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Is female preference for male repertoires due to sensory bias?

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There are several possible explanations for the female preference for male repertoires in birds. These males are older, and have better territories; thus there are functional reasons for females to prefer these males. However, there is an alternative explanation; females may habituate less quickly to song repertoires than single songs. I tested whether females have a non-functional, sensory bias for male song repertoires, by testing female preference for a repertoire in zebra finches (*Taenopygia guttata*), a species in which males possess a single stereotyped song. Females chose between a male repertoire of four different phrases created from the song phrase of one individual and that of one of those phrases repeated four times (natural zebra finch song). Females were also given a choice between the above repertoire and a song made from the phrases of four related males ('family' stimulus). I tested female preference by training females to press a button for presentation of a song stimulus, and counting the number of button presses. Females preferred the song repertoire to a single phrase song, and did not differentiate between the repertoire and song phrases from four males. Evidence from the Estrildidae indicates that having a single song is the ancestral state for zebra finches, so the preference is not ancestral.

Keywords: zebra finch; female preference; sensory bias; repertoire

1. INTRODUCTION

In many species of birds females prefer males that have a larger repertoire (Buchanan & Catchpole 1997; Kroodsma 1976; Searcy & Marler 1981). The size of the repertoire may indicate male qualities such as age (Mountjoy & Lemon 1995), or experience (Yasukawa *et al*. 1980). These males also tend to have better territories (Yasukawa 1981) and provide better paternal care (Yasukawa *et al*. 1990). Repertoire size can thus be used by females to assess male quality. Males with larger repertoires are also preferred as extra-pair copulation (EPC) partners (Hasselquist *et al*. 1995), suggesting that there may be indirect benefits for females to mating with males with larger repertoires.

However, another possible explanation for female preference for large repertoires is that males are exploiting a sensory, or perceptual, bias of the females (Endler & Basolo 1998). The role of receiver bias, and subsequent sensory exploitation (Ryan & Rand 1993) in driving the evolution of signal form has received more attention in recent years (Guilford & Dawkins 1991; Endler 1992; Ryan 1998). Pre-existing bias models propose that the evolution of many traits can be explained by features of the female nervous system that predispose a female to respond more strongly to certain male characteristics. If receiver bias has a part in signal evolution, preference for the signal is not expected to be functional and there may be no intrinsic benefit to choosing males producing the favoured signal, but there is a mating advantage to the male in possessing that signal.

The receiver bias exploited by a male repertoire may be the fact that habituation occurs to repeated presentation of a stimulus (Krebs 1976), i.e. response intensity declines to a stimulus that is not reinforced. With a repertoire the stimulus changes more frequently and female response increases after each song change (Searcy *et al*. 1994). Therefore, habituation of females to stereotyped song may be the mechanism favouring the evolution of repertoires. Possession of a repertoire may reduce female habituation (Krebs & Kroodsma 1980) and increase overall female response to male song (Catchpole *et al*. 1984; Baker *et al*. 1986). To test for an intrinsic bias among females towards repertoires, females from species in which males normally have only a single song have been studied. In field sparrows (*Spizella pusilla*) and white-throated sparrows (*Zonotrichia albicollis*) males do not possess a repertoire and females show no preference for a repertoire over a single song (Searcy & Marler 1984). However, Searcy (1992*a*) showed that female common grackles (*Quiscalus quiscala*) prefer the artificially combined song of four males (repertoire stimulus) to that of the song of a single male. The preference for the repertoire (a stimulus that does not occur naturally), in Searcy's study, was assumed to show that there was a pre-existing bias in this species and by extension the potential for a bias in many species. However, after reconstructing the phylogeny, analysis showed that the single song found in common grackles is most likely the derived state (Gray & Hagelin 1996). All other icterid species studied possess a repertoire, so the preference could be the ancestral condition.

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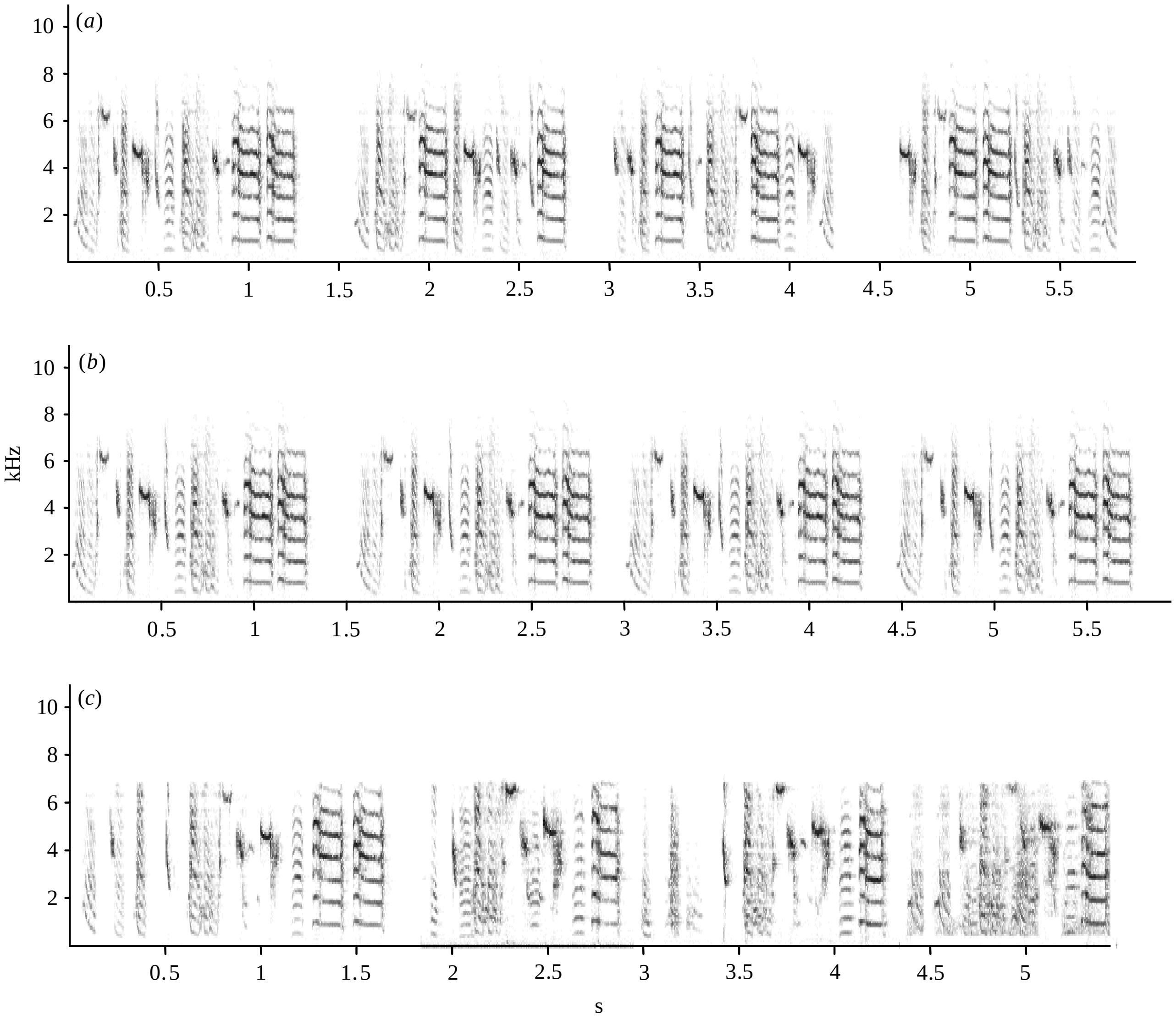

Figure 1. Sonograms of (*a*) repertoire, (*b*) control and (*c*) family stimulus songs for a male.

To test whether the evolution of repertoires is due to female sensory bias it must be shown that there is preference for a male repertoire in a species in which males do not have a repertoire, and thus the preference is unlikely to be functional. In addition the phylogeny should support the hypothesis that possessing a single song is the ancestral state. Zebra finches (*Taenopygia guttata*) fit the above criteria. In zebra finches, each male sings a different song learnt from an adult tutor, usually the father; songs are individually distinct, but stereotyped. Only two of the African groups of estrildid finches have a repertoire, *Lagnostica* (three species) and *Pytilla melba* (Goodwin 1982; R. B. Payne, personal communication). All close relatives of the zebra finch have stereotyped songs (Zann 1976; Immelmann 1969). The study of one estrildid group, the *Lagnostica* genus, and the song types produced by these species, suggests that estrildid songs developed from calls into stereotyped sequences of call notes, which then developed into stereotyped songs containing some call notes (Baptista 1996). A phylogeny is currently being constructed for the estrildid finches, but is not yet published. Given the rarity of repertoires in the estrildid finches in general and their absence among the immediate relatives of zebra finches, it seems unlikely than any direct ancestor of zebra finches possessed a repertoire.

The repertoire in this study was not constructed from the song of different males (e.g. Searcy 1992*a*; Searcy & Marler 1984), a shortcoming in previous studies, but from rearranging the notes in the song of one individual. Each female was presented with two stimulus songs, one a song made up of a repertoire of four different song phrases (ABCD, ABCD), and the other a song with only one repeated phrase (AAAA etc.), the natural state (see figure 1). Each phrase in the artificial repertoire contained identical notes, but in each exemplar the notes were in a different order. This type of repertoire was chosen because it is a type of change that could evolve in zebra finches. Juvenile song (plastic song) contains many of the notes that will be used when the male is adult, but the order is not yet stereotyped (Slater *et al.* 1991). I also compared preferences for the artificial repertoire and a song of four phrases one from each of four related males, known as the 'family' stimulus. Females were trained to

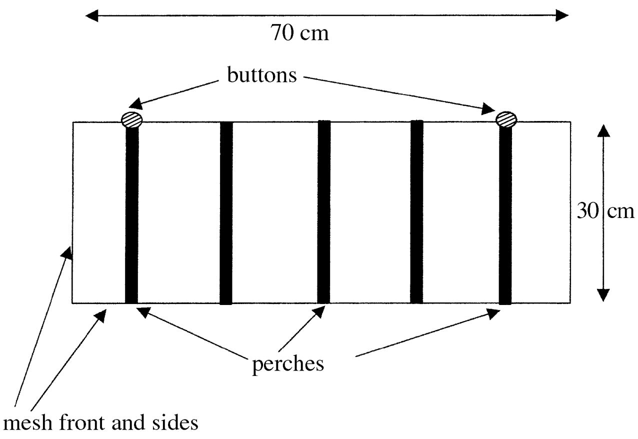

Figure 2. Skinner box apparatus.

press a button in order to be presented with a song stimulus. A similar technique was used to measure song preference in chaffinches (Riebel & Slater 1998). The number of presses was used as a measure of preference, rather than injecting the females with oestradiol and measuring copulation solicitation displays (e.g. Vallet *et al.* 1998; see references in Searcy 1992*b*), as this may change relative preferences as well as overall receptivity (but see Searcy & Capp 1997). Zebra finches are opportunistic breeders and females are always receptive to males (Zann 1996), so artificially increasing receptivity is not necessary for sexual preferences to be expressed.

2. MATERIAL AND METHODS

(a) *Stimuli males*

Males were kept in a large holding room with a 16 L:8 D cycle, with freely available food and water; grit and egg food were provided weekly. All males had breeding experience and were housed in pairs with a female. None of the males was breeding at the time of recording.

Songs were recorded in a soundproof chamber using a Sennheiser MKH 70 microphone and a Sony TC D5 tape recorder. All songs recorded were undirected song (Zann 1996), i.e. song produced when the male was not in visual contact with a female. Songs were then recorded onto a Macintosh computer as a Canary 1.2 sound file for editing and analysis.

(b) *Subjects*

Ten adult female zebra finches (two years old), with no breeding experience were used as subjects. The females were unrelated and from two breeding colonies, one in Leiden, the other from Groningen (The Netherlands). They were housed in single sex groups of five individuals, in the same room as the males, in auditory but not visual contact, and under the same conditions. Females had been trained one year previously to press a button in a Skinner box apparatus (see figure 2) in order to be presented with a male zebra finch, and had retained the ability to press the button. All females had been trained with the same male.

(c) *Preparation of stimuli*

Ten male songs were chosen from the pool of recorded songs to make the stimuli for the subsequent female preference tests. Songs were chosen on the basis of clarity and duration of recording. In addition the songs of three relatives of each stimulus male were chosen to provide the phrases for the 'family' stimulus (see figure 1).

Zebra finch song consists of a repeated phrase (repeated one to eight times) made up of individual notes (3–14, Zann 1993). Songs are separated by a gap of about 5 s, and phrases within a song by about 0.1 s (Zann 1996) (figure 1*b*). The phrase is the usual unit of investigation due to the fact that the number of phrases in a song is variable, but the phrase itself is remarkably consistent within an individual (Zann 1996).

The following three stimuli songs were created from the original recordings using the Canary 1.2 sound analysis program.

(i) *Repertoire*

One example of a phrase from an individual was chosen for manipulation. I rearranged notes from the phrase, by cutting and pasting, to produce four different versions of the phrase (figure 1*a*). The four versions were combined to produce a song consisting of four phrases. Each phrase was of equal length and contained the same notes, but note order varied. Care was taken to keep the structure of the song similar to normal zebra finch song (Zann 1993), in that call-like notes should be found at the end of a song and high notes never found at the end of a song.

(ii) *Control*

One of the four modified phrases from the repertoire stimulus was chosen at random. This was copied four times to make a song (figure 1*b*). Thus, the stimulus contained the same notes, at the same amplitude, and was of the same length as the repertoire.

(iii) *Family*

For each of the ten males used above, the songs of three relatives were chosen. One phrase from each of the four (including the stimulus male) was used in order to make a stimulus song consisting of four phrases (figure 1*c*). Phrase lengths were kept similar, editing where necessary. In addition notes were cut and pasted in each song, back into the same place, so that all songs had been manipulated in some way.

All the above thirty stimuli songs of four phrases were saved as '.wav' sound files for recording onto the registration devices used in the preference tests.

(d) *Preference tests*

Each of the ten females was given two preference tests in a 'Skinner box' (figure 2) which was visually and vocally isolated from other zebra finches. The Skinner box consisted of a cage (70 cm × 30 cm × 45 cm) containing two buttons connected to a registration device, which in turn was connected to a Blaupunkt CB 4500 speaker placed on top of the cage. When the female pressed a button one of the stimulus songs, consisting of four phrases, was played once over the speaker, one button corresponding to each stimulus song (controlled by the registration device). The females remained in the apparatus for one day and then the buttons were switched to correct for any side preference, after which the females remained in the Skinner box for another day.

The preference tests were as follows: experiment A, repertoire versus control—each stimulus male was used once; experiment B, repertoire versus family—the same ten males as for experiment A were used. The repertoire stimulus was paired with the family stimulus of a different male, i.e. the males of the family

Table 1. *Female button presses for the different stimuli over two days (2 × 12 h periods)*

	repertoire versus control (experiment A)		repertoire versus family (experiment B)	
female	repertoire	control	family	repertoire
1[a]	75	72	27	55
2[a]	94	81	577	473
3	407	179	344	339
4[a]	685	401	847	980
5	38	37	158	143
6[a]	227	125	138	204
7	50	42	122	49
8	156	57	95	110

[a] Female received experiment A first.

stimulus were not related to the male providing the repertoire stimulus. Female preference was calculated as the percentage of button presses for the repertoire.

Half the females started with experiment A and half with experiment B. Females were presented with a different male stimulus song in each condition. One female died halfway through the experiment and another only pressed on one side and was thus discarded.

(e) ***Analysis***

All statistical tests were conducted using SPSS v. 7.9. (SPSS for Windows, SPSS Inc., Chicago).

3. RESULTS

Table 1 shows that there was considerable individual variation in the number of presses females made over the two days of each experiment, therefore the percentage rather than number of presses was used in analysis. The percentage of presses for the repertoire stimulus was arcsine converted (Sokal & Rohlf 1994) to normalize the data. The converted percentage was then tested with a one-sample t-test for a deviation from 0.5. (i) Repertoire versus control—the percentage of presses was significantly above 50% for the repertoire stimulus ($t = 3.75$, d.f. $= 7$, $p = 0.007$, mean ± s.d $= 64.7 \pm 11.1$; figure 3). (ii) Repertoire versus family—females showed no significant preference ($t = 0.757$, n.s., mean ± s.d. $= 53.5 \pm 13.04$; figure 3).

There was no correlation between the preference for the repertoire in the two experiments for individual females (Pearson's correlation n.s.). There was also no effect on whether a female received experiment A or B first, for the number of button presses, or the percentage preference (Mann–Whitney U—order 1 or 2 independent variable, preference measure dependent variable, $n = 8$; n.s. all tests)

I tested whether there was an association between the total number of button presses (female 'activity level') in a particular experiment and the percentage preference for the repertoire in that experiment. Females were categorized into those that pressed more than 100 times and those that pressed less. The test was significant for the repertoire versus control condition (t-test: $t = -2.5$, d.f. $= 6$, $p = 0.05$; less than 100 times, mean preference $= 55\%$; more than 100 times, mean preference $= 68\%$). This large individual variation has been found in previous experiments using female button pressing as a measure of preference (S. A. Collins, unpublished observations; K. Riebel, personal communication). The t-test was rerun with only those females that pressed over 100 times, the result was still significant ($t = 3.94$, d.f. $= 5$, $p = 0.01$; repertoire versus control).

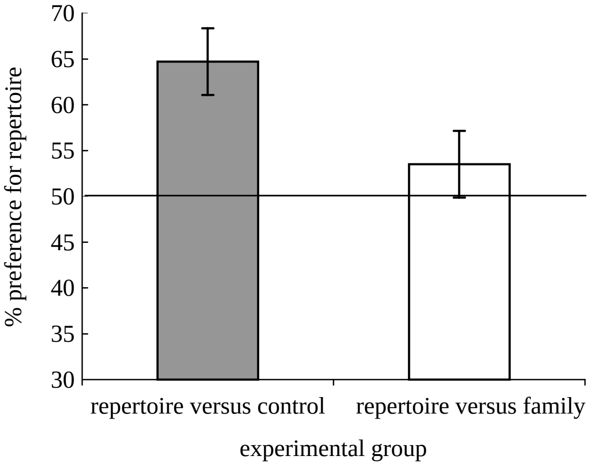

Figure 3. Percentage preference of females for repertoire stimulus ± s.e. ($n = 8$, repertoire versus control, shaded bar; $n = 8$, repertoire versus family, open bar).

Females pressed at a fairly constant rate throughout the experiment, except for a peak before lights out and after the lights went on in the morning.

4. DISCUSSION

Zebra finch females prefer repertoires to stereotyped song, but show no preference for the repertoire of four phrases compared with a song made of phrases from four males from the same family. Possession of a single stereotyped song is most likely to be the ancestral condition in this group (see Baptista (1996) for work on *Lagnostica*). Therefore, preference for a repertoire in female zebra finches cannot be a functional preference. Zebra finches are estrildid finches, a group which evolved in Africa and then spread via Asia to Australia (Goodwin 1982). Only three species of *Lagnostica* (although not all species are recorded) and *Pytilla melba* possess a repertoire and these are found in Africa (Goodwin 1982; Immelmann 1969; Zann 1976). Some estrildid finches have two song types, undirected and directed song (only directed song is sung to the female). In zebra finches these songs are identical, but in some species they are not. However, having identical song types is most common.

The most likely explanation for the preference is that females habituate less quickly to the more complex stimulus (Krebs & Kroodsma 1980). There are other possibilities; perhaps complex songs indicate male learning ability (Jacobs 1996), or fitness (Nowicki *et al.* 1998). More complex natural songs (songs with a greater number of different note types) may be preferred by female zebra finches, and by extension the more complex repertoire is also preferred by the females. There is some evidence that males with more complex songs have larger brain areas associated with song learning

(MacDougall-Shackleton *et al*. 1998; Ward *et al*. 1998), but not that they possess greater general learning ability. It is unknown whether remembering notes in a number of different orders (repertoire stimulus) could require more brain 'space', as is the case for remembering a larger number of notes (long complex songs). However, even if females are shown to prefer more complex natural songs, sensory bias for the more complex stimulus rather than a functional preference for complexity could still determine this preference. A further possibility, that females prefer songs containing particular note types (Vallet *et al*. 1998), is not important for this experiment, as repertoire and control contain the same note types. Finally, females may react to the repertoire as if to the song of four individual males. Although I used the song of one individual, it is possible that females treat variable songs as indicating a number of males. Females could be showing a preference for a group of males. To resolve this question it is necessary to show that females can recognize individuals even when the note order is changed. Individual recognition when note order varies has been shown in starlings (*Sturnus vulgaris*) (Gentner & Hulse 1998; but see Beecher *et al*. 1994), but this is a species where males naturally produce a repertoire. However, if females prefer to listen to the song of four males, then any male that produces a song that sounds like four males would be preferred. If this preference leads to increased reproductive success for the male singing this song type, then repertoires may evolve. In this case the preference arises through the exploitation of a functional choice to be near a group of four males rather than a sensory bias.

In this study I also found that there was no difference between female response to the song phrases of four related males and the repertoire of four phrases from the same male. There are again several possible explanations for this. Females may treat both stimuli as being from four males, and prefer them equally. Another possibility is that the females prefer the song of four males equally to that of the four-phrase repertoire for one of two reasons. Both 'family' and 'repertoire' stimuli may have had a similar level of variability and if the preference mechanism works through differential habituation, then the origin of the phrases may not be important, only their complexity. Finally, females may identify one stimulus as being from four individuals, but not prefer songs from four individuals.

The use of button pressing as an indicator of female preference allows the study of song preferences without the confounding effect of male behaviour. It is possible that a non-sexual preference is being measured, but females press the button a similar number of times for the presentation of a live male (number of presses from 76 to 1060 in two days, data from a previous experiment with the same females (see table 1 for comparison); S. A. Collins, unpublished data). Therefore I believe the most likely explanation is that the females are expressing a sexual preference for the male song.

This study indicates that the evolution of repertoires would be favoured by female preference in zebra finches. The reason that repertoires have not evolved in this species may be due to constraints on the brain, or learning ability of the males. In the wild the median life span for a zebra finch is about one year, although they may live up to five years, the environment is very unpredictable and zebra finches have many adaptations for reaching maturity quickly (Zann 1996). This may reduce the possibility of the evolution of repertoires, due to the pressure of being capable of breeding as soon as possible. There may be some cost to possessing a repertoire, in terms of the brain area required (DeVoogd *et al*. 1993), or in terms of the costs of not being individually recognized. Miller (1979) suggests that one function of the zebra finch song is for individual recognition. Possessing a repertoire may mean that individuals can no longer be consistently recognized by partners.

The results of this study show that male repertoires in many species could evolve, without a functional benefit to the female from choosing, due to the general preference bias in females. Although, in a number of species the preference may well be functional, allowing identification of older more experienced males etc., the bias would increase the strength of the preference.

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