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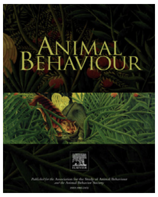

# Same-sex partner preference in adult male zebra finch offspring raised in the absence of maternal care

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An important component of mate choice is the sex of the potential partner, yet little is known about the factors that cause an individual to pair with the opposite sex. In the current study, we addressed the role of exposure to adult females during development in adult mate choice using a socially monogamous and biparental avian species, the zebra finch, *Taeniopygia guttata*. In our experimental set-up, zebra finch offspring were either raised in the presence of adult males and females in their aviaries (control) or in the absence of all adult females including their mothers (female-deprived). The female-deprived subjects were raised successfully by the male parents and showed no growth deficits compared to controls. When we tested partner preference of control and female-deprived subjects as adults, 57% of males that had been raised without females paired with each other. In contrast, 76% of male offspring that were raised with adults of both sexes paired with females. The most likely interpretation of this dramatic effect on pairing outcome is imprinting on adult males in the aviary in the absence of all adult females. These results thus suggest that sexual imprinting or some other form of social learning is a key developmental process for sexual partner preference in addition to preference for species and individual characteristics.
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The choice of a mate is critical in species that are socially or genetically monogamous and biparental and form long-term pair bonds, as an individual's fitness depends, in part, on the quality or characteristics of the mate (Black & Hulme, 1996). Previous studies have shown that birds accrue information about their conspecifics during a sensitive period early in development. These acquired preferences are then consolidated as the birds reach reproductive maturity and guide their choice of mates. This phenomenon is known as sexual imprinting (Bischof & Rollenhagen, 1999; Immelmann, 1972; Kruijt, 1985).

Sexual imprinting is often studied by cross-fostering offspring of one species to another, and has been shown to be important for the formation of partner preferences in pigeons, doves, ducks, geese, galliform birds and estrildid finches as well as other vertebrate species (Immelmann, 1975; ten Cate & Vos, 1999). Both sexes have been shown to choose mates based on sexual imprinting with the parent or parents as important models (sources of cues for imprinting). It was initially thought that in dimorphic species with solely maternal care, such as ducks, only the male offspring would imprint on the parent (the mother) with respect to future mating, in contrast to monomorphic biparental birds such as geese, where both sexes of offspring would be subject to sexual imprinting. This hypothesis was not supported, however, and instead both sexes are guided by learned cues from the single parent, although not necessarily by the same cues (ten Cate & Vos, 1999). In the wild, cross-fostering of offspring between two species of tits, the blue tit, *Cyanistes caeruleus* and the great tit, *Parus major*, resulted in heterospecific pairing between them (Slagsvold, Hansen, Johannessen, & Lifjeld, 2002). In fish, mate choice in female adult guppies is influenced by the phenotype of the male with which they are raised during development, as females that are raised with colourful males have higher choice scores for colourful males in mate choice tests (Breden, Novinger, & Schubert, 1995). Even an invertebrate (a wolf spider) has been shown to base mating preference on prior exposure to and memory for conspecifics (Hebets, 2003). In humans too, there is evidence for opposite-sex imprinting between sons and their mothers, based on facial similarities between female partners and mothers of the male subjects (Marcinkowska & Rantala, 2012). One study has demonstrated that women who were adopted chose partners who resembled their adoptive fathers, suggesting that they may have imprinted on their adopted fathers' physical features (Wiszewska, Pawlowski, & Boothroyd, 2007). Moreover, when the subjects rated their early relations with their fathers highly, there was a strong positive relationship

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between facial proportions of their fathers' faces and facial proportions of faces they found attractive (Wiszewska et al., 2007).

In socially monogamous and biparental zebra finches, *Taeniopygia guttata*, which form pair bonds for life, there are two stages of sexual imprinting. During the acquisition phase, which occurs during the first 40 days posthatching, specific partner preferences are formed by zebra finch offspring based on features of their parents. During the consolidation phase, which extends from day 60 to adulthood, acquired preferences are cemented by exposure to adult birds (Bischof, 2003; Bischof & Clayton, 1991; Kruijt & Meeuwissen, 1991; Oetting, Prove, & Bischof, 1995). Within species, preferences for conspecifics and specific colour morphs have been shown to result from sexual imprinting (Immelmann, 1969; Vos, Prijs, & Tencate, 1993; Witte & Caspers, 2006).

In addition to species and colour morph recognition, it is also critical that birds recognize and prefer individuals of the opposite sex as mates (sexual partner preference). Little is known about how socially monogamous animals, including socially monogamous birds, learn to prefer individuals of the opposite sex within their own species. Sexual partner preference is particularly interesting with social monogamy, because the pair has a close social relationship that goes far beyond simply mating. Most of what is known about the development of sexual partner preference in socially monogamous species comes from studies of zebra finches (Adkins-Regan, 2002). These studies have demonstrated that both hormones and early social environment influence the development of sexual partner preference in this species. Females treated with oestradiol benzoate during the first 2 weeks after hatching preferred to pair with other females, but only if they had been housed in all-female aviaries as juveniles, suggesting that sexual partner preference was masculinized by oestradiol treatment in combination with some kind of social experiential effect (Adkins-Regan, 2002; Mansukhani, Adkins-Regan, & Yang, 1996).

A role of early parental environment was seen when zebra finches were raised without adult males in the aviaries (by removing those males when the chicks were still in the nest). Both sexes raised without adult males failed to show as pronounced a sexual partner preference as the controls (Adkins-Regan & Krakauer, 2000). This effect was relatively modest (38% of males and 25% of females raised without fathers paired with same-sex partners, compared with 13% of control males and 0% of control females), was equivalent in magnitude in the two sexes and was only statistically significant if both sexes were combined.

The effect of uniparental rearing by males alone (by removing adult females) has not been determined before. We hypothesized that if sexual imprinting and the learning of mate choice are facilitated by observing and interacting with adult conspecifics, female-deprivation during development should alter mate choice of zebra finch offspring. Here we addressed the role played by exposure to adult females during early development in adult pairing preference by removing all adult females from breeding aviaries when chicks were 2–12 days old.

## METHODS

### *Breeding Colonies, Female Deprivation, Manipulation and Subsequent Housing*

Male and female zebra finches that were raised in the laboratory in the same colony and had prior breeding experience were allowed to pair in aviaries. Each breeding aviary (0.94 × 0.76 × 0.94 m) was divided into two halves. In one half, both male and female birds raised their young (control offspring), whereas in the other half, male birds raised the young alone (female-deprived offspring). Adult females were removed from this half of the aviary when the chicks were between 2 and 12 days old. All the eggs in the aviaries hatched within 10 days of each other. The age range of the chicks at removal occurred because zebra finches show asynchronous hatching within clutches. The youngest chicks had to be 2 days old before removing the females, and the first-hatched chicks in a few of those nests were 10 days older. Subsequently, the adult males raised the fledglings to independence when the offspring were 45–55 days of age. Chicks did not need and were not provided with supplemental crop feeding. Although the female-deprived offspring had no tactile contact with adult females after the manipulation, they had visual and auditory contact with adult females in the adjacent half of the aviary, once they fledged. Three such breeding cycles were carried out successively with different breeding pairs for each cycle to generate adequate numbers of male and female offspring ($N = 24$ control females, $N = 24$ female deprived females, $N = 21$ control males, $N = 21$ female-deprived males). At 45–55 days posthatching, the offspring from both groups were moved into unisex aviaries. At this age, zebra finches are no longer dependent on their parents for food and can be sexed based on their plumage coloration (Zann, 1996). The unisex male and female aviaries were in the same room and therefore birds could see and hear individuals of the opposite sex. Subjects of control and female-deprived groups were not mixed prior to mate choice tests at adulthood. All animal procedures conformed to Federal and State regulations and were approved by the Institutional Animal Care and Use Committee of Cornell University.

### *Offspring Growth*

Offspring were weighed, and tarsus length was measured, every 5–7 days from hatching until they were at least 40 days old, to determine any differences between groups. In addition, the number of mortalities was noted in both groups. Few chicks died (control = 4, female-deprived = 3).

### *Behavioural Tests*

Zebra finches reach reproductive maturity between 60 and 90 days (Zann, 1996). We performed partner preference and mate choice tests when the birds were at least 100 days of age. The tests lasted for 2 weeks, wherein days 1–5 were the early pairing phase and days 10–14 were the late pairing phase. The testing cages were aviaries (0.94 × 0.76 × 0.94 m) containing nestboxes and nest material. Each aviary contained a biased sex ratio of birds consisting of 2:1 males:females for male subjects and 2:1 females:males for female subjects. This was to ensure that subjects would have to compete for their preferred partners. Hence, if the treatment had simply affected the overall attractiveness of a bird, it would likely remain unpaired in these tests. Each testing aviary had either three control males, three female-deprived males and three stimulus females, or three control females, three female-deprived females and three stimulus males. Stimulus males and females were sexually experienced, unpaired birds that were unrelated to subjects.

#### *Behavioural observations*

We observed all birds for 15 min per day during the early (days 1–5) and late (days 10–14) pairing phases to confirm pairing status.

#### *Scoring behaviour*

During each observation period, an observer blind to the subject's treatment also scored five behaviours that have been established as indicators of courtship, aggression or pairing (Zann, 1996; see below) using a computerized event coder (Event Coder 1.0).

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