Sexes of a monomorphic species differ in preference for mates with a novel trait

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We investigated the different roles of the sexes in the origination of novel traits in the sexually monomorphic Javanese mannikin *Lonchura leucogastroides*. We introduced a red feather as an evolutionarily novel trait in both sexes and tested their preferences for prospective mates with this trait. Males rejected females bearing the red feather and preferred to court unadorned females. In contrast, females partly preferred adorned males. Specifically, previously unattractive males gained in attractiveness and could increase their reproductive success when bearing the ornament, whereas previously attractive males lost in attractiveness, but this did not affect their reproductive success. We introduced two other novel traits in males and investigated the females' response to these in mate choice tests. Each of the three new traits interacted with the natural attractiveness of males. The more attractive a male was before ornamentation, the more it lost in attractiveness after ornamentation and vice versa. Thus, the position of the trait did not affect the interaction. Because males rejected adorned females and females partly preferred adorned males, novel traits might evolve by intersexual selection in males rather than in females. This can lead to a sexual dimorphism with conspicuous traits in males. Our study reveals a new insight into the mechanism of the evolution from monomorphism to dimorphism with ornamental traits in males. *Key words:* female mate choice, male mate choice, novel traits, origination of sexual dimorphism. *[Behav Ecol 10:15–21 (1999)]*

Theories of intersexual selection predict that one sex generates selection on the opposite sex (Andersson, 1994). In many species females invest more energy, resources, and time in the offspring and are therefore the choosy sex (Trivers, 1972). Females often choose males on the basis of secondary sexual male traits and prefer the male bearing the most elaborate trait (Andersson, 1994). Experimental studies have shown that females prefer males with artificially exaggerated traits to males with traits within the natural range of variation (Andersson, 1982; Andersson, 1992; Petrie et al., 1991). This indicates that females may be a major force in the elaboration of existing male traits.

In species in which males provide a substantial amount of parental care to the young, males are expected to exercise mate choice as well (Trivers, 1972). Several studies in biparental species have shown that males discriminate between females and that they base their mate choice on display traits in females (e.g., Hill, 1993; Johnson, 1988; Wynn and Price, 1993). Therefore, male mate choice can lead to conspicuous traits in females. In the crested auklet *Aethia cristatella* both males and females based their mate preference on the same trait in the opposite sex (Jones and Hunter, 1993). This shows that in biparental species, both sexes may generate selection on morphological traits in the opposite sex. This selection pressure can lead to maintenance or elaboration of already existing traits.

However, the origin of ornamental traits is still poorly understood. What happens when a novel trait appears in a population? How do indivduals respond to a novel trait in prospective mates? Do the sexes differ in their response to such mates? To examine these questions we used a sexually monomorphic species lacking any conspicuous ornamental traits as a model for the ancestral form of an ornamented species and introduced an evolutionarily novel trait to both sexes.

For this study we used a monomorphic, socially monogamous estrildid finch with biparental care, the Javanese mannikin *Lonchura leucogastroides*. Both sexes bear drab plumage with only black, brown, and white feathers. Males provide 50% of parental care (Witte K, personal observation) and should therefore exercise mate choice. In both sexes we introduced a red feather standing upright like a crest as an evolutionarily novel and highly conspicuous trait. The entire extant family of estrildid finches lacks crests, and genera closely related to the Javanese mannikin are similarly colored (Goodwin, 1982; Wolters, 1979–1982). Additionally, the Ploceidae, the sister family of Estrildidae, lacks crests as well, with one exception. The males of the crested malimbe *Malimbus malimbicus* have short feathers on the head, which protrude slightly from the neck (Serle et al., 1977). Therefore, it is likely that the red feather is an evolutionarily novel trait in the Javanese mannikin. Additionally, we introduced two other novel traits in males, two red stripes under the tail and a red bill, and tested these traits in female mate-choice tests.

METHODS

Study species

Our birds were bred in captivity. We kept the birds in large aviaries (3.0 m × 1.6 m × 2.5 m) in mixed gender groups on 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 white cloth from other aviaries. Each bird had a unique combination of black and white commercial leg bands, which were cut into three thin rings before banding. Because colors of leg bands have a strong effect on mate choice in zebra finches (Burley et al., 1982), we used only colors which occur in the plumage and used thin rings to minimize any effect of banding on mate choice. To determine the sex of individuals we observed the birds repeatedly. In the Javanese mannikin only males sing courtship and undirected song (Goodwin, 1982). Birds were identified as males when we observed them singing. A bird was identified as a female if three different males showed courtship display to the same bird and if we had never seen that bird singing.

Test and stimulus birds were selected from different aviar-

ies, so that test birds had not been exposed to stimulus birds before testing. All test and stimulus birds had previous breeding experience and were at least 12 months old.

Ornamentation
We adorned birds with one of three different kinds of red ornaments: a feather on the forehead, two stripes under the tail, or a red bill. The 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 bird's forehead with double-sided tape so that it stood upright like a crest. The feather was easily removed without damaging the plumage. For decorating the tail we used two pieces of red tape cut the size of the outermost tail feathers and attached them under the tail. The stripes could be removed from the tail without disarrangement of tail feathers. We painted the bill red with vermilion "Pelican" watercolor paint. Like the unmanipulated birds, none of the artificial ornaments reflected ultraviolet light (Witte, 1995).

The adorned birds were allowed to get accustomed to the novel trait at least for 17 h before test, though they showed normal behavior after 2 h. The adorned birds did not appear to exhibit comfort behavior (like cleaning the plumage) more frequently than the unadorned birds and did not fly around more than unadorned birds.

Female mate choice

We performed female mate-choice tests in cages and measured the attractiveness of males before and after ornamentation with the novel trait. In two control experiments we tested for consistency in female mate choice and order effect. Additionally, we measured the reproductive success of males before and after ornamentation.

General methods
Two cages containing males were placed side by side. A female cage was placed centrally in front of both male cages. 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 intermediate-height perches parallel to the sides of the cage (=perches of choice) 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 screens beside and behind excluded any other visual stimuli. For familiarization, all birds were kept in test cages for at least 1 day before testing in visual but not in acoustic isolation. Before the test began the female's cage was hidden behind another screen in front of the male cages. Immediately after removing this screen, tests started and lasted 40 min, with a break after 20 min, switching the males' cages to control for side preference in females. A 15-cm wide baffle attached at 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. During tests, singing and courtship rates in males and tail quivering in females as well as the positions of the three birds were recorded every 5 s in instantaneous sampling. The attractiveness of males was measured as the time (second) the female spent perching in a very restricted area: on the first third of the perches of choice adjacent to the males when facing one of 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 cages but below the perches, as it was not clear if she was interested in the male or only in food. When females changed perches within an interval, it was scored as 2.5 s, otherwise as 5 s. Tests were

performed daily from 0900 h to 1700 h, with a break from 1200 h to 1400 h, when most birds were inactive. Between tests, birds were kept in unisexual groups. For each experiment we used new naive test individual females and males.

We tested the effect of three different new ornaments in males on female mate preferences. Before testing, all test females had seen another, nontest male adorned with a novel trait used in the test, and so they were allowed to habituate to such a new male type. None of the females was frightened by the adorned, nontest male.

Red feather: most attractive versus least attractive male
To investigate whether the highly conspicuous red feather has any effect on female mate choice, we first adorned only the most attractive and the least attractive male for each female. We used 11 females and 5 males. To determine the most attractive and least attractive male for each female, we tested each possible male pair combination in front of each female. The most attractive male was that male with whom the female spent on average the most time in all tests. The least attractive male was that male with whom the female spent on average the least time in all tests. After this, we placed the red feather on the forehead of the most attractive male and tested him against all other males. We did the same with the least attractive male. The order of tests with the adorned, most attractive and the adorned, least attractive males was randomized. We compared the new attractiveness of each most and least attractive male when bearing the red feather with their natural attractiveness before ornamentation in the same male pair combinations.

Red feather: males of all degrees of attractiveness
In another experiment we investigated the effect of the red feather in general by adorning males of all degrees of natural attractiveness. We tested new individual females ($n = 11$) in front of pairs of new males ($n = 6$). Each female was tested twice in front of the same pair of males. In the first test both males were unadorned, in the second test one randomly chosen male was adorned with the red feather. We compared the natural attractiveness with the new attractiveness of each adorned male.

Red stripes under the tail
The red stripes were a semicryptic novel trait in males. Females could only see the stripes when males were sitting on a higher perch than the female and facing the female, or on the opposite perch of choice when facing the female, or when male and female were next to each other but the female had bent down to see the stripes. We tested 14 females in front of 14 pairs of males ($n = 14$ males). Each male was used in two trials with different partners and was used as an adorned male only once. Each female was tested twice in front of the same pair of males. In the first test both males were unadorned; in the second test one randomly chosen male was adorned with the red stripes under the tail. We compared the natural attractiveness with the new attractiveness of each adorned male.

Red bill
A red bill is very common within the estrildid family but is lacking in close relatives of the Javanese mannikin. Thus, we considered a red bill a heterospecific trait in males. Ten females were allowed to choose first between two males with normally colored bills ($n = 10$ pairs of males). In the second test a randomly chosen male was given a red bill. We compared the time the female spent with a male when his bill was red and when it was naturally colored.

Control for order effect

In the experiments described above, females were allowed to choose between two unadorned males, first followed by tests of the same males, and then as one adorned and one unadorned male. In this experiment, we tested whether our previous results were due to an order effect. We reversed the order and gave a female a choice between an adorned and unadorned male first and in the second test between the same two unadorned males. As an ornamentation we painted the bill red and used new individual females ($n = 12$) and males ($n = 12$ pairs of males).

Control for consistency

To test whether a change in attractiveness in males is due to inconsistency in female mate choice, we tested females ($n = 10$) twice in front of each pair of males ($n = 10$ pairs of males), but this time without adding a novel trait and without any manipulation in between and measured the repeatability, r (Lessells and Boag, 1987), of time females spent in front of a male. We compared this r value with the repeatability of female time spent with males before and after ornamentation in the red bill experiment ($n = 10$ females, $n = 10$ pairs of males). This experiment served as a control for all female mate-choice tests with adorned males.

Red feather: reproductive success

To investigate whether the red feather had any effect on the reproductive success of males, we performed mate choice tests in an aviary (2.1 m × 1.6 m × 2 m). The aviary was visually but not acoustically isolated from other aviaries. It contained food, water, and sand ad libitum, 10 nest-boxes, and plenty of coconut fibers as nest building material. Over the period 1991–1995, we used 32 females and 64 males in 6 experimental and 2 control experiments, each lasting about 6 months. The birds within each group had not been housed together before testing. In each group four females could choose between eight males and breed with them. We defined unmated males as unattractive and mated males as attractive. We measured the reproductive success of each male as the number of offspring in his nest. We defined that male as the father of a brood, as the one that copulated most often with the mother of the brood during her fertile period. We observed the birds with binoculars (8 × 21 mm) 3 h per day between 1000 h and 1200 h and between 0330 h and 0430 h, when most copulations take place (Witte K, personal observation). Birkhead and Møller (1992) found that, in birds, the more a male copulates with a female, the higher the probability of his paternity.

After a pair has formed, both sexes contribute to nest building, with the female mostly in the nest and the male carrying material to the nest. When the nest is finished the female lays two to six eggs. Both sexes incubate the eggs for about 14 days. Once hatched, the young fledge after 21 days and are dependent on parental feeding for a further 16 days. After the offspring are independent of their parents, we removed them from the group and separated the adult males from the adult females for 3 weeks. We then placed a red feather on two attractive (=mated) males and two unattractive (=unmated) males and released the same females back into the same group of males. We observed the groups daily and again measured the reproductive success of the same males.

The two control groups tested whether the separation from the partner for 3 weeks could cause changes in bonding. We performed two controls, in which four females could choose between eight males. After a separation of 3 weeks we placed all birds together in the same aviary but without any ornamentation of males.

Male mate choice

Red feather: experiment

Previous experiments have shown that males do not show a mate preference when given a choice between two females in cages (Witte K, unpublished data). Therefore, we performed the male mate-choice experiments in an aviary (2 m × 1.1 m × 2.5 m), which contained food, water, and sand ad libitum, several nest-boxes, natural branches, and coconut fibers 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 acclimation, and two females were kept together in a cage visually isolated from the aviary. One of the females was adorned with a red feather on the forehead; the other female remained unadorned. The adorned females were allowed to get accustomed to the feather, and the unadorned female in the cage was also allowed to habituate to the new female type during the 17 h before tests. Before testing, all test males had seen another, nontest female adorned with a red feather; thus they were habituated to such a new female type. None of the males was frightened by the adorned nontest female (Witte, K, personal observation).

We performed tests between 1000 h and 1200 h, with one test per day. Tests began immediately after simultaneously releasing both females into the aviary and lasted 1 h. During tests we measured the number and duration (seconds) of courtship displays by the male to each female. Each male was tested once, and each female pair was tested twice, but the second time with another male. We tested 14 males and used 14 females.

Red feather: control

As a control we tested whether the manipulation itself could have an effect on female behavior, which could influence male mate-choice decisions. Here the unadorned females were manipulated in the same way as the adorned females. We put a piece of double-side tape of the same size as used for the adorned females on their heads and covered the white tape with a tip of a tail feather from other females not being used in these experiments. All other conditions were the same as in the experiment. We tested six males and used six different pairs of females with one female adorned with the red feather and the other female with the brown cover on her head.

Analysis

In female mate-choice tests we used the Wilcoxon matched pairs test to test for a change in time a female spent in front of the same male with and without the novel trait and to test for a change in the total time a female spent in front of both males in two tests. With a Fisher's Exact test we investigated the change in solicitation display of females in front of adorned males. We used a linear regression to test whether the ornamentation had the same effect on previously unattractive and previously attractive males. To test for an interaction between the natural attractiveness of males and ornamentation, we used a repeated-measures ANOVA, with attractiveness as a between-male and ornamentation as a within-male factor. For this test, we divided the males into attractive and unattractive groups and compared their attractiveness before and after ornamentation. In male mate-choice tests we used the Wilcoxon matched pairs test to investigate which type of female the males preferred to court. All p values are two tailed.

RESULTS

Female mate choice

Red feather: most attractive versus least attractive males

The red feather resulted in a significant change in attractiveness in the most and least attractive males. Females spent sig-
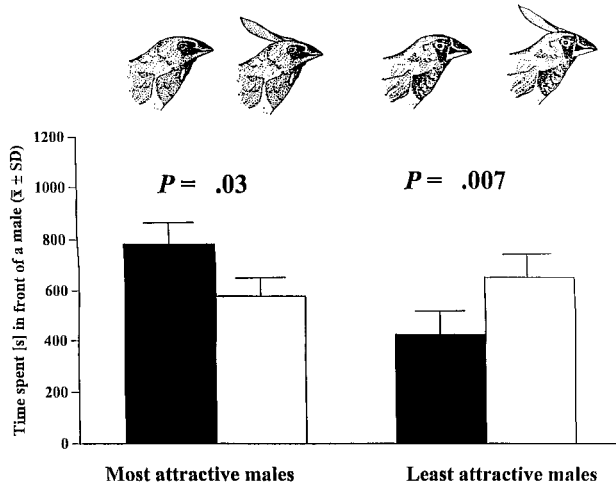
Figure 1
Change in attractiveness of most attractive and least attractive males before and after ornamentation with a red feather. Attractive males lost in attractiveness; unattractive males gained in attractiveness.

nificantly less time with most attractive males when bearing the red feather (Figure 1; $n = 11$ females, $z = -2.13$, $p = .03$). However, the same females spent significantly more time with the unattractive male when bearing the red feather (Figure 1; $n = 11$ females, $z = -2.66$, $p = .007$). The total time a female spent in front of both males did not change after ornamentation of one male ($n = 11$, $z = -0.53$, $p = .55$). Females spent on average 1523.4 ± 288 s with two unadorned males and on average 1643.2 ± 215 s with one adorned and one unadorned male. The singing rate did not differ before and after ornamentation in either more attractive or less attractive males, but previously unattractive males showed courtship display to the female significantly more often when adorned (Wilcoxon matched-pairs test: $n = 5$ males, $p = .01$). This probably results from the increased time females spent in front of them, rather than due to self-recognition, because a male is only able to court a female after she has decided to sit in front of him. Additionally, males could not see the red feather on their head and saw no other male with this ornament. So it would not seem that the red feather could have affected the males' assessment of himself directly.

Females performed solicitation display by tail quivering in front of most attractive males before ornamentation but not after ornamentation. In front of the previously least attractive males, however, females tended to perform tail quivering more often when males were adorned (Fisher's Exact test: $n = 11$, $p = .0571$). This suggests that females were indeed sexually motivated during tests and reacted differently to most attractive and least attractive males after ornamentation with the red feather.

Red feather: males of all degrees of attractiveness
In the experiment with adorned males of all degrees of attractiveness, we found a significantly negative relationship between the natural attractiveness of males and the change in attractiveness (after minus before ornamentation; Figure 2a; linear regression: $F_{1,9} = 15.97$, $n = 11$, $p = .003$, $y = -1.0x + 716$). The more attractive a male was before ornamentation, the more he lost in attractiveness after ornamentation. The less attractive a male was without the red feather, the more he gained in attractiveness when bearing the red feather. The repeated-measures ANOVA showed a significant interaction between natural attractiveness and the change in attractiveness in males ($F_{2,9} = 14.59$, $p = .004$; Table 1). Females
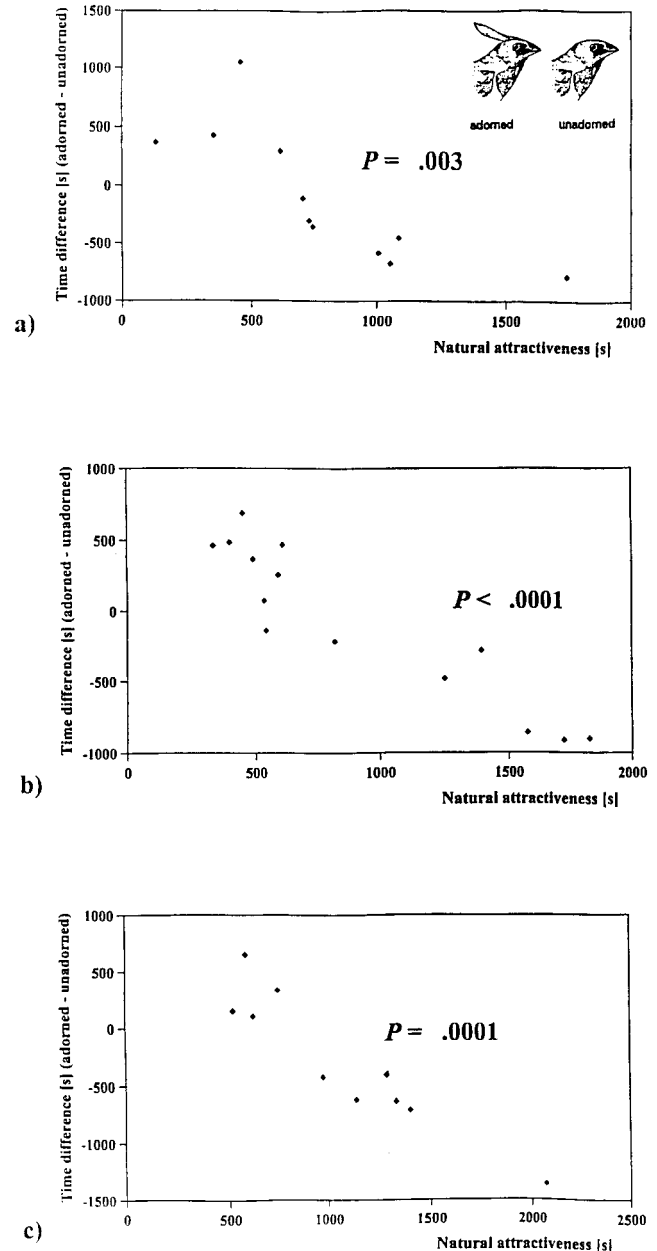

Figure 2
(a) Males of all degrees of attractiveness: negative relationship between the natural attractiveness of males and the change in attractiveness before and after ornamentation with a red feather. (b) Negative relationship between the natural attractiveness of males and the change in attractiveness before and after ornamentation with red stripes. (c) Negative relationship between the natural attractiveness of males and the change in attractiveness before and after ornamentation with a red bill.

spent on average 1732.5 ± 512 s with two unadorned males and on average 1689 ± 488 s with one adorned and one unadorned male. Thus the total time spent did not change due to manipulation ($n = 11$, $z = -0.43$, $p = .68$).

Red stripes under the tail
When males were adorned with the semicryptic red stripes under the tail, females often bent down to see the stripes when males sat on a perch at the same height as the females. We found a similar significantly negative relationship between

Table 1
Repeated-measures ANOVA of change in male attractiveness due to ornamentation with a novel trait, measured as the time a female spent with a male when he was adorned and unadorned

Trait		Source	df	Mean	F	p
Red feather	Between subjects	Attractiveness	1	217,818.330	1.60	.238
		Error	9	136,256.30		
	Within subjects	Ornamentation	1	107,929.70	1.58	.24
		Attractiveness*ornamentation	1	996,075.15	14.59	.004
		Error	9	68,249.35		
Red stripes	Between subjects	Attractiveness	1	1,423,356.00	20.25	.001
		Error	12	70,303.89		
	Within subject	Ornamentation	1	35,571.57	0.43	.523
		Attractiveness*ornamentation	1	1,040,657.30	12.66	.004
		Error	12	82,228.89		
Red bill	Between subjects	Attractiveness	1	456,775.31	7.46	.026
		Error	8	61,265.16		
	Within subjects	Ornamentation	1	418,327.81	5.88	.041
		Attractiveness*ornamentation	1	1,038,540.30	14.61	.005
		Error	8	71,084.84		

the natural attractiveness of males and the change in attractiveness as we found in the experiment with the red feather (Figure 2b; linear regression: $F_{1,12} = 77.7$; $n = 14$, $p < .0001$, $y = -0.9x + 796$). Additionally, the change in attractiveness depended on the natural attractiveness of males (repeated-measures ANOVA: $F_{2,12} = 12.66$, $p = .004$; Table 1). The total time a female spent with both males in a test did not change between tests ($n = 14$, $z = -0.56$, $p = .57$). Females spent on average 1567.4 ± 554 s with both unadorned males and on average 1635.3 ± 347 s with one adorned and one unadorned male.

Red bill
When the male's bill was painted red, we again found a significantly negative relationship between the natural attractiveness of males and the change in attractiveness (Figure 2c; linear regression: $F_{1,8} = 54.08$; $n = 10$; $p = .0001$; $y = -0.9x + 949$). As before, the red bill interacted significantly with the natural attractiveness of males (repeated-measures ANOVA: $F_{2,8} = 14.61$, $p = .005$; Table 1). Females spent on average 1723.8 ± 412 s with both males before ornamentation and on average 1490.3 ± 361 s with both males after ornamentation ($n = 10$, $z = -1.78$, $p = .08$).

Control for experimental order
In all experiments with adorned males, females chose first between two unadorned males, and second between one adorned and one unadorned male. We always found a significantly negative relationship between the natural attractiveness of males and the change in attractiveness, regardless of which trait was used. It could be that this relationship was due to an order effect in our experiments. If so, we would expect a positive relationship upon reversing the order of the test. However, when females chose first between a male with a red bill and a male with a natural bill and a second time between two unadorned males, we also found a significantly negative relationship between the natural attractiveness of a male and the change in attractiveness (red bill minus natural bill; linear regression: $F_{1,10} = 5.17$; $n = 12$; $p = .04$; $y = -0.6x + 788$). This result suggests that there was no order effect in our experiments. Again, females spent on average a similar amount of time with both males with (1819.13 ± 425 s) and without (1911.8 ± 352 s) ornamentation ($n = 12$, $z = -0.62$, $p = .53$).

Control for consistency
When females chose between the same pair of unadorned males twice without any manipulation in between, the repeatability was high ($r = .95$). Thus, females were consistent in their choice, and the change in time a female spent with the same male in the experiments with adorned males was likely not due to inconsistency in female mate choice. As a comparison, in the red bill experiment the repeatability was .17.

Red feather: reproductive success
Attractive males had 31 offspring before ornamentation and 26 offspring after ornamentation (Figure 3; $z = -1.47$, $p = .14$). Thus, we could detect no effect of the red feather on the reproductive success of attractive males. Unattractive birds were by definition unmated and had no offspring before ornamentation. With the ornament, however, 6 out of 12 unattractive males mated with a female and had in total 10 offspring (Figure 3; $z = -2.2$, $n = 12$, $p = .02$). In the control experiment all previously mated birds rebonded with the same partner after the separation. Therefore, the separation itself did not cause any changes in pair bonding.

Male mate choice

Red feather: experiment
Almost all males initiated courtship display with females after we released the females in the aviary. All males ($n = 14$) showed a clear preference for females without the red feather: males courted more often in front of unadorned females (Figure 4a; $z = -3.06$, $p = .002$) and on average for a longer period of time in front of unadorned females (Figure 4b; $z = -3.06$, $p = .002$). One adorned female showed tail quivering as a solicitation display to the male in both tests she was used in, and both males copulated with her. The copulation indicates that males recognized the adorned females as a conspecific female and that females showed the complete sexual behavior to stimulate a male.

Red feather: control
In the red feather control experiment, all six males courted only in front of the females with the brown tape on the head ($n = 6$ males, $z = -2.23$, $p = .03$). Thus, the rejection of females bearing the red feather was even stronger than in the first experiment. This result suggests that the mechanics of manipulation itself had no effect on male mate choice. In
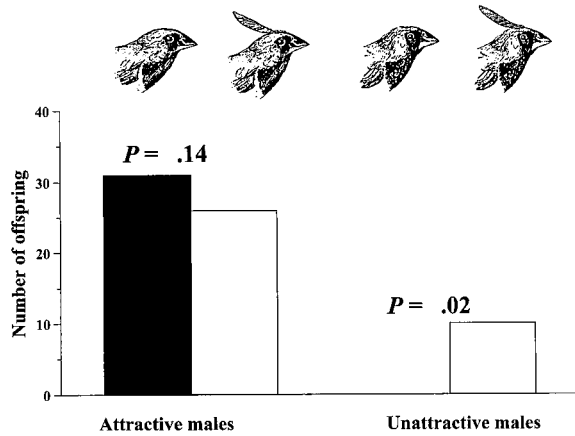
Figure 3
Number of offspring of attractive and unattractive males before and after ornamentation with a red feather.

summary, males preferred to court unadorned females and therefore rejected females bearing a red feather on the head.

DISCUSSION

Our results demonstrate that male and female Javanese mannikins differ in their responses to prospective mates adorned with an evolutionarily novel trait, a red feather on the head. Males rejected adorned females and courted in front of unadorned females more often than in front of adorned females. Javanese mannikin females, however, partly preferred males adorned with the red feather. Previously unattractive males gained in attractiveness and could increase their reproductive success when adorned with the red feather. Previously attractive males lost in attractiveness when bearing the red feather. But this loss in attractiveness did not affect their reproductive success. In the monomorphic double-bar finch (*Poephilia bichenovii*), Burley (1986a) tested the response of males and females to conspecifics with blue leg bands, red leg bands, and unbanded individuals. Males and females rejected red-banded conspecifics of the opposite sex and preferred blue-banded individuals. The blue bands might amplify the blue bill of the double-bar finch. In an experiment cited by Trivers (1985), Burley adorned males of the dimorphic zebra finch *Taeniopygia guttata* with a feather of different colors on the head. A male with a white "hat" was more attractive to females than a "hatless" male. However, no quantitative data are available. In contrast to our study, zebra finch plumage naturally contains white color, and the zebra finch is a dimorphic species.

Burley et al. (1982) extensively investigated the effect of colored leg bands in the zebra finch. They found that red-banded males were most attractive to females. Males preferred black-banded females. Both sexes avoided conspecifics with blue and green leg bands. Red leg bands may reinforce the red bill in males, and the black leg band may reinforce the black vertical eye-stripe in the female's face. In addition, males with red leg bands and females with black leg bands had a much higher reproductive success than individuals with other leg band colors (Burley, 1986c). The color of leg bands even affected the sex ratio of offspring, with a bias toward the gender of the more attractive parent when one of them was rendered attractive (Burley, 1981, 1986b). Thus, in the zebra finch males and females preferred different color leg bands in the opposite sex. This is not surprising because the zebra finch is a sexually dimorphic species, and selection on mate preferences based on sex-specific traits has been acting for a
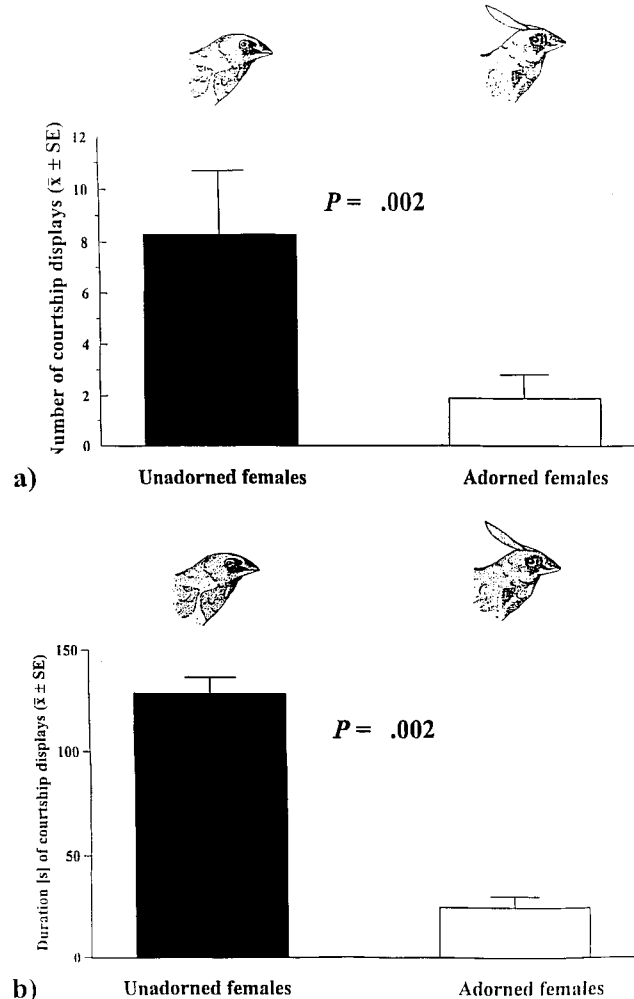

Figure 4
Male mate choice tests: (a) number of courtship displays of males to unadorned and adorned females. Males showed significantly more courtship displays to unadorned females. (b) Average (±SE) time (seconds) males spent courting in front of unadorned and adorned females. Males courted significantly longer in front of unadorned females.

long time. In our sexually monomorphic estrildid finch, it is unlikely that selection has acted on mate preferences based on different morphological traits in both sexes. It is therefore surprising that the sexes differed in their preferences for the same novel trait.

We found that the natural attractiveness of males interacted with the new ornamentation. The more attractive a male was before ornamentation, the more he lost in attractiveness after ornamentation and vice versa. This was true for all three different kinds of novel traits we introduced in males. Thus, the position of the trait did not affect the interaction. This interaction has not been documented and results in new predictions for the evolution of novel traits in males. Although this interaction is described here for the first time, our study is not the only one showing an interaction between natural attractiveness and a manipulation. In a reanalysis (Witte and Lubjuhn, submitted) of a study by Burley (1986a), an interaction was found between the natural attractiveness of zebra finch males and the change in attractiveness with red leg bands. In contrast to Burley's interpretation that red leg bands always increase the attractiveness of males, our reanalysis

showed that red leg bands increased or decreased the attractiveness of males depending on their natural attractiveness. In a study of facial attractiveness in humans and asymmetry, Swaddle and Cuthill (1995) found that previously unattractive faces became more attractive after being changed into more symmetrical faces, but previously attractive faces became less attractive when being changed to more symmetrical. Therefore, the interaction between the natural attractiveness and any manipulation may be a general phenomenon and should be taken into account when manipulating already existing traits or introducing novel traits regarding mate choice. A possible mechanism for this interaction might be that females possess an imaginary representation of an attractive male and compare this representation with real males. Attractive males resemble this representation. Adding any kind of trait would lower the resemblance and therefore lower their attractiveness. Unattractive males are dissimilar to this inner representation and can gain in attractiveness by adding a novel, conspicuous trait.

When a novel trait appears in a population of a monomorphic species, two scenarios are possible. Both sexes could prefer the novel trait in the opposite sex. This would lead to a more conspicuous but still monomorphic species, as in the case of the crested auklet *Aethia cristatella* (Jones and Hunter, 1993). Or the sexes could differ in their responses, which might lead to a dimorphic species with a novel trait in only one sex, or the same trait expressed to different degrees in both sexes. Our results show that in the Javanese mannikin, males and females play counteracting roles in the evolution of novel traits. Males rejected females adorned with a novel trait, but females partly preferred males with the same novel trait. This might lead to a dimorphic species with a conspicuous trait in males only. It would still be possible that the novel trait would be expressed in females as well, because of genetic correlation between male and female traits (Halliday and Arnold, 1987; Lande, 1980). However, these adorned females would have no chance to reproduce.

Our results show that the sexes of this monomorphic species differ in their preference for mates with a novel trait. This offers a new insight into the mechanism of the evolution from a monomorphic species to a dimorphic species with ornamental traits in males.

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