



Removal of adult males from the rearing environment increases preference for same-sex partners in the zebra finch

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The developmental processes producing preferences for opposite-sex mating partners are not well understood. Zebra finches, *Taeniopygia guttata*, are colonial and socially monogamous with biparental care. To determine whether the early social environment contributes to sexual partner preference, we removed adult males from breeding colonies when the oldest chicks were less than 1 week old (male-removal rearing) or left them in the breeding cage (control rearing). At independence, male-removal and control offspring were moved to unisex cages. As adults they were given two-choice tests with male versus female stimuli followed by group aviary tests. Male-removal subjects, unlike controls, did not prefer opposite-sex stimuli in the two-choice tests. Male-removal subjects were less likely than controls to successfully pair with opposite-sex birds in the group aviary tests; 38% of them paired with a same-sex bird. Thus early social experience may contribute to a critical component of mate choice, choosing the opposite sex, in this pair-bonding species.

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One of the most salient and robust features of mate choice is a preference for individuals of the opposite sex. While the adaptive significance of such a preference is obvious, the developmental processes that lead to such a preference are not at all obvious. For species that develop in a social context, early experience with conspecifics, including parents, siblings and other members of the social group, is a potential contributor to adult sexual partner preference (preference for mating or pairing with females versus males).

Experiments with a variety of species have shown that animals reared without normal social experience during development (for example, without mothers or in unisex social groups) may show deficits in sexual behaviour as adults when tested with opposite-sex stimuli (Larsson 1978; Leonard et al. 1993; Wallen 1996). There have been few attempts, however, to determine whether these or other manipulations of social experience alter an animal's sexual partner preference. Those few studies that have given subjects a choice of male versus female stimuli seem to be limited to species of mammals that do not form pair bonds (de Jonge et al. 1987; Slob et al. 1987; Matuszczyk & Larsson 1994; Perkins & Fitzgerald 1997).

Animals that are socially monogamous and pair for life raise particularly interesting questions about the processes that operate during development to yield opposite-sex pairs. Few choices are made in a lifetime and the first choice is made in young adulthood without benefit of prior breeding experience. Thus unless the incidence of extrapair parentage is high, lifetime reproductive success depends importantly on the initial choice; an error would be costly. Furthermore, the association between males and females is not limited to copulation or to the breeding season. Pairing for life occurs in a few invertebrates such as termites (Thorne 1997), a few mammals (Komers & Brotherton 1997), and a number of birds such as geese and swans (Black 1996).

The zebra finch, *Taeniopygia guttata*, like most estrildine finches, breeds colonially and exhibits social monogamy with obligate biparental care (obligate in the sense of universal within the species); pairs last until one of the partners dies (Immelmann 1967; Zann 1996). Paired birds in wild and captive colonies are readily identifiable, because they spend much time in physical proximity, including clumping together, preening each other (allo-preening), and spending time in a nest or nestbox together, activities that are seldom part of the social interactions of other dyads in the colony.

It has been well established in this species that social experience during development is critical for the singing of normal songs by males and for the normal adult preference for conspecific pairing partners. Males learn

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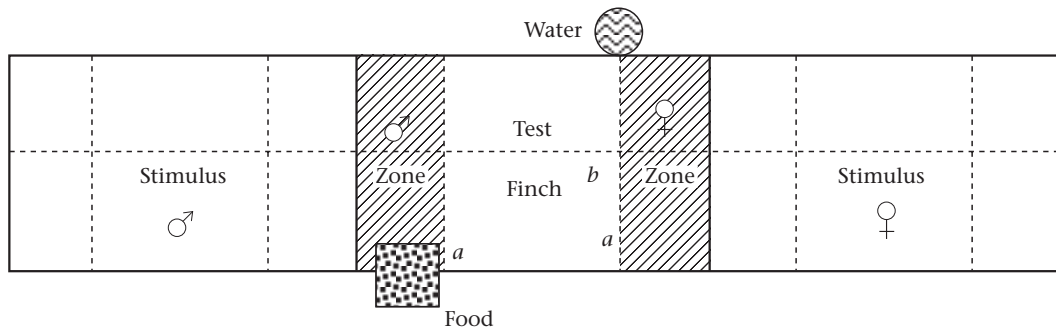


Figure 1. Design of the two-choice testing cages. Each compartment measured 61×36 cm and 41 cm high. The test subject was housed in the centre compartment. For testing, a male and female stimulus were introduced into the side compartments. Solid lines are hardware cloth; dotted lines are perches. Perches labelled *a* were 16 cm from the sides of the compartment and 11 cm from the floor; these defined the male- and female-stimulus proximity zones. Perch *b* was 21 cm from the front of the compartment and 31 cm from the floor. The stimulus compartments had the same perch configuration.

their song from their father and other adult males in the colony during the period between fledging and independence from the parents (Immelmann 1969; Böhner 1983; Slater et al. 1988; Williams 1990; Zann 1997). This process requires interaction or visual contact with the song tutor; simply hearing adult males in the same room is not sufficient for copying (Eales 1989). Both sexes acquire a preference for mates of their own species and subspecies through a process of sexual imprinting. In cross-fostering experiments, birds later choose partners of the same type as the parents that reared them (Immelmann 1972; Bischof 1994).

Zebra finches also learn to tell males from females in part through experience with the parents occurring prior to 65 days (Vos 1994). The ability to discriminate between the sexes, however, is necessary but not sufficient for a sexual partner preference to be expressed. Does social experience with parents and other adults contribute to the normal development of a heterosexual partner preference? We removed adult males from breeding colonies, thus eliminating opportunities for young birds to experience paternal care, interact with adult males, or see male–female pairs, opportunities that would be available to all wild zebra finches.

METHODS

Breeding Colonies and Rearing Manipulation

Adult breeders were obtained from local pet shops and from Canary Bird Farm, Elizabethtown, New Jersey. They were given supplements of greens and hard-boiled eggs. All juvenile and adult birds were given food and water ad libitum. All animal procedures were approved by the Cornell University Institutional Animal Care and Use Committee and met all applicable state and federal guidelines.

There were three breeding colonies, each consisting of six to seven pairs housed in a cage $1.8 \times 1.8 \times 1$ m. Breeding was synchronized by withholding nest material for several weeks and then supplying it to all cages on the same day. In two colonies, all adult males were removed

when the oldest nestlings in the cage were 5–7 days old. Fledging occurs at about 16 days. At 5–7 days eyes are still closed or only partially open, and thus nestlings have not yet had significant visual experience with other birds. Birds hatched and reared in these colonies will be referred to as male-removal subjects (or birds). Adult males were not removed from the third (control) colony. After the young were old enough to be removed (see below), the adult males were returned to the colony and a new breeding cycle was initiated as before. This process was repeated twice with the same cage assignments until all male-removal and control subjects had been generated.

Nestlings and Juveniles

Both male-removal and control nestlings were checked daily and crop fed with warm hard-boiled egg yolk if the crop was empty. At 10–14 days they were given plastic leg bands, avoiding colours that may influence attractiveness (Burley et al. 1982). At 40–45 days of age, when offspring normally become independent of parental feeding and can be sexed by plumage, they were transferred to unisex cages ($1.8 \times 1.8 \times 1$ m). These cages were in a room containing other birds but were separated from them and from each other by curtains. Thus they could hear but not see or contact birds of the opposite sex. Unisex housing at this age does not by itself alter sexual partner preference in either sex (Adkins-Regan et al. 1996).

Adults

Eight birds in each of the four groups (two sexes \times two rearing conditions) were tested. White birds were excluded. Birds were from 21 different clutches; the number of clutches per group ranged from five to seven.

At a minimum of 100 days, we transferred each subject to individual housing in the centre compartment of a three-compartment testing cage (Fig. 1). The other two compartments were empty, and the birds could hear but not see other birds in the room. Two weeks later, two-choice tests began.

Behavioural Testing

Two-choice tests

Birds were given one 15-min test at the same time of day for 5 consecutive days. For each test, we placed a stimulus male and female on opposite sides of the compartment housing the test subject. Birds used as stimuli were untreated birds that had been housed in unisex group cages that were different from those housing the test subjects and thus were unfamiliar to the subjects being tested. Different stimulus pairs were used each day for a given subject, and no stimulus was used more than once per day. The locations (left or right) of the male and female stimuli were reversed each day, with half the subjects beginning with the male on the left and half with the male on the right. In addition, the positions of the two stimuli were reversed halfway into the 15-min test. We recorded the total time that the subject's head was in the male and female proximity zones (see Fig. 1) with stopwatches. Proximity has been shown to be a valid measure of partner preference in this species (Clayton 1990; Houtman 1992). In addition, we recorded the number of song bouts given by male subjects while facing the male and female stimuli. A song bout is a period of continuous audible singing separated by at least 1 s from other singing. Directed singing by males predicts pair formation in free-choice settings and is widely used as one measure of partner preference in this species (ten Cate 1985).

Group aviary tests

Four subjects of the same sex (two controls and two male-removal subjects) were introduced together with five stimulus birds of each sex into an aviary ($1.8 \times 1.8 \times 1$ m) containing nestboxes and nest material and left there for 2 weeks. The stimulus birds were untreated birds that had been housed in different unisex cages from those housing the subjects, and thus were unfamiliar to the subjects being tested. Subjects were identified by the unique colour combinations of their leg bands. We observed each subject for 15 min per day for 4 consecutive days and then again on 4 nonconsecutive days ending on day 14, with the first observation occurring as soon as possible after all birds were placed in the aviary. We recorded the following behaviours.

(1) Directed singing: the number of song bouts directed at another bird.

(2) Undirected singing: the number of song bouts not directed at any particular bird.

(3) Courtship dancing: the number of times the subject performed the male-typical courtship display, in which the bird hops along the perch with an erect posture making 180° turns as it moves towards the stimulus bird.

(4) Allopreening: the number of times the subject preened another bird.

(5) In nestbox with: the number of times the subject was in a nestbox with another bird. To be recorded, the birds had to be in the nestbox together for at least 5 s.

(6) Following: the number of times the subject followed another bird nonaggressively. Following is a

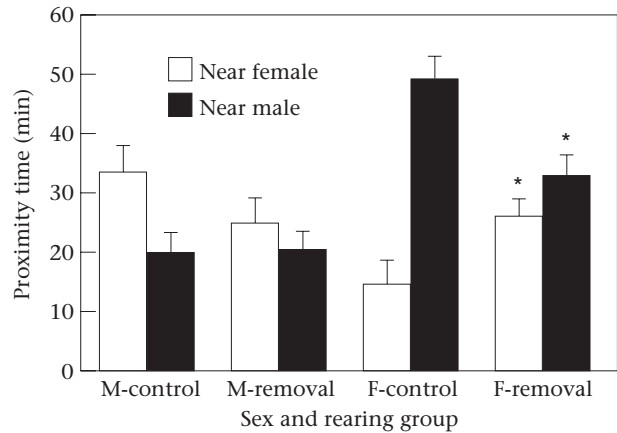


Figure 2. Total time (min) spent in female- and male-stimulus proximity zones ($\bar{X} \pm SE$) by control and male-removal birds in five 15-min, two-choice tests. $N=8$ per group. * $P < 0.05$ compared with controls of the same sex.

mate-guarding behaviour performed more frequently by males (Birkhead et al. 1988).

(7) Chasing: the number of times the subject chased another bird. Chasing is an aggressive behaviour performed by both sexes. Birds chase others in order to defend mates, nest sites, nest material and other reproduction-related resources.

Allopreening, following and being in a nestbox with another bird are all indicators of attempted or successful pairing (Zann 1996). The observer also noted whether the subject seemed to have a particular preferred partner (consistent object of these behaviours) and whether the preferred partner reciprocated or tolerated these behaviours.

Data Analysis and Statistics

We summarized results from the behavioural tests as the total behaviour frequency or duration of behaviours in all tests of the same kind (two-choice or group aviary). We analysed differences between control and male-removal groups using Mann-Whitney U tests. All probabilities reported are two tailed. Because a relatively large number of behaviours from group aviary tests were analysed using multiple U tests, these probabilities were corrected by a sequential Bonferroni procedure. Because siblings from the same clutch did not resemble each other (see Sibling Similarity results), the N for statistical analysis was the number of birds, not the number of clutches.

RESULTS

Two-choice Tests

Most control males (6/8) spent more time near female stimuli, and all control females spent more time near male stimuli (Fig. 2). Also as expected, most control males (7/8) sang more to female stimuli (Fig. 3). Male-removal birds did not show these preferences. Female subjects in the male-removal group spent as much time in proximity

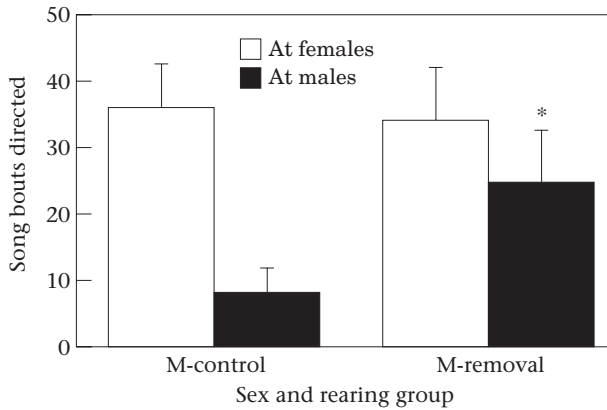


Figure 3. Total number of song bouts ($\bar{X} \pm SE$) directed at female and male stimuli by control males and male subjects in the male-removal group in two-choice tests. Females do not sing. Mean \pm SE song bout frequencies of male subjects in group aviary tests were: 8.4 ± 2.8 (control group song bouts to female stimuli), 1.1 ± 0.6 (control group song bouts to male stimuli), 7.1 ± 3.3 (male-removal group song bouts to female stimuli) and 7.0 ± 3.3 (male-removal group song bouts to male stimuli). * $P < 0.05$ compared with control males.

zones as control females (were as interested in the stimuli), but divided their time more evenly between male and female stimuli, resulting in a significant increase in time spent near females and a significant decrease in time spent near males. Although male subjects in the male-removal group sang to female stimuli as much as control males did, they sang significantly more to male stimuli than control males did.

Group Aviary Tests

Control males were more likely to dance, to allopreen, be in a nestbox with, and follow female stimuli than they were male stimuli (Table 1). Male subjects in the male-removal group directed more of all of these behaviours to male stimuli than control males. None of these differences remained significant after Bonferroni correction, but the overall pattern was notable none the less.

As in the two-choice tests, most control males (6/8) sang more to females, whereas male subjects from the male-removal group sang equally to males and females (see Fig. 3 legend). However, because of the greater variability in group aviary behaviour, this difference was not significant.

Control females, as expected, tended to direct their pairing preference behaviours at males (Table 1). Female subjects in the male-removal group did not differ significantly from control females for any of the measures in Table 1.

Chasing was not affected by the rearing manipulation (Table 1). Males from both groups mainly chased other males, and females from both groups mainly chased other females.

Figure 4 shows the pairing status of the subjects during the second week of observations, when pairing preferences have stabilized, unsuccessful relationships have ended and most trios have resolved (Silcox & Evans

1982). Overall, birds from the male-removal groups were significantly less likely to be paired with an opposite-sex partner. Those that attempted to pair or succeeded in pairing with a same-sex bird never had another male-removal group bird as the preferred partner.

Sibling Similarity

Although some male-removal subjects were siblings from the same clutch (as was the case for some control subjects), male-removal siblings did not tend to resemble each other with respect to any measure of sexual partner preference. None of the male-removal subjects that paired with same-sex birds had a sibling that also paired with a same-sex bird.

DISCUSSION

Both males and females reared without adult males in the breeding cage directed more partner preference behaviours to same-sex birds than control birds. For females, this altered preference was most pronounced in the first set of tests (the two-choice tests) and thus could reflect avoidance of novel stimuli (neophobia) or an initial inability to discriminate or recognize sex. At the beginning of the two-choice tests, female subjects were encountering adult male zebra finches for the first time since their first week of life. Adult males look very different from females and younger males. This distinctive appearance, combined with male-typical behaviours such as singing at the female, may have required some time to become attractive or to be an acquired basis for sex discrimination. Even if temporary, however, such an influence of the rearing environment could have lasting consequences for females of any species that forms long-term pair bonds, because of missed opportunities to claim high-quality males.

The altered preference of the males is less likely to be due to neophobia. They were already familiar with female conspecifics from the rearing cage in which they lived until 40 days. They were already familiar with adult males because they were group housed in an all-male cage until 100 days, by which time all the birds were physically and behaviourally adult.

In laboratory colonies of zebra finches, it is not uncommon to see an occasional same-sex pair among nonexperimental birds, especially among females with limited access to males (Adkins-Regan et al. 1996), which would explain the low, but nonzero, interest in same-sex birds seen in the control groups here. The significantly elevated incidence of this behaviour in the male-removal groups is none the less striking. The behaviour of the males in the group aviary tests (Table 1) suggests that they were actively seeking out male mates. To our knowledge, this is the first experiment showing that the early social environment affects preference for opposite-sex partners in a pair-bonding species.

These results raise two interesting questions of interpretation that would require further work to answer. First, what was it about the rearing manipulation that

Table 1. Behaviour of control and male-removal subjects towards females and males in group aviary tests

Group/measure	Behaviour											
	Dance to		Allopreen		In nestbox with		Follow		Chase			
	F	M	F	M	F	M	F	M	F	M		
Males												
Control												
The number displaying behaviour	4	1	6	1	7	2	6	3	7	8		
Total frequency	1.8±0.9	0.1±0.1	3.4±1.1	0.1±0.1	18.8±5.4	2.0±1.7	12.4±4.5	0.4±0.2	4.3±1.5	38.5±11.0		
Male removal												
The number displaying behaviour	4	5	4	4	4	5	4	6	8	8		
Total frequency	1.1±0.5	3.4±1.8*	3.6±1.9	1.9±1.0	8.4±4.4	4.0±1.8	13.1±7.2	7.6±3.1*	8.8±3.8	35.9±10.08		
Females												
Control												
The number displaying behaviour	0	0	3	4	2	7	1	4	8	6		
Total frequency	—	—	1.3±0.8	2.9±1.5	3.3±2.1	7.3±1.6	0.1±0.1	3.9±2.1	16.4±5.0	3.9±1.6		
Male removal												
The number displaying behaviour	0	0	3	3	4	5	1	5	8	6		
Total frequency	—	—	1.3±0.6	2.1±1.2	6.3±3.0	9.0±4.2	0.3±0.3	2.0±0.9	17.6±5.2	5.4±3.1		

Frequencies are $\bar{X} \pm SE$. $N=8$ for each group. See Fig. 3 legend for song bout results.

* $P<0.05$ compared with controls of the same sex.

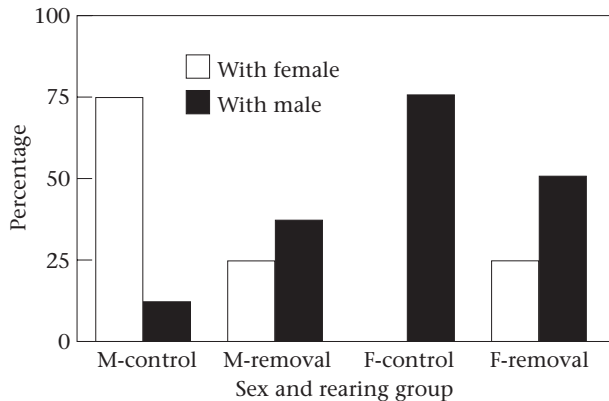


Figure 4. Percentage of control and male-removal birds that were paired with a female or with a male during the second week of the group aviary observations. Overall, 12 of 16 controls were paired with an opposite-sex bird, whereas six of 16 male-removal birds were paired with an opposite-sex bird (chi-square test: $\chi^2_1=4.57$, $P<0.05$).

altered the adult behaviour of the subjects? There are several possibilities. Male-removal birds grew up in breeding cages with fewer adult birds, and thus possibly fewer social interactions overall. This does not seem a likely explanation for the altered sexual partner preference, however, because there is much variation in the size of the breeding units between laboratories that produce behaviourally normal birds (some even breed birds in isolated pairs). Male-removal birds did not receive paternal care or interact with a father after the first week of life. Zebra finch fathers feed nestlings nearly as much (domesticated birds) or as much (wild birds) as the mothers do (Zann 1996), and juvenile males interact more with the father than with the mother (Williams 1990; Houx & ten Cate 1998). Also, removal of the fathers could have changed the interactions with the mother, or may have altered the physiology of the developing birds. There are remarkably few studies of the effect of fathers on the future reproductive behaviour of their offspring in non-human species with biparental care (Wuensch 1985; Roberts & Carter 1997). Male-removal birds were almost certainly fed less. In sexual imprinting studies in which zebra finch young were fostered to parents of the same or a different species, young that were fed more showed a stronger preference for the parental species when choosing mates as adults (Bischof & Clayton 1991; Oetting et al. 1995). Another possibility is that the critical feature of the rearing manipulation was that birds were not exposed to any adult male models between the first week of life and the age at which their peers in the group-housing cage reached maturity (males) or the age at which testing began (females). Zebra finches are colonial and thus are normally exposed to many adult male models in addition to the father. Furthermore, although male subjects in the male-removal group were exposed to females (the mothers) and to males (their age peers), they did not experience the two together, either spatially or temporally, until testing began.

The second question of interpretation is what aspects of the subjects' behaviour were changed by the male-removal manipulation that accounts for the test outcomes? Vos (1994), using two-parent rearing, showed that morphological cues are important in sex recognition and that some of these cues are learned from the parents, suggesting a failure to recognize or discriminate sex should be considered. However, both sexes of male-removal subjects showed excellent sex discrimination in their chasing (aggressive) behaviour in the group aviary tests (Table 1). All male subjects in the male-removal group sang abnormal songs, in agreement with reports of Eales (1989), Jones et al. (1996) and Collins (1998). Did these abnormal songs contribute to the altered sexual partner preference of these males? Female zebra finches prefer males with high song rates (Collins et al. 1994). Males with abnormal songs showed considerable interest in other males, but it is possible that their abnormal songs made them less likely to be chosen by females.

Paternal care is common in birds (Silver et al. 1985). It has often been assumed that paternal care must be required for offspring survival and that this is the selective pressure that has led to social monogamy, the most common avian mating system. Beginning with Gowaty (1983), researchers have conducted male-removal experiments to test some of these assumptions. Surprisingly, in some cases male removal has had little effect on offspring survival or condition at fledging (reviewed in Gowaty 1996). Such an experiment has not been reported in wild zebra finches. Our subjects survived the removal of their fathers with the assistance of some crop feeding by humans, but might not survive in the wild where a single mother's task is more difficult.

Regardless of whether zebra finch fathers are required for the young to survive, the absence of adult males in our experimental laboratory colonies did alter the behaviour of the offspring in ways that would negatively impact their future reproductive success. The fact that adult males are normally present sets the stage for them to be a part of the package of reliable environmental information used by the developing young for the programming of behaviour (ten Cate 1994; Elman et al. 1996). One would not expect such a role for adult males to be universal across species, however, because adult presence or paternal presence is not universal. Nor can it be assumed that early social experience is a universal contributor to adult sexual partner preference. In both sheep and macaque monkeys, the preference for opposite-sex partners seems to be relatively impervious to manipulations of social experience prior to adulthood (Perkins & Fitzgerald 1997; Wallen & Parsons 1997), unlike the preferences of the finches in our experiment.

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