



Female zebra finches require early song exposure to prefer high-quality song as adults

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Song learning in songbirds has been studied extensively in males but not in females. Females prefer songs previously heard, but it is not known whether opportunity for learning during the juvenile period affects the ability of females to judge song quality. We show that early exposure to adult song is required in the development of normal adult female zebra finch, *Taeniopygia guttata*, song preferences. Females were reared in conditions that varied in the exposure to song. As young adults, these females were tested for song preference using a two-choice speaker protocol with unfamiliar song stimuli. Females reared with adult males preferred tutored (normal-quality) song, whereas females reared without adult males were as likely to prefer untutored (abnormal-quality) song as tutored song. All three groups of females preferred conspecific to canary song but showed no preference for songs that were temporally reversed or played forward. Our results suggest that a normally reared female's preference for songs with more notes and spectral complexity is learned during early exposure to adult males that produce such songs.

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Learning plays an essential role in the adult singing behaviour of male songbirds, but what about the effects of learning on adult behaviour in females? Vocal learning in females has been studied in a few species where both sexes sing, such as Nuttall's white-crowned sparrow, *Zonotrichia leucophrys nuttalli* (Cunningham & Baker 1983) and northern cardinals, *Cardinalis cardinalis* (Yamaguchi 1998, 1999; reviewed in Riebel 2003). Much of the literature on song learning has focused on highly sexually dimorphic species such as the zebra finch, *Taeniopygia guttata*, in which only the males sing. Female songbirds often use song to choose mates (Zann 1996; Nowicki et al. 2002), but little is known about how females establish song preference. We tested the hypothesis that auditory learning by female zebra finches during development shapes their later song preferences.

Zebra finches are an estrildid species in which pairs of birds form lifelong pair bonds and display biparental care, making the choice of a high-quality mate crucial (Zann 1996). In the wild, both male and female zebra finches generally disperse from their natal colony (Zann 1996). Females, then, must be able to judge the quality of unfamiliar males using a variety of cues, including song. Indeed, female zebra finches are able to discriminate between pairs of unfamiliar songs as well as between pairs of familiar songs (Cynx & Nottebohm 1992).

Song learning in male zebra finches is a multistage process (Nottebohm 1999). The male zebra finch learns song from a tutor during a sensitive period for model acquisition (25–60 days of age), then practises and perfects this song during a sensorimotor phase (40–75 days of age) (Slater & Jones 1995; for review, see DeVoogd & Lauay 2001). The song becomes stereotyped by approximately 80 days of age, after which it remains unchanged for the remainder of the male's adult life (Marler 1997). If denied access to a tutor during the sensitive period, a male's song as an adult is similar to normal zebra finch song in segmentation, duration and frequency range, but has fewer distinct phrases and inconsistent frequency modulations (Price 1979; Eales 1987). Young adult zebra finches of both sexes prefer the song of their father over that of a male with dissimilar song (Clayton 1988) or that of an unfamiliar male (Riebel et al. 2002), but those who are

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given new tutors after the close of the sensitive period for song acquisition in males (first at 35 days of age and another at 120 days of age) prefer the song of the most recent tutor (Clayton 1988). After the sensitive period for model acquisition has closed, males continue to learn song for the purposes of recognition and discrimination, suggesting that an early sensitive-period learning for song production can be distinguished from recognition and discrimination learning that occurs into adulthood (Clayton 1988; Riebel et al. 2002).

Adult female zebra finches can make complex song discriminations. They recognize and prefer the song of their father or their mate to the song of an unfamiliar male (Miller 1979a, b; Clayton 1988; Riebel et al. 2002). Adult females who had tutors from 35 to 65 days of age preferred their tutor's song over the song of an unfamiliar male, whereas untutored females showed inconsistent preferences, suggesting that females have a sensitive period for model acquisition (Riebel 2000). In males, song learning early in life (song production) can be distinguished from learning later in life (song recognition). However, there is no evidence to date that females undergo a model acquisition phase in early development that differs from recognition learning later in life. That is, an adult female preference for a previously heard (familiar) song, such as the song of her father or her mate, over an unfamiliar song may indicate that a female is capable of song recognition and discrimination but does not provide direct evidence for sensitive-period learning in females.

We tested the preferences of adult female zebra finches for unfamiliar songs as a function of exposure to adult male song during rearing using two-choice speaker tests. These females were tested for their preference for unfamiliar tutored versus untutored zebra finch songs to determine: (1) whether females reared with adult males would prefer high-quality (tutored) over poor-quality (untutored) song and (2) whether the removal of adult males during development would affect female song preference, specifically, whether females hearing song for the first time as adults would prefer tutored or untutored song.

In adult males, neurons in several song system nuclei are less responsive to the bird's own song (BOS) temporally reversed compared with BOS played forward (Vicario & Yohay 1993; Lewicki 1996; Doupe & Solis 1997). This attenuation of responsiveness to reversed song appears during the sensorimotor phase, suggesting a relationship between song-order selectivity and development and, possibly, learning (Volman 1993; Doupe 1997; Solis & Doupe 1997). By testing the preference of female zebra finches for complete song played forward versus the same song played in reverse, we gain insight into the salience of temporal order and/or overall complexity of song for females.

Finally, we tested female preference for conspecific versus canary song to determine whether there are constraints on the song template that females can learn. We know that they can learn to prefer the song of foster finch species (Clayton 1990), and that they prefer to hear conspecific song as early as 28–53 days of age when reared by their mothers (Braaten & Reynolds 1999), but we do not know how strong or lasting this bias might be.

METHODS

Animals

Subjects were 46 female zebra finches hatched and reared in the laboratory at Cornell University, Ithaca, New York, U.S.A. Eight to 10 breeding pairs of zebra finches were housed in wire-mesh, free-flight aviaries ($1.8 \times 0.8 \times 1.0$ m) equipped with nestboxes. Nesting material was made available for the duration of the experiment. A diet of dry seed, water, grit and shell was available *ad libitum*, supplemented daily with fresh greens and hard-boiled eggs crushed with shell. All animal procedures were approved by the Cornell University Institutional Animal Care and Use Committee (IACUC) and met all applicable state and federal guidelines.

Experimental Manipulations

Within each aviary, the day the first chick hatched was designated day 1. We recorded the hatch dates of all nestlings and applied leg bands, colour-coded for hatch date, when nestlings were 10–14 days of age. We performed experimental manipulations on days 18 and 50, as described below. We removed unhatched eggs daily from all nestboxes beginning on day 32.

Group names (below) designate categories of birds present in the aviaries in which subjects were reared, such that uppercase letters represent adult birds (M = adult male, F = adult female) and lowercase letters represent offspring (m = male offspring, f = female offspring).

MFmf group

Females were reared in multiple-nest aviaries by both parents along with male and female siblings. Females remained in these aviaries until testing was complete.

Fmf group

Females were reared in multiple-nest aviaries along with male and female siblings, but with all adult males removed on day 18, prior to the sensitive period for model acquisition in males. Females remained in these aviaries until testing was complete.

Ff group

Females were reared in multiple-nest aviaries along with their siblings, but with all adult males removed on day 18, prior to the sensitive period for model acquisition in males. Female and male offspring were removed from their home aviaries on day 50 (when the appearance of adult plumage allowed sexing of the juveniles) and placed into same-sex aviaries ($1.8 \times 1.8 \times 1$ m) that were acoustically isolated from all other aviaries. Offspring that were too young to sex when the oldest chick had reached day 50 were monitored on a daily basis and removed to the appropriate same-sex aviary when adult plumage was evident. Females remained in the same-sex aviary until testing was complete.

Thus, females in the MFmf group were able to interact with their fathers throughout the juvenile period, whereas

females in the Fmf and Ff groups did not have access to their fathers during and after the sensitive period. Females in the Fmf group were exposed to the plastic and untutored full song of their male nestmates and other males of the same hatching cohort. Females in the Ff group did not hear complete song before testing as adults, but may have heard some subsong. Because the ages of chicks in the aviary ranged from 18 to 50 days of age (eggs might continue to hatch until the oldest chick was 32 days), it is unlikely that many males were producing subsong and it is also unlikely that females heard very many such vocalizations. To later test for possible effects of such experience on adult female preference, we used the hatch date information for each aviary to calculate the number of days that each female may have been exposed to song from either adult males or young males in the same hatch cohort.

Song Stimuli

Song clips for the preference tests were generated using Canary software (v.1.2.4; Charif et al. 1998) from archived recordings of males previously housed in the DeVogd laboratory (ca. 1990) to ensure that stimuli were unfamiliar to the subjects. We used all possible combinations of song pairs from five tutored and seven untutored males to create stimuli. For the forward versus reverse test, the song of each tutored male was paired against his own song temporally reversed using SoundEdit (v.2.0.7; Macromedia 1992). We used a 10-s clip of male canary song, *Serinus canaria*, as the heterospecific song stimulus.

We created zebra finch song stimulus clips by selecting three to four bouts of song from each male, for a total clip length of 10 s. These clips were matched for amplitude and used to create 1-min song loops consisting of two songs: 10 s of song A from side 1; 5 s of silence; repeat (e.g. tutored song on left track) followed by 10 s of song B from side 2; 5 s of silence; repeat (e.g. untutored song on right track) and stored on compact discs. Tests were counter-balanced for song type order and side of presentation in testing cage.

Preference Test Arena

The testing arena (Fig. 1) consisted of an elongated wire-mesh aviary (197.5 × 37.5 × 46 cm) subdivided into a large central neutral zone and two 30-cm zones at either end that defined the sites at which the bird's presence would indicate a preference (Miller 1979b). A Sony SRS-A37 speaker was concealed behind a cloth at each end of the arena. Three perches were arranged in front of each speaker so that they appeared symmetrical from the start area. The arena was physically divided into three equal areas, with a central start area bracketed by gates that could be lifted by the observer seated behind a curtain (Neubauer 1999). Painted wooden models of male zebra finches were placed on a segment of a perch extending outside of the aviary to encourage female response (Tchernichovski et al. 1998). The speakers were connected to a Sony Walkman portable compact disc player operated by the experimenter. The volume at the centre of the

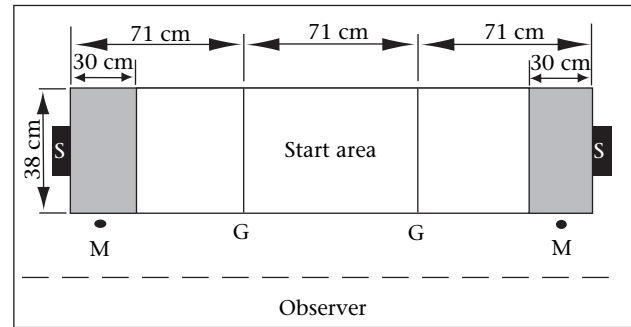


Figure 1. The song preference arena consisted of a wire-mesh aviary subdivided by movable wire-mesh gates (G). Painted male models (M) were placed near each of the speakers. Song stimuli were broadcast over speakers (S) at each end of the arena. The time spent near each speaker (shaded area) was recorded.

testing arena fell between 58 and 66 dB, which is within the range of normal male song intensity (as measured in mixed-sex aviaries by the experimenter).

Preference Test Protocol

We tested females with tutored versus untutored song stimuli at 120–127 days of age, forward versus reverse song at 127–145 days of age and zebra finch versus canary song at 134–150 days of age, with a minimum of 7 days between each test. To test the hypothesis that females reared with and without exposure to song would differ in their preference for tutored versus untutored song required that the first test be that of tutored versus untutored song. All tests were performed between 0900 and 1200 hours. Song stimuli were randomly assigned to each subject, with novel stimuli presented during each test. Females were caught during the afternoon of the day prior to testing and held overnight in individual transport cages (20 × 22 × 40 cm) covered with cloth to visually isolate each female.

Each test consisted of two blocks. In block 1, the female was placed into the start area and given 10 min to adjust to her new surroundings. The song stimuli were played for 2 min so that the female heard each song twice before being allowed to respond, then the gates were opened. The amount of time the female spent within 30 cm of each end of the cage was recorded for the next 8 min. The female was returned to the start area and given another 10 min of quiet. Block 2 was identical to block 1, except that the songs were presented from the opposite sides.

Statistical Analyses

Within each of the three preference tests, we calculated the percentage of time that each female spent with a given song type (tutored song, forward song and zebra finch song) for blocks 1 and 2. The percentage of time from blocks 1 and 2 were averaged to yield a value from 0 to 100 indicating the direction and strength of preference for each female. A value of 100 would indicate that a female showed an absolute preference for tutored, forward or

conspecific song, a value of 0 would indicate an absolute preference for untutored, backward or canary song and a value of 50 would indicate that the female showed no preference for either stimulus (i.e. either flew back and forth during the test or showed a place preference, having gone to the same side of the arena in blocks 1 and 2). One female did not enter either timed zone and was excluded from the analysis.

For each preference test, we tested the effect of rearing environment on female song preference using one-way ANOVA followed by planned comparisons between females in the MFmf group and each of the experimental groups using independent *t* tests. We analysed song type preference for each group as a deviation from 50% with one-sample *t* tests. The proportions of females showing a song preference and showing a place preference within each group were compared using chi-square statistical tests. Possible effects of age at testing, the number of days spent with adult males and the number of days spent with young on adult female song preference were analysed using Pearson correlation coefficients. All statistical analyses were two-tailed and conducted with the SPSS statistical package (v.10.0.7a; SPSS 2002).

RESULTS

Tutored versus Untutored Song

Statistical analyses showed a significant effect of rearing environment on female preference for tutored versus untutored song (ANOVA: $F_{2,43} = 3.30$, $P = 0.05$; Fig. 2). Females in the MFmf group spent significantly more time near tutored song compared with females reared without adult males in mixed-sex aviaries (Fmf) (independent *t* test: $t_{30} = 2.07$, $P = 0.05$) and females reared without adult males in same-sex aviaries (Ff) ($t_{28} = 2.30$, $P = 0.03$; Fig. 2). In addition, females in the MFmf group showed a significant preference for tutored song (one-sample *t* test: $t_{15} = 3.71$, $P = 0.002$). There was no

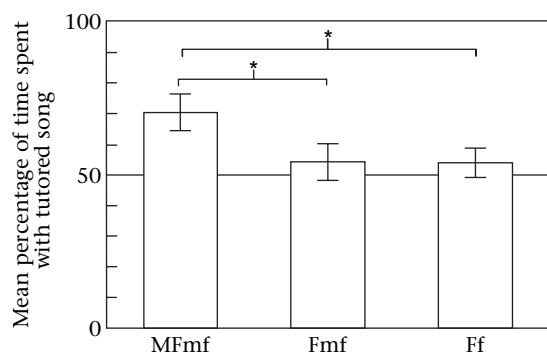


Figure 2. Tutored versus untutored song. Mean \pm SE percentage of time spent near the tutored song for subjects reared in the MFmf ($N = 16$), Fmf ($N = 16$) and Ff ($N = 14$) groups, where M and F refer to adult males and females, and m and f refer to male and female offspring, respectively. A score of 100 indicates an overall strong preference for tutored song, 0 indicates an overall strong preference for untutored song and 50 indicates no song preference. * $P < 0.05$ (independent *t* test).

significant preference for song type shown by females in the Fmf ($t_{15} = 0.77$, $P = 0.45$) and Ff ($t_{10} = 0.92$, $P = 0.38$; Fig. 2) groups. The proportions of females showing a song preference versus a place preference did not differ significantly between groups (chi-square test: $\chi^2_2 = 1.19$, $P = 0.564$). The time spent near tutored song did not significantly correlate with age at testing (Pearson correlation: $r_{46} = -0.011$, $P = 0.942$), the number of days with adult males ($r_{46} = -0.211$, $P = 0.159$) or the number of days with juvenile males ($r_{46} = 0.180$, $P = 0.231$).

Forward versus Reverse Song

There was no significant effect of rearing environment on female preference for forward versus reverse song (ANOVA: $F_{2,27} = 0.22$, $P = 0.80$; Fig. 3). There was no significant preference for song type in the MFmf (one-sample *t* test: $t_{11} = 0.67$, $P = 0.52$), Fmf ($t_8 = 0.60$, $P = 0.56$) and Ff ($t_8 = 0.20$, $P = 0.84$) groups (Fig. 3). The proportions of females showing a song preference versus a place preference did not differ significantly between groups (chi-square test: $\chi^2_2 = 0.40$, $P = 0.56$). The time spent near forward song did not significantly correlate with age at testing (Pearson correlation: $r_{30} = 0.311$, $P = 0.95$), the number of days with adult males ($r_{30} = 0.161$, $P = 0.395$) or the number of days with juvenile males ($r_{30} = -0.096$, $P = 0.615$).

Zebra Finch versus Canary Song

There was no significant effect of rearing environment on female preference for zebra finch versus canary song (ANOVA: $F_{2,26} = 0.76$, $P = 0.47$; Fig. 4). Regardless of rearing environment, females showed a significant preference for zebra finch song (one-sample *t* test: MFmf: $t_{10} = 4.98$, $P = 0.001$; Fmf: $t_7 = 4.73$, $P = 0.002$; Ff: $t_9 = 3.37$, $P = 0.008$; Fig. 4). The proportions of females showing a song preference versus a place preference did not differ significantly between groups (chi-square test: $\chi^2_2 = 0.40$, $P = 0.56$). The time spent near zebra finch song did not significantly correlate with age at testing (Pearson correlation: $r_{29} = 0.117$, $P = 0.544$), the number of days

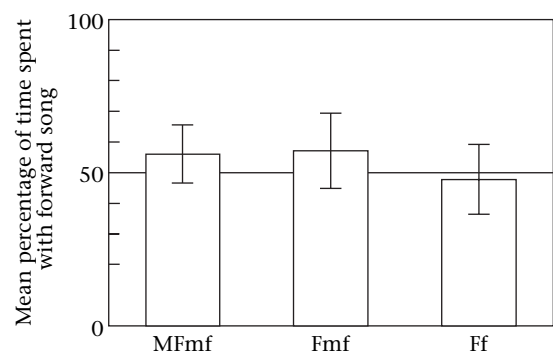


Figure 3. Forward versus reverse song. Mean \pm SE percentage of time spent near the forward song for subjects reared in the MFmf ($N = 12$), Fmf ($N = 9$) and Ff ($N = 9$) groups (see Fig. 2 for category designations).

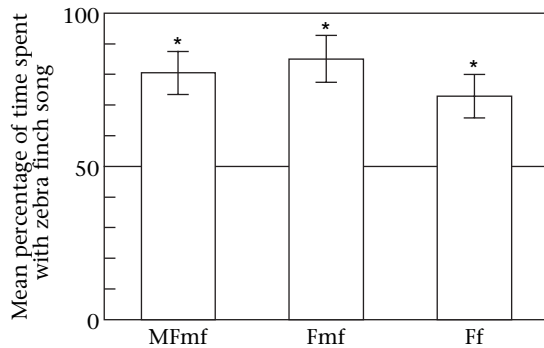


Figure 4. Zebra finch versus canary song. Mean \pm SE percentage of time spent near the zebra finch song for females reared in the MFmf ($N = 11$), Fmf ($N = 8$) and Ff ($N = 10$) groups (see Fig. 2 for category designations). * $P < 0.01$ (one-sample t test).

with adult males ($r_{29} = -0.195$, $P = 0.311$) or the number of days with juvenile males ($r_{29} = 0.257$, $P = 0.179$).

DISCUSSION

The results of the present study show that the opportunity that a juvenile female zebra finch has to learn song from adult males affects her adult song preference. Females reared with adult males preferred normal-quality song, whereas females reared without adult males did not act on song quality. Within each of the experimental conditions, some females chose tutored song and some chose untutored song, suggesting that the tutored song stimuli varied in quality and/or that our untutored song stimuli contained elements that were attractive to females. A more robust effect of rearing condition on female preference for tutored versus untutored song may be possible by using computer-generated song stimuli where elements of song can be varied systematically. Females reared without adult males did not differ from control females in their likelihood to show a preference. Rather, they were equally likely to choose an untutored or a tutored song. These results suggest that song learning that occurs in juvenile female zebra finches is critical in the formation of a song template and later aids the adult females in judgments of song quality.

Females reared with juvenile males appeared unable to take advantage of the learning opportunity afforded by the males' vocalizations. Volman & Khanna (1995) found that young males learn from each other if no adult male tutors are available. When housed together from day 10 posthatch, the songs of the males share several characteristics (sequence similarity, shared syllables, frequency modulations). In contrast, females in our study that were exposed to the plastic and crystallized untutored songs of their brothers (and other males in their hatch cohort) showed no preference for untutored over tutored song. Rather, their responses resembled those of females that had at most heard the first days of subsong before being placed in all-female aviaries. In fact, the number of days spent with juvenile males did not correlate with adult

song preference in either song-deprived group. Thus, the sensitive period for auditory learning in females may close before males in their hatching cohort begin to sing (approximately 40 days of age), regardless of auditory experience. Alternatively, females may have a sensitive period that is open during the time that males in their cohort begin to sing, but they are unable to learn sufficiently from untutored and/or uncrystallized song. Young males may not be considered appropriate tutors, or interaction with an adult male tutor may be critical for learning in females. Given that the number of days spent with adult males did not correlate with adult song preference and that adult males were removed at day 18, it would appear that females are unable to learn from their fathers before 18 days of age. Thus, the sensitive period for song acquisition in females appears to open after 18 days of age (perhaps at the same age as for males) and closes by 40 days of age.

Females were as likely to prefer forward or reverse song, regardless of rearing environment. Because females tended to make a choice (i.e. did not show a place preference), it may be that song is equally attractive played forward and in reverse. These results are also consistent with earlier song discrimination research done using an operant task (Cynx 1993). Males and females first learned to discriminate between a pair of songs, then were presented with the same stimuli temporally reversed. While males were able to re-learn the discrimination, females were unable to do so, performing at chance levels (Cynx 1993). Unlike males, female zebra finches may be relatively insensitive to the temporal order of song, perhaps attending to overall complexity and spectral composition when evaluating song. Further investigation is necessary to understand the importance of complexity and temporal order in female song preference.

It is unlikely that the females experience a general deficit in perception as a result of their rearing environment. Sturdy et al. (2001) reared zebra finches in one of three conditions: (1) with both parents (normal rearing environment), (2) with fathers removed at 4 days posthatch and mothers removed at 33–35 days posthatch or (3) with fathers removed at 4 days posthatch and fledglings moved to individual cages at 33–35 days posthatch. Males and females were tested at adulthood for their ability to discriminate frequency range, which is important for species recognition (Weary et al. 1986), frequency ratio, or relative pitch, which is important for recognition of the songs of conspecifics (e.g. black-capped chickadees, *Poecile atricapillus*, Ratcliffe & Otter 1996) and song notes, which is important for recognition of the calls and songs of individual conspecifics, for example, song note learning in males (Beecher 1996) and mate recognition in females (Searcy & Yasukawa 1996). Both males and females reared without adult males (but with siblings and mothers) showed deficits in frequency range discrimination, which is important in classifying song as conspecific and for song recognition. However, only males and females reared without adult males (and isolated from siblings and mothers) showed additional deficits in frequency ratio and song note discrimination (Sturdy et al. 2001). The females in our study who were reared without adult males

may have shown deficits in frequency range discrimination, as did the song-deprived birds in the Sturdy et al. (2001) study. However, all of the juveniles in our experiment experienced a rich social and acoustic environment regardless of rearing environment, comparable to the first and second groups from the above experiment. Thus, there were probably no deficits in either frequency ratio or, perhaps most important for this discussion, song note discrimination in the females in our experimental conditions.

All females preferred zebra finch to canary song, regardless of rearing condition. Like males, females appear to have a bias for characteristics of conspecific song that is modified by auditory learning. Canary song is quite unlike zebra finch song in structure, so additional preference tests comparing zebra finch song with songs of more closely related species are needed to confirm this hypothesis. Because the order of the tests was not counter-balanced, females were exposed twice to adult zebra finch song prior to the zebra finch versus canary song preference test. The earlier tests may have affected the preferences for zebra finch song over canary song in the females reared without exposure to adult males. Future research confirming a bias for conspecific song in adult zebra finches previously not exposed to song is necessary.

Our results show that female songbirds do learn about song early in life. Access to an adult male appears to be critical for this learning, much as it is in male song learning. In addition, the present work establishes that the sensitive period for song acquisition in females may begin at approximately the same age as it does in males. However, females differ from males in that they appear unable to learn from young males and the sensitive period may close earlier in females regardless of auditory experience. Further research must be done to distinguish learning done during the sensitive period for song acquisition from processes subsequent to a female making a mate choice based on song quality, leading to a preference for the song of her mate.

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