we added one adult female and one adult male which resembled the parental type of the young birds. We presented these adult birds to the test birds, because it is known that experiences later on in development can also influence mate preferences (ten Cate et al. 1984; Bischof & Clayton 1991; Domjan 1992; Bischof 1994; Oetting & Bischof 1996). The young of the group 'parents unadorned' remained in their aviary where other adult birds served as model birds. We observed the birds daily to determine the sexes as described above.

There is evidence that siblings can influence the development of sexual preferences (Kruijt et al. 1983). Kruijt et al. investigated the sexual preferences of zebra finch males when they were raised by Bengalese finches as parents with no or up to four zebra finch siblings as nest mates. They found an effect of siblings on the development of sexual preferences, but the parents had the dominant influence on the development of later sexual preferences of the zebra finch males.

Mate Choice Tests with Males

Previous experiments have shown that males do not show a mate preference when given a choice between two females in cages (Witte & Curio 1999). We therefore performed the male choice experiments in an aviary (2 m × 1.1 m × 2.5 m) which contained food, water, and sand *ad libitum*, several nestboxes, natural branches, and coconut fibres for nest building. The aviary was illuminated with two halogen lamps (300 W) from above. Each day before testing, one male was released into the aviary for familiarization while two females were kept together in a cage visually isolated from the aviary. One randomly chosen female was adorned with a red feather on the forehead; the other female remained unadorned. The adorned female was allowed to become accustomed to the feather

for at least 5 h. Directly after manipulation females preened their plumage more frequently than unadorned females and flew around more. However, after only 2 h adorned females showed behaviour similar to that of unadorned females.

Tests began immediately after releasing both females into the aviary simultaneously and lasted 1 h. We measured the number of courtship displays performed by the male in front of each female as a score of his mate preference. A female was scored as chosen by a male when the male performed at least 55% of all courtship events in front of that female. If a male did not display to one of the females, we tested the male again with a different pair of females. Each pair of females was used twice, but the second time with another test male. We tested 13 males of the group 'mother adorned'. All males were tested only once. Males never saw stimulus females before testing. One male showed courtship displays to females less than three times during the test and was excluded from the analysis. In the group 'parents adorned' we tested 12 males, but three of them did not court in front of females and were excluded from the analysis. Unfortunately, we could not test males from the group 'father adorned'. In the imprinting group 'father adorned' we had only seven offspring. Two fledglings died and the five remaining chicks were females. In the group 'parents unadorned' we tested 10 males.

Mate Choice Tests with Females

All female mate choice tests were performed in cages from 10:00 to 12:00 h and from 14:00 to 17:00 h (Fig. 1). Two cages with one male each stood side by side in front of a female's cage. Each cage (43.3 cm × 49.0 cm × 40.0 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) and one high perch near and

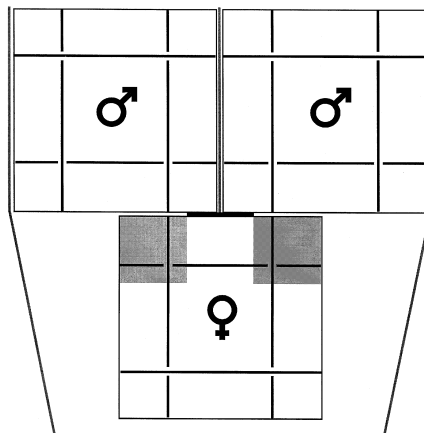


Fig. 1: Top view of the female mate choice situation. The stippled areas show the preference zone

parallel to the back. A wooden partition between the males' cages excluded visual male-male contact and other screens beside and behind the cages excluded other visual stimuli. For familiarization, all birds were kept in test cages for at least 3 h 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 males' cages. Immediately after removing this screen, tests began and lasted 40 min, with a break to switch the position of the males' cages to control for side preference in females after 20 min. A baffle of 15 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. The attractiveness of males was measured as the time (in seconds) the female spent perching in a very restricted area: on the first third of the perches of choice adjacent to the males when facing them, or on the mesh above these perches in front of the males (stippled area in Fig. 1). Other positions were scored as no-choice positions, even when the female was near a male's cage but below the perches, because it was not clear whether she was interested in the male or in the food. During tests we recorded the position of the female every 5 s. It was scored as 2.5 s when the female changed perches within an 5-s interval, and otherwise was scored as 5 s. Time spent in front of a male is an indication of sexual preference for that male in the Javanese Mannikin. Witte (1990) found, in the same choice situation, 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 observed tail quivering, but it was very rare, so we could not use it as a measure of sexual preference. A male was scored as being chosen when a female spent at least 55% of the time with him. Tests in which females spent less than 30% of the total time in front of both males or showed side biases were excluded from the analyses.

Each female was tested only once. One randomly chosen male was adorned with the red feather, and the other remained unadorned. Each adorned male was allowed to acclimatize to the feather for at least 5 h before testing. Males showed normal behaviour within 2 h after manipulation. They did not seem to preen their plumage more often than the unmanipulated male. In a previous study Witte & Curio (1999) showed that the singing rates of Javanese Mannikin males adorned with a red feather and those unadorned did not differ. Each male was used only once in a test. Test females had never seen stimulus males before testing.

We tested nine females of the group 'mother adorned', 14 females of the group 'parents adorned', five females of the group 'father adorned', and 13 females of the group 'parents unadorned'.

Analysis

We used a Wilcoxon matched pairs test to detect female mate preferences for adorned or unadorned males for each imprinting group, as measured by the relative time spent in front of each male in a test. We measured male mate preference by comparing the number of preferred females using a binomial test. We compared

the results for conspecific preference in female and male mate choice tests between same-sex groups with a Fisher's exact test. We also investigated the strength of female preference for adorned males (= time the female spent with the adorned male – the time she spent with the unadorned male) for all imprinting groups with a Kruskal Wallis H-test. All *p* values are two-tailed.

Results

Mate Choice Tests with Males

In the group 'mother adorned', four of the males tested were from the same clutch, there were three pairs of brothers, and the remaining two males came from different clutches. We found no significant difference between intra- and inter-clutch variation regarding a preference for adorned females (one-factor ANOVA, $df = 5$, $F = 0.4$, $p = 0.831$). Thus, we combined the data for all 12 males. These males courted in front of an adorned female significantly more often than in front of an unadorned female (binomial test, $p = 0.039$; Fig. 2).

In the group 'parents adorned', only two males were from the same clutch.

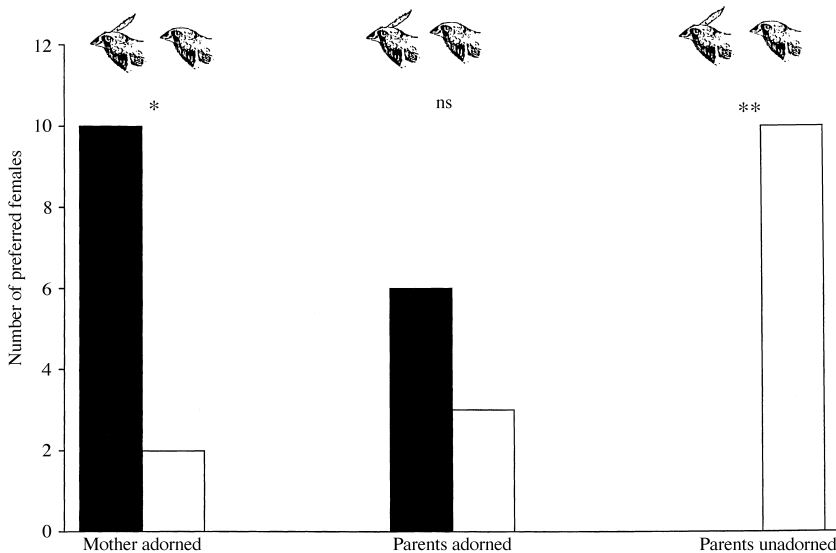


Fig. 2: The effect of parental adornment on male mate choice, measured as the number of preferred females that were adorned (solid bars) and unadorned (open bars), in tests where males could choose between adorned and unadorned females. Males of the group 'mother adorned' significantly preferred adorned females over unadorned females. Males of the group 'parents adorned' did not discriminate between adorned and unadorned females. Males of the group 'parents unadorned' significantly preferred unadorned females over adorned females. ** $p < 0.01$; * $p < 0.05$; ns, not significant

Males of this group showed no significant preference for adorned females (binomial test, $p = 0.5$; Fig. 2), although six out of nine males courted in front of adorned females more often than in front of unadorned females. For the group ‘unadorned parents’ raised in an aviary we did not know which test males were relatives and which were not. Males raised by ‘unadorned parents’ significantly preferred unadorned females over adorned females (binomial test, $p = 0.002$). When we compared the mate preferences of males raised by ‘unadorned parents’ with mate preferences of males raised by at least one adorned parent, we found that the latter preferred adorned females significantly more often (Fisher’s exact test, ‘mother adorned’, $p < 0.001$; ‘parents adorned’, $p = 0.006$, after Bonferroni correction). Thus, we can conclude that males of the two imprinting groups were sexually imprinted on females with a red feather.

Mate Choice Tests with Females

In the group ‘mother adorned’, only two of nine females were from the same clutch. Females of this group spent significantly more time in front of adorned males than in front of unadorned ones (Wilcoxon matched pairs test, $n = 9$, $z = -2.66$, $p = 0.008$; Fig. 3). In the group ‘parents adorned’ we had two clutches with

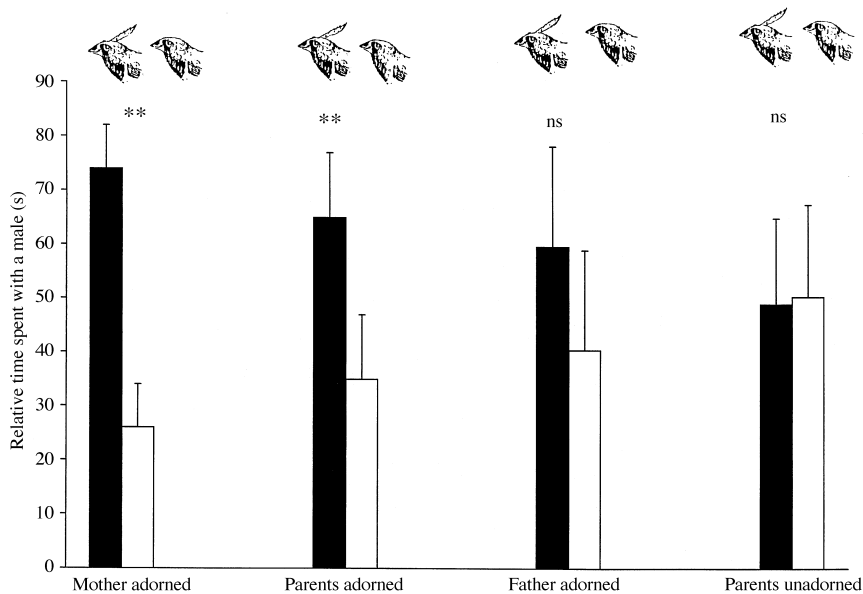


Fig. 3: The effect of parental adornment on female mate choice, measured as the relative time ($\bar{x} + \text{SD}$) spent by females in front of each male in a test (adorned males, solid bars; unadorned males, open bars). Females of the group ‘mother adorned’ significantly preferred adorned males. Females of the group ‘parents adorned’ significantly preferred adorned males. Females of the group ‘father adorned’ and ‘parents unadorned’ did not prefer adorned males. ** $p < 0.01$; ns, not significant

three females each, one clutch with two females, and six females from different clutches. The inter-clutch variation did not significantly differ from the intra-clutch variation (one-factor ANOVA, $df = 8$, $F = 1.35$, $p = 0.385$). Thus we combined data for all 14 females. Females of the group 'parents adorned' also spent significantly more time with adorned males (Wilcoxon matched pairs test, $n = 14$, $z = -2.789$, $p = 0.004$; Fig. 3). Females of the group 'father adorned' showed no significant preference for adorned or unadorned males (Wilcoxon matched pairs test, $n = 5$ [from four different clutches], $z = -1.21$, $p = 0.23$; Fig. 3). Females of the group 'parents unadorned' showed no preference for adorned males or unadorned males (Wilcoxon matched pairs test, $n = 13$, $z = -0.25$, $p = 0.81$; Fig. 3). For this group we did not know the number of clutches from which the birds were derived. Females of the group 'both parents adorned' and females of the group 'mother adorned' did not differ significantly in their preference for adorned males (Fisher's exact test, $p = 0.253$). When we compared the female mate choice of the imprinting groups with at least one adorned parent with the mate choice of females raised by unadorned parents, we found that females of the groups 'mother adorned' and 'parents adorned' preferred adorned males significantly more often than females raised by unadorned parents (Fisher's exact test, $p = 0.012$, after Bonferroni correction). Thus, we conclude that females of those imprinting groups were sexually imprinted on the red feather. We could not reject the null hypothesis that females of the group 'father adorned' did not differ in mate choice from the females raised by 'unadorned parents' (Fisher's exact test, $p = 1.0$). It seems that females of the group 'father adorned' were not imprinted on the red feather, or were imprinted in a less obvious way than females of the other groups. However, the sample size is very small and the findings should be interpreted with caution.

Females of different imprinting groups significantly differed in the strength of preference for adorned males (Kruskal Wallis H-test, $\chi^2 = 14.23$, $df = 3$, $p < 0.05$ after Bonferroni correction; Sokal & Rohlf 1995; Fig. 4). Females of the group 'mother adorned' showed the strongest mate preference for adorned males.

Discussion

Methodological Problems

We realize that there are a number of weaknesses in our experimental design that could potentially weaken our conclusions. We are convinced, however, that these flaws do not influence the validity of our results in any important way.

The offspring of imprinting groups with at least one adorned parent were raised in cages whereas offspring of the fourth group 'unadorned parents' were raised in an aviary. However, we believe that the different rearing conditions did not greatly influence our results. A previous study in Javanese Mannikins (Witte 1995) indicated that differences in rearing conditions (aviary or cage) have no detectable influence on mate preferences. In this study, Witte investigated whether the red feather had any effect on reproductive success in males. She performed

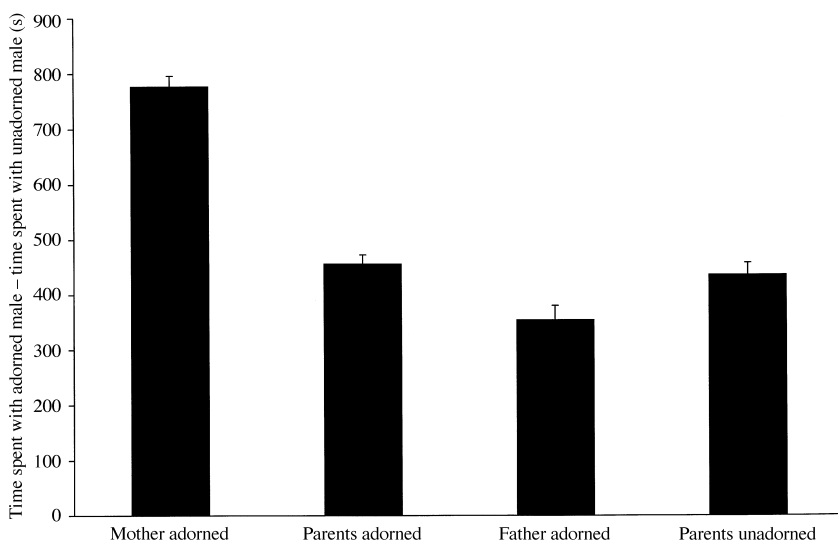


Fig. 4: Strength of female mate preference as measured by the difference in time ($\bar{x} + \text{SE}$) spent with the adorned male and the unadorned male in tests. Females of the group 'mother adorned' discriminated most strongly between an adorned and an unadorned male

mate choice tests in an aviary. Each group consisted of eight males and four females. Females could choose between males and reproduce with them. Four males were adorned with the red feather. This aviary experiment was performed with six different groups. Additionally, two control experiments with unadorned males only were performed. All offspring stayed together with parents and other adults until the age of 60 d. Daughters of adorned fathers and unadorned mothers in these aviary experiments and daughters of unadorned parents of the control experiment were tested for a preference for adorned males or unadorned males in double-choice tests. Daughters ($n = 11$, from 10 different clutches) of adorned fathers preferred significantly more often adorned males than daughters ($n = 13$, from eight different clutches) of unadorned fathers which had no experience with adorned males before tests (χ^2 test: $\chi^2 = 2.81$, $df = 1$, $p_1 = 0.045$). This showed that, in an aviary situation, females became imprinted on a novel adornment, although they had also seen other unadorned males. Additionally, a comparison of the two studies, in which females were raised by an adorned father in an aviary (Witte 1995) or raised by an adorned father in cages (this study), showed that there was no influence of different rearing conditions on female mate preference [Mann Whitney U-test: $n(\text{this study}) = 5$, $m(\text{Witte 1995}) = 11$, $z = -0.51$, $p = 0.6$]. This again indicates that different rearing conditions have no detectable influence on later mate preferences. Unfortunately, we have no evidence that rearing in an aviary or a cage environment has no influence on mate preferences in males, but we are confident that the rearing conditions have a very weak influence, if any.

In mate choice tests, only one of two stimulus birds was adorned with the red feather and therefore manipulated. It is possible that the manipulation changed the behaviour of the bearer in such a way that it became more attractive to males. In a previous study Witte & Curio (1999) tested whether the manipulation itself could have an effect on female behaviour. They manipulated unadorned females in the same way as females adorned with the red feather. They put a piece of double-sided tape on the head of the female and covered it with the tip of a brown tail feather from another female. When males raised by unadorned parents in an aviary were allowed to choose between a female with a red feather and a female with the brown tape on the head, they preferred females with the brown head. Apparently, the manipulation itself had no influence on male mate choice. Additionally, the bearer cannot see the feather and therefore does not know what is on its head.

As test birds we used birds of the same clutch within an experimental group and treated the response of siblings to stimulus birds as independent data. A particular adorned parent may be attractive because of the red feather, but also because of another independent trait that it happens to have. Offspring may learn to associate this trait with the feather and therefore develop a preference for adorned mates. Thus, the response of siblings to adorned mates may not be independent. We found, however, that the intra-clutch variation did not differ significantly from the inter-clutch variation in response to adorned mates. Thus, we believe that the responses of siblings in tests can be treated as largely independent. It would have been better to use just one individual from each clutch in order to avoid pseudo-replication.

Discussion of Results

Our results demonstrate that male and female Javanese Mannikins raised by at least one adorned parent showed a significantly stronger preference for adorned conspecifics of the opposite sex than males and females raised by unadorned parents with no experience of the red feather. We conclude, therefore, that males and females became sexually imprinted on the red feather. Males of the groups 'mother adorned' and 'parents unadorned' preferred females which resembled their mother. In Javanese Mannikins the male initiates courtship display in front of a female. Thus, it is important for a male to distinguish between the sexes before courting. Weary et al. (1993) proposed a mechanism by which, during the course of sexual imprinting, discriminative associative learning enables the bird to discriminate between the sexes. Here, for a male the mother could act as a positive stimulus and the father as a negative stimulus. This mechanism could explain our findings in the male mate choice tests. For males of the group 'mother adorned' the adorned mother might have served as a positive stimulus while the unadorned father might have served as a negative stimulus. Thus, males of this group showed a strong preference for adorned females, which resembled their mother. In the group 'parents adorned' the adorned mother also served as a positive stimulus and

the adorned father as a negative stimulus. As an outcome of exposure to both stimuli, however, males of this group merely showed a non-significant tendency to prefer adorned females. One would expect males raised by an adorned father and an unadorned mother to prefer unadorned females as did males raised by unadorned parents. Unfortunately, we had no sons of an adorned father and an unadorned mother to test. It is possible that Javanese Mannikin males learn to recognize the sexes by sexual imprinting. We cannot conclude from our results that males learn to recognize gender during sexual imprinting because we could not test males of the group 'father adorned'. There is, however, an indication of how males of the group 'father adorned' would have responded to adorned and unadorned females. In another study, Hörster et al. (unpubl. data) investigated sexual imprinting on a red bill in the Javanese Mannikin. Males raised by a father with a red bill and a mother with a normal-coloured bill significantly preferred females with a normal-coloured bill over females with a red bill. If we can extrapolate from this result to our study we would expect males raised by a father adorned with the red feather and an unadorned mother to prefer unadorned females. An alternative would be that males just learn to recognize the more conspicuous sex.

There are some indications from other studies (on the zebra finch *Taeniopygia guttata*, Vos 1994; the great tit *Parus major*, Slagsvold 1993; the pied flycatcher *Ficedula hypoleuca*, Sætre & Slagsvold 1992) that males learn to recognize sexes during imprinting. In the dimorphic zebra finch, many imprinting experiments have been performed using both the normal morph and the white morph as parents. These experiments have shown that zebra finch males learn to recognize the sexes by sexual imprinting (Immelmann 1975; Vos 1994). Moreover, males raised by mixed morph pairs developed not only a mate preference for females resembling their mother, but also a sexual dislike for females resembling their father (Vos et al. 1993). Males of the group 'unadorned parents' rejected all adorned females in the test. We think that it is extremely unlikely that this strong rejection was due to rearing in an aviary. It is more likely that lack of experience with adorned parents led to this rejection of adorned females.

In female mate choice tests we found that females of the groups 'mother adorned' and 'parents adorned' preferred males bearing the red feather. These males, however, resembled the mother's type. This shows that the mechanism of discriminative associative learning, with a father serving as a positive stimulus and a mother serving as a negative stimulus, cannot explain female preferences. Females raised by 'adorned fathers' did not discriminate between adorned and unadorned males. The sample size is too small for interpretation, however. In another experiment, Witte (1995) tested Javanese Mannikin females ($n = 11$) that were raised by a male adorned with the red feather and a normal female in mate choice tests with adorned and unadorned males and compared these tests with tests performed with females raised by unadorned parents. Females raised by an adorned father and unadorned mother showed a tendency to prefer adorned males more than females raised by unadorned parents (Fisher's exact test, $p = 0.06$; Witte 1995). This result and the comparison of all imprinting groups suggests that females became attracted to the red feather independently of which sex bore the ornament. It seems that

females did not learn sex recognition in combination with the red feather during imprinting. In the zebra finch, Weisman et al. (1994) found that females preferred males with the same bill colour as their father's to males with the bill colour of their mother. However, this preference was unstable and was only found on the first day of testing. When zebra finch females were raised by parents representing the white and the normal morph, females preferred males which resembled their mother's type (Vos 1995). This is similar to our findings in the Javanese Mannikin females, since females raised by an adorned mother preferred males with the mother's trait.

Females of the group 'parents unadorned' did not significantly reject adorned males, although they had no experience with adorned males before the test. Witte & Curio (1999) investigated the female response to Javanese Mannikin males with a red feather as a novel adornment. They found that some females rejected males with the novel adornment, although they had preferred those males before manipulation, and some females preferred males with the novel adornment, although they had rejected these males before manipulation. This means that the novel adornment interacted with the natural attractiveness of males. Naturally attractive males lost in attractiveness when adorned with the red feather, and naturally unattractive males gained in attractiveness when adorned. This interaction could explain our result. Because some males lost and some males gained in attractiveness due to the red feather, we found no difference in response to adorned and unadorned males.

Females of the group 'mother adorned' showed the strongest preference for adorned males among the imprinting groups. The reason for this may be that females of this group had already seen both 'morphs' whereas females of the group 'parents adorned' and 'parents unadorned' had seen only one type. Females of the group 'father adorned' had seen the two types as well, but the sample size is too small to allow interpretation of the result. Early experience with both 'morphs' may increase the ability to discriminate between unadorned and adorned mates.

In summary, our study shows that males and females raised by one adorned or two adorned parents showed a stronger preference for adorned conspecifics of the opposite sex than birds raised by unadorned parents. Thus, both sexes became sexually imprinted on the new type, but in different ways. Males might have learned the novel adornment in relation to sex or just in relation to the more conspicuous parent. Females, however, learned the novel adornment independent of the sex of the parent. Sexual imprinting on a novel adornment is possible and might support the spread of a novel trait within a population in both sexes. Sexual imprinting might be a mechanism for the evolution of a monomorphic species without any ornamental traits into a species with conspicuous traits in both sexes.

Acknowledgements

We thank H.-J. Bischof, T. Meijer, and three anonymous reviewers for helpful comments on the manuscript. KW was supported by the Deutsche Forschungsgemeinschaft (WI-1531/1).

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Received: December 10, 1998

Initial acceptance: September 4, 1999

Final acceptance: October 10, 1999 (R. Noë)