

Time spent with a male is a good indicator of mate preference in female zebra finches

KLAUDIA WITTE

Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Morgenbreede 45, 33615 Bielefeld, Germany (E-mail: Klaudia.Witte@uni-bielefeld.de)

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The time a female spends in front of a male is a commonly assumed but rarely tested measure of female mate preference in mate choice experiments. I investigated whether the mate preference in zebra finch females *Taeniopygia guttata castanotis* measured as the number of solicitations directed towards a male was related to the time females spent with that male. In a binary choice situation within an aviary, females were allowed to fly freely and visit two individually caged males over a whole day. I measured the females' solicitation displays as the number of tail quivering and/or presentations of nesting material. I also measured the time the females spent in front of each male. Females that solicited did so exclusively to one of the two males and when they did they spent almost twice as much time with that male than with the other. The time these females spent in front of a male correlated positively with the number of solicitation displays directed to that male. The study shows the first experimental link between mate preference measured by courtship displays and preference measured as the time a female spends with a male. Hence, time spent with a male, the most common measure of female mate preference in zebra finches choice experiments is a good indicator of female mate preference.

KEY WORDS: sexual selection, mate preference, mate choice experiment, female solicitation displays, zebra finches.

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INTRODUCTION

According to sexual selection theories, females in most species are the choosy sex because they invest more in reproductive effort than males (TRIVERS 1972). Therefore, female mate preference is a driving force in sexual selection and responsible for the evolution of ornamental traits in males of many species. The evolution and maintenance of female mate preference is still one of the central questions in sexual selection (JENNIONS & PETRIE 1997).

Female mate preference has been extensively investigated in many studies with the focus on different aspects of the phenomenon (overview in ANDERSSON 1994). In most experimental studies of female mate preference, the design is a binary choice situation in which the females have no physical contact with the stimulus males, and preference is determined by the time a female spends with a male. It is assumed that time is costly such that females should spend more time with the male they have chosen as a potential mate. The male with whom the female spends most time or more than some given threshold, is scored as the attractive male and hence the male with whom she would copulate.

Time spent (= the time a female spends in front of a male during a choice test), however, is only an indirect measure of the mate preference of females. For instance it could also be a measure of female sampling behaviour. Females often visit several males before deciding (JANETOS 1980, PARKER 1983, REAL 1990, GIBSON & LANGEN 1996). In the satin bowerbird, *Ptilonorhynchos violaceus*, for instance, females visit up to eight males before deciding (UY et al. 2001) and female great reed warblers, *Acrocephalus arundinaceus*, visit a median of six males before choosing a mate in the field (BENSCH & HASSELOQUIST 1992). This type of sampling behaviour is also noted in experimental binary choice situations. In fish, for instance, females often swim several times to both males presented in a test, while in birds they commonly hop several times back and forth on the perches in front of stimulus males. Thus, by measuring time spent it is often difficult to distinguish between sampling behaviour and the actual mating decision (WAGNER 1998).

A more direct and therefore more reliable measurement of female mate preference is to measure their sexual behaviour by quantifying their solicitation displays. Canary females *Serinus canaria*, for example, show a typical copulation solicitation display (CSD) in front of a loud speaker playing specific syllables of the male song, and they do not habituate to those syllables. Thus, the CSD is a valuable quantitative and direct measure of mate preference in canary females and is frequently used to investigate the function of different song types in canaries (VALLET et al. 1992, VALLET & KREUTZER 1995, LEITNER et al. 2001).

The zebra finch is one of the most commonly used bird in studies regarding female mate preference of male ornaments such as: chest plumage (SWADDLE & CUTHILL 1994), beak colour (BURLEY & COOPERSMITH 1987, HOUTMAN 1992, but see COLLINS & TEN CATE 1996, COLLINS et al. 1994, BLOUNT et al. 2003), artificial traits (BURLEY et al. 1982, BURLEY 1986, TYLER BURLEY & SYMANSKI 1998), display behaviour (COLLINS 1994), song (RIEBEL 2000) and sexual imprinting (IMMELMANN 1975, TEN CATE 1985, VOS 1995, WITTE & SAWKA 2003, WITTE & CASPERS 2006).

Solicitation displays in female zebra finches

Within the estrildid finches, females show tail quivering as a specific solicitation display towards a courting male (GOODWIN 1982). In the display the female bends its legs, lowers its body in a horizontally aligned position involving the beak, head, back and tail. She then moves the tail feathers very quickly up and down. Females can direct this tail quivering towards a male after he has started displaying to her, or they can sometimes initiate courtship by tail quivering before the male begins its own display courtship (MORRIS 1954, TEN CATE & MUG 1984, ZANN 1996, WITTE pers. observation). Female tail quivering clearly shows her willingness to copulate with the male and is, therefore, an unambiguous indicator of her mate preference.

Zebra finch females can also signal their mate preference by presenting nest building material to a male. I observed a female picking up a coconut fibre from the ground with the bill, flying to her preferred male and presenting the coconut fibre to him. The presentation was performed while the female exhibited tail quivering and after some time the female dropped the nest material. During this presentation the male courted the female intensively but because he was caged they could not copulate. This behaviour has been described by MORRIS (1954: 307) as nest building displacement: "The female flies up to the nest, which is half finished, and pulls at a protruding piece of straw. The male, who was feeding, immediately flies up and lands nearby. She fiddles with a piece of straw and begins to solicit. The male hops over and he too tugs at a piece of nest material. Then he begins to court. She stops displaying and appears to give all her attention to the straw in her beak, but then drops it and solicits again". Presenting nest material to a male is, therefore, a second direct indicator of the mate preference in females.

Most mate choice experiments with zebra finches use the time a female spends in front of a male to measure her mate preference. Only two studies have explored the use of female courtship displays but both of these involved females that were likely to have had unusually high levels of motivation for mating. One study was concerned with whether zebra finch females exhibited a mate preference bias for their own species (TEN CATE & MUG 1984). The authors measured the time a female spent with a male within a 40-min test and they also measured her number of tail quivering displays. They found that for females cross-fostered by Bengalese finches *Lonchura striata*, the time spent was not directly correlated to the number of tail quivering but for females raised by parents of their own species the time spent ratio (time spent near zebra finch male / time spent with both males) and tail quivering ratio (tail quivering in front of zebra finch males / tail quivering in front of both males) were correlated. However, females were kept isolated before testing for an unusually long period for zebra finches, a full 70 days, and so females could have been over stimulated by the test situation. In the second study the tail quivering of female zebra finches was measured while a loud speaker played male courtship songs (CLAYTON 1990). However these females had been treated with oestradiol before testing and so were unusually over stimulated by hormonal treatment. Because time spent is the most commonly used measure of mate preference in zebra finches, and because the only two studies that measured the association between time spent and sexual behaviour in zebra finch females involved unusual experimental conditions (TEN CATE & MUG 1984, CLAYTON 1990), it appears necessary to show that the time a female spends with a male indicates her proper mate preference under more normal conditions.

In the present study, therefore, I measured the non-manipulated sexual responses of zebra finch females to males without a prior isolation period or hormonal treatment and asked whether these were correlated to the time these females spent in front of the caged males.

METHODS

Study species

For each experiment, males and females were randomly selected from the stock population of Australian zebra finches of about 300 birds at the Department of Animal Behaviour, University of Bielefeld. Test birds were F_4 -descendants of wild caught Australian zebra finches and kept in several aviaries before the experiment. Males and females wore numbered orange coloured leg bands, a colour assumed to be neutral in mate choice in this species (BURLEY et al. 1982). The birds were separated by sex 2 months before the experiment began and were kept in distinct aviaries. The males and females used were sexually experienced, aged at least 18 months and had not seen each other before the experiment.

Female mate choice experiments in an aviary

Mate choice experiments were performed under natural light conditions and outdoor temperature between 27 April and 15 June 2004 on a terrace (5.90 m \times 15.30 m and 2.80 m high) covered by a clear plastic roof offering partial protection against rain and wind at the sides. The temperature varied between 5 and 19 °C (on average 9.9 °C) during the night and between 10 and 35 °C (average 23.1 °C) during the day. Experiments were performed in two side by side aviaries (1.85 m \times 1.85 m, 1.85 m high) 14 cm apart separated by a wooden wall. In each aviary, I fixed two male cages (60 cm \times 31 cm, 42 cm high) with a cable: one cage in the upper left corner and the other cage in the upper right corner in the back of the aviary (Fig. 1). The two male cages were 60 cm apart from each other and cloth covering the sides of each male's cage prevented them from seeing each other. Each male cage contained a wooden nest box (14.5 \times 14.5 \times 14.5 cm) with an entrance hole of 7 \times 12 cm and 12 g coconut fibres as nest material. In each cage, I provided food, water and sand *ad libitum* in small dishes. Food was a mixture of seeds containing Senegal, red, yellow and Canary millet. Each male cage had two perches fixed at height of 21 cm within the cage. The perches were 50 cm long and each protruded 19 cm from the male cage. Within each aviary, I fixed two natural branches, each 1 m long, at a height of 1.50 m above the floor in the forward part of the aviary, one fixed at the left and one at the right side of the aviary (Fig. 1). Food, water and sand were provided for the female in dishes on a small table (33 \times 50 cm, 60 cm high). Additionally, I provided 12 g coconut fibres on the floor.

A mate choice experiment consisted of three observation periods per day and measurements took place between 10.30 a.m. and 11.30 a.m., 2 p.m. and 3 p.m., and 4 p.m. and 4.30 p.m. Males were released into the cages at 10 a.m. before starting the experiment. Females were released into the aviary shortly before starting the experiment. I conducted two experiments simultaneously. At a position of 2 m from the aviaries I could easily observe all six birds simultaneously and recorded the position of females and the behaviour of males and females at 10 sec sampling intervals. For females, I recorded whether they showed tail quivering or presented coconut fibres to a male within a 10 sec sampling interval. A choice was scored for a male when the female perched on one of the perches sticking out of its cage or hung on the mesh at the front side of the male cage. Other positions of the female were scored as no-choice positions. Perch time was scored as 10 sec when a female did not change her position within a 10 sec sampling interval, otherwise it was scored as 5 sec. Within a

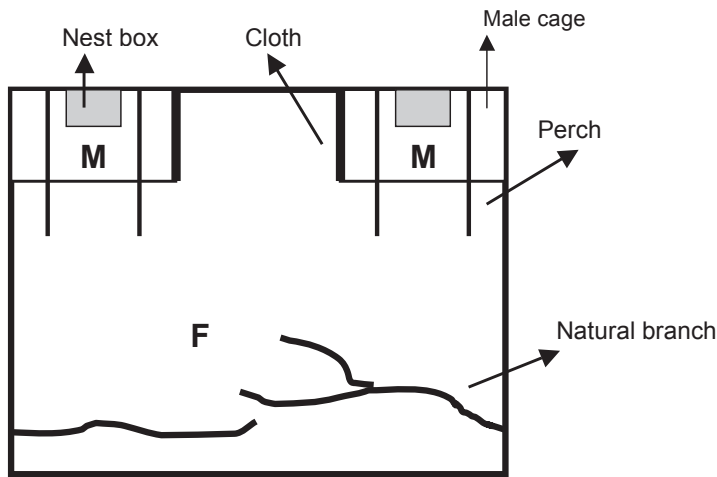


Fig. 1. — Top view of the aviary. A female could choose between two males, each in separate cages. The females were provided with 12 g coconut fibres, food, water and sand ad libitum. They could perch on two natural branches (no choice position) or on the perches protruding from the male cages (choice position). Each male had a nest box, coconut fibres and food, water and sand ad libitum. The sexual behaviour of females (tail quivering, presenting coconut fibres to males) and males (courtship displays toward females) were measured within each 10 sec sampling interval. Additionally, the time a female spent in front of each male was recorded. In the figure, M = male, F = female.

sampling interval, I recorded whether males sang a non-directed song, i.e. a song not directed to the female, or showed courtship display including song directed to the female. After the experiment, I weighted the males and females and measured their tarsus and wing length. After these experiments, the birds were kept in the laboratory for other experiments.

In the experiments, the males ($N = 62$) were generally used twice, but paired with a different male on the second presentation, although four males were used only once. Females ($N = 58$) were used only once in the mate choice experiments.

Data analysis

A male was scored as sexually preferred by a female when she showed tail quivering in front of him and/or presented a coconut fibre to him. A male was scored as preferred when the female did not show any solicitation displays but spent more time with that male than with the other male in the test. A male was scored as non-preferred when the female spent less time with him and never showed tail quivering and/or presented a coconut fibre towards him in a test. I compared the number of sampling intervals with tail quivering and/or presentation of coconut fibres to males within a test using a paired *t*-test. I compared the absolute and relative time a female spent in front of a sexually preferred male with the time she spent in front of the non-preferred male within a test by using a Wilcoxon signed-ranks test. Additionally, I correlated the time females spent in front of sexually preferred males with the number of sampling intervals with tail quivering and/or presentation of nest material using a Spearman rank correlation. With an ANOVA, I calculated the repeatability (after LESSELS & BOAG 1987) as a measure of the consistency in female absolute time spent in front of a sexually preferred or a preferred male over the 2.5 hr test period separated into five 30 min-test periods. I used a Mann Whitney U-test to compare morphological traits in males. Unless otherwise stated values presented in the text are mean \pm SD.

RESULTS

Female mate preference

The females exhibited a clear preference for one of the two males presented in the test. They spent on average $71.05 \pm 16.22\%$ (68.94 ± 23.80 min) of their time with the sexually preferred or preferred male and only $28.94 \pm 16.2\%$ (27.31 ± 17.5 min) of their time with the non-preferred male (Wilcoxon signed-ranks test: $Z = -6.027$, $N = 58$, $P < 0.001$).

Thirteen females showed tail quivering and/or presented a coconut fibre to one of the two males in an experiment. Females showed tail quivering up to 10 times within an experiment, but always exclusively to one of the two males (Paired t test: $t_{12} = 4.9$, $P < 0.001$). Four of 13 females presented coconut fibres to one of the two males in a test and showed tail quivering in front of that same male. Seven of 13 females showed only tail quivering to one of the two males (Paired t test: $t_{12} = 2.94$, $P < 0.012$), and two females presented coconut fibres, without showing tail quivering, to one of the two males in a test. Additionally, another female picked up a coconut fibre, flew to one of the branches and then let it fall. The females spent almost twice as much time in front of the sexually preferred male, on average 63.40 ± 26.53 min as in front of the non-preferred male, on average 36.68 ± 21 min (Wilcoxon signed-ranks test: $Z = -1.99$, $N = 13$, $P = 0.046$). When comparing the relative time a female spent in front of males, females spent $62.56 \pm 20.2\%$ of their time in front of the sexually preferred males and only $37.43 \pm 20.2\%$ of the time in front of non-preferred males (Wilcoxon signed-ranks test: $Z = -2.04$, $N = 13$, $P = 0.039$, Fig. 2). The time these females spent in front of sexually preferred males correlated positively with the number of sampling intervals with tail quivering and/or presenting nest material (Spearman rank correlation: $r = 0.572$, $N = 13$, $P = 0.041$).

Consistency in female mate choice

When comparing the absolute time females spent in front of sexually preferred males during the 2.5 hr experimental period, females were quite consistent in the amount of time that they spent perching in front of the same male in the five 30 min-test periods. The repeatability was 0.46 (ANOVA: $F_{12;52} = 5.37$, $P < 0.001$). Thus females were quite consistent in their time spent in front of the same sexually preferred male over the day. This was also true for the other females that showed no tail quivering and that did not present nest material to a male, although the repeatability was lower with $r = 0.24$ (ANOVA: $F_{45;52} = 2.60$, $P < 0.001$).

Male behaviour and morphology

Males that were sexually preferred by females showed courtship displays including songs directed to the female in a significantly higher number of sampling intervals (24.36 ± 7.98) than did the non-preferred males (11.50 ± 9.42) (Wilcoxon signed-ranks test, $Z = -2.76$, $N = 13$, $P = 0.006$). Both males in the tests showed a similar level of activity in singing songs undirected to the female. Undirected songs by sexually preferred males were emitted in 19.93 ± 33.02 sampling intervals while the non-

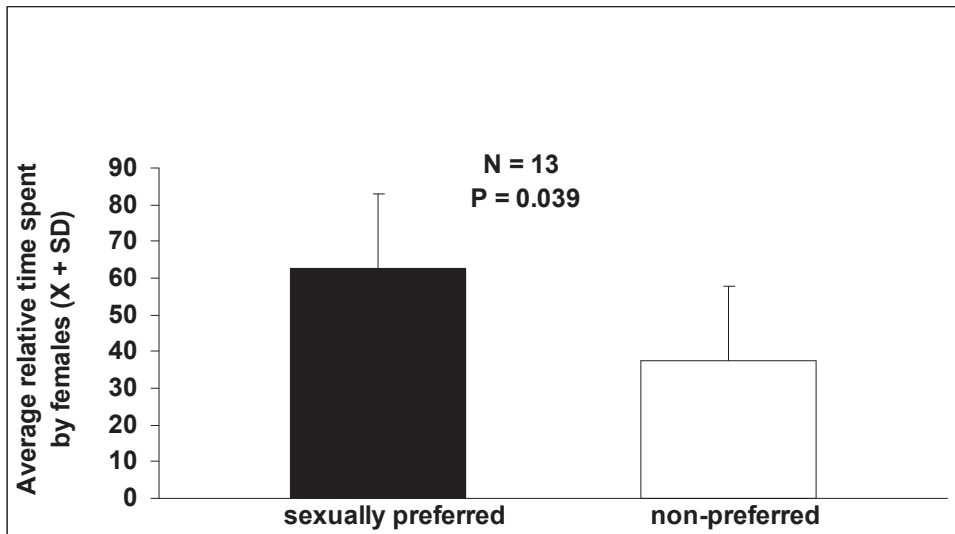


Fig. 2. — The results of the mate choice experiment shown as the average relative time spent by females in front of sexually preferred males and in front of non-preferred males. A sexually preferred male is defined as a male in front of whom the female has shown tail quivering and/or presentation of coconut fibres. A non-preferred male is defined as a male in front of whom the female has not shown solicitation displays within the same test.

directed songs of non-preferred male companions were emitted within 21.5 ± 16.93 sampling intervals (Wilcoxon signed-ranks test: $Z = -1.33$, $N = 13$, $P = 0.18$).

When analysing the behaviour of males in tests that did not involve solicitation by females, the preferred males (i.e. males in front of whom females spent more time during a test) showed on average significantly more courtship displays to females (20.16 ± 17.19) than non-preferred male companions (7.89 ± 9.83) (Wilcoxon signed-ranks test: $Z = -3.97$, $N = 45$, $P < 0.001$). There was no significant difference in the number of non-directed songs (Wilcoxon signed-ranks test: $Z = -1.51$, $N = 45$, $P = 0.13$) as preferred males emitted non-directed songs in 18.49 ± 23.73 sampling intervals and non-preferred males did so in 24.69 ± 27.34 sampling intervals.

Attractive males, whether based on solicitation or time spent, did not differ from unattractive males in wing length or tarsus length (Mann Whitney U-test: wing length $Z = -0.832$, $N = 58$, $P = 0.405$, tarsus length $Z = 0.861$, $P = 0.389$, respectively). Females weakly preferred heavier males skipp (Mann Whitney U-test: $Z = 1.805$, $N = 58$, $P = 0.071$).

DISCUSSION

This study shows that the time a zebra finch female spends in front of a caged male is a reliable indicator of her mate preference for that male. The proportion (13 out of 58) of females showing solicitation displays in this aviary experiment is impressive given that the test females were not treated with either hormones nor

long periods of isolation before testing. Without any such manipulation zebra finch females rarely show sexual behaviour in a mate choice situation (Vos 1995). When females can fly freely within an aviary and visit caged males, many females showed tail quivering that allowed me to demonstrate that under more natural conditions, the time spent in front of a male's cage can be a reliable measurement of female zebra finch mate preference.

Females that solicited in front of males spent almost twice as much time with that male than with the other male in the test. Test females that exhibited solicitation displays showed this behaviour exclusively in front of only one of the two males within an experiment. These females showed tail quivering and/or presented coconut fibres to a specific male. Presenting nest material as a female solicitation display has been described by MORRIS (1954) but it has never been used as an indicator of mate preference in zebra finches females. For future mate choice experiments, I suggest that females are provided with nest material in order to give them the opportunity to exhibit this sexual behaviour which can be used as a valuable indicator of their mate preference.

In the present experiment, females could choose between two males over a day. To test whether females choose consistently over a day, I divided the total observation time of 2.5 hr into five 30 min periods. When comparing the mate choice decisions of all females across those five 30 min periods, there was no difference in time spent with the sexually preferred or preferred male between the five test periods. Thus, females chose consistently over the day. That also means that the first 30 min period represents the same mate choice decision as that recorded after a day. Thus, a day long test period can be shortened to 30 min without losing information regarding mate choice.

Sexually preferred males showed on average significantly more courtship displays to females than non-preferred males. Both males in a test showed a similar amount of activity in singing undirected songs. The same was true for preferred males and their non-preferred male companion. However, the fact that attractive males showed more courtship displays towards a female is more the consequence than the cause of female mate preference. In the test situation, a male could only court a female after the female had decided to perch in front of him. Thus, the number of courtship displays in males reflects the female mate preference (COLLINS 1994).

Another approach to investigate female mate preference is to measure pair formation between males and females, or to allow and observe with whom the female copulates. This has been done in previous studies (e.g. SILCOX & EVANS 1982, CLAYTON 1990). SILCOX & EVANS (1982) investigated pair formation in the zebra finch. They kept two females and two males within a cage and observed social contact, body contact, courtship behaviour in males during pair formation. CLAYTON (1990) allowed zebra finch females to choose between males in an aviary. These experiments are of course important, however, they have three disadvantages. First, it depends on the question in focus whether it is appropriate to allow the female physical access to a male because this offers an opportunity to copulate with the male. Second, in an aviary there is male-male competition and female-female competition for mates, and sometime male-male competition overrides the outcome of female choice. In the Javanese Mannikin, *Lonchura leucogastroides*, WITTE (unpublished data) investigated the influence of male-male competition on female mate choice in three situations. First, females ($N = 8$) were allowed to choose between two males, each in a separate cage (no male-male competition, for details see WITTE & CURIO 1999, WITTE et al. 2000). Second, the same females could choose between

the same two males in an aviary for a day (allowing male-male competition). Only two of eight females chose the same male as in the cage experiment. Males were aggressive to each other and chased the other away. In a third experiment, the dominant male was kept in a cage within the aviary and the female and the subordinate male could fly freely within the aviary (male-male competition excluded). In this situation, five of eight females chose the same male as in the previous cage experiment. Thus, male-male competition can mask female mate choice in this species.

A third disadvantage of aviary experiments is that in a biparental species it is likely that males are also choosy (HILL 1993, WYNN & PRICE 1993, JONES et al. 2001). Thus, male mate choice can be a confounding factor when investigating female mate preferences in an aviary in which all birds have physical access to each other.

The present study provides experimental evidence that time spent is a reliable indicator of mate preference in zebra finch females and validates time spent as the most commonly used measure for female mate preference in previous and future mate choice experiments with zebra finches.

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