



Female choice for song characteristics in the house finch

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Song has been proposed to function in mate choice, and such a role has been demonstrated experimentally in a number of species. We presented captive female house finches, *Carpodacus mexicanus*, with a choice of two songs, each of which was identical except for a single parameter that had been either accentuated or minimized. To ensure that our playback tapes offered choices within the normal range of variation in house finch song, we recorded wild male finches, then created playback tapes using values for the song parameters under consideration that were above or below the mean for the local population, but within the natural range of variation. We presented females that had not previously mated with choices between songs that (1) were long or short, (2) were given at fast or slow rates, and (3) included a large or small repertoire of unique song elements. Females showed significant preferences for long songs and for songs presented at a faster rate, but there was no significant preference for large or small repertoires of unique song elements. Song length and rate each seem likely to indicate a male's energy reserves, and thus could be important sources of information for females choosing mates.

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Growing evidence suggests that song is an object of female mate choice in a variety of bird species (Andersson 1994). Playback studies, primarily conducted in the field, have demonstrated that females are more likely to approach nestboxes with broadcasts of their species' song rather than no song, and prefer to associate with males that sing either the local dialect or the same dialect as their father (reviewed in Searcy 1992a; Searcy & Yasukawa 1996). Clearly, female birds seem interested in the broad-scale characteristics of song, but we know less about the specific aspects of vocalizations that make them attractive in mate choice.

Many studies of female choice relative to song characteristics have focused on song complexity, and several studies have shown that song complexity plays a role in female mate choice (e.g. Howard 1974; Catchpole 1980; Searcy 1992b). Song complexity can be defined as the number of different song types performed by a male or, in species with reduced song repertoire sizes, by considering the number or structure of individual elements (sometimes called notes) within a song. Each element can vary in structure from simple tonal whistles to extended noises containing numerous frequency modulations, and the type and quality of elements that are produced may convey information about the neuromuscular coordination of the individual producing them (Suthers et al. 1999). Other studies have examined the role of temporal characteristics

of song in mate choice. An emerging theme from these previous studies is that females prefer longer songs (Wasserman & Cigliano 1991; Balzer & Williams 1998) and higher song rates (Gottlander 1987; Alatalo et al. 1990; Westcott 1992; Möller et al. 1998; Gentner & Hulse 2000). Thus, females have repeatedly shown a preference for increased song complexity, and there is growing evidence of female choice for long songs and fast song rates.

In this study we tested female mate preferences relative to different aspects of song in the house finch, *Carpodacus mexicanus*, a small passerine bird with sexually dichromatic plumage that has been studied extensively (Hill 2002). Male house finches do not defend territories (Thompson 1960; Hill 1993, personal observation), so song is not used to establish or maintain spatial boundaries. Therefore, if song is sexually selected in house finches, it is likely to function primarily in mate attraction.

We tested mate preferences of captive female house finches relative to male song by providing females with dichotomous choices between songs that varied along a single parameter. In three experiments, we tested for female preferences relative to song length, song rate and song element repertoire size.

METHODS

Definitions: Song, Song Types and Song Elements

We defined the most basic component of a song, the note or song element, as a tracing on a sonogram that

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could be drawn without lifting a pencil from the paper, and that was temporally separated from other elements by background amplitude levels. We defined a song as being a vocalization containing at least four different types of song elements, none of which were separated from any other element by more than 1 s of background amplitude levels. Like the performance of other behaviours, an individual house finch's production of a given song is fairly stereotyped each time it is produced, but consecutive iterations of the same song are rarely identical. On some occasions, a given song may include several elements that are dropped from use on other occasions. These slight variations in production are typically not considered to constitute a distinctly different song, but rather to represent variation within a song 'type' (discussed in Spector 1994).

Natural Song Variation in Wild Males

To assess natural variation in the parameters to be tested, we recorded song opportunistically from 45 uniquely colour-banded finches, recording each male as long as he continued to sing. We used no playback to elicit any vocalizations, and made recordings during all daylight hours. We included a reference tone of 440 Hz in each recording as a calibration of the recorder's fidelity. We used a Marantz PMD-222 cassette recorder, side A of 60-min chromium oxide cassettes (with bias equal to that of the Marantz), and a Sennheiser MKH-70 directional microphone to make recordings. We then entered those recordings into a Power Macintosh computer using SoundEdit software (Farallon Computing, San Francisco, California, U.S.A.). This software allowed removal of extraneous background noise, yielding files of song that we imported into Canary software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.) for generation of sonograms. We used the following settings to generate sonograms: clipping level = -120 dB, fast Fourier transformation (FFT) = 512 points, filter bandwidth = 176 Hz, sampling rate = 22 000 Hz and frame length = 23 ms. We used the sonograms generated in Canary to measure the mean song length, song rate (number of songs/min) and frequency range based on 10–20 songs from each of the males recorded. We calculated the mean number of unique song elements comprising the first 20 songs for a random subset of 15 of the males.

Captive Maintenance

In each of the 3 years of our study (1998–2000), we caught 13 hatch-year male and 40 hatch-year female house finches on the campus of Auburn University, in east-central Alabama, by placing wire-mesh traps around bird feeders. Hatch-year birds were identified by their distinctive plumage (Hill 1993); their use as test subjects ensured an equal level of breeding experience for all birds in the study (i.e. no prior breeding experience). We captured all birds in August–September of 1997–1999, then held them in captivity through the winter. Therefore, our study subjects were 2–5 months old at the time of

capture, and approximately 8–11 months old when tested. We examined all birds for the presence of pox lesions and infection with *Mycoplasma gallisepticum* (Nolan et al. 1998; Roberts et al. 2001). No infected birds were used in this study.

We housed all birds in outdoor flight cages ($1.5 \times 3.7 \times 2.4$ m) at the Auburn University aviary, fed them an ad libitum diet of birdseed, and supplied water supplemented with vitamins (Nolan et al. 2000). Each cage housed fewer than 20 birds. Females were isolated visually, but not acoustically, from the male house finches used in this study and from males used in other studies. Therefore, females were exposed to vocalizations of male conspecifics for up to 5 months before their capture and for the duration of their time in the aviary. Hatch-year males maintained in the same aviary developed a species-typical song, suggesting that there was sufficient acoustic stimulation for the captive birds of both sexes during any critical learning periods.

Mate Choice Trials

We ran a total of 120 90-min mate choice trials between dawn and 1800 hours at the beginning of the annual breeding seasons (between mid-February and early May) of 1998–2000. These 120 trials represented 40 trials addressing each of the three song parameters for which we tested female preferences (i.e. 40 tests of preference for song length, 40 tests of preference for song rate and 40 tests of preference for element repertoire size). The timing of our trials corresponded to a period when female finches in the local wild population were seeking males and forming pair bonds (Hill 1993). To increase female receptiveness to the males, we implanted all females with a 4–5 mm length of silastic tubing filled with 2–3 mm of oestradiol at least 2 weeks before the first mate choice trial. Each female participated in only one trial.

We conducted our trials in an outdoor mate choice arena adjacent to the campus of Auburn University. This arena had four parallel lanes ($3.7 \times 1.5 \times 2.4$ m each) for holding males, and a fifth lane ($3.0 \times 6.0 \times 2.0$ m) that ran perpendicular to the others (for a diagram of the mate choice pens, see Figure 2 in Tobias & Hill 1998). Placement of a female into the fifth lane allowed her to fly back and forth and examine each of the males. The males could see the female when she was in front of their cage, but the walls between the four parallel lanes prevented the males from seeing each other. Of the four parallel flight cages, stimulus males were placed in the middle two.

A loudspeaker in each male's cage broadcast songs we had manipulated so that they differed along only one parameter relative to the song in the other male's cage. Songs were broadcast simultaneously in both cages for the entire 90 min, meaning that some of the songs in each treatment were overlapped temporally by the other loudspeaker. Because the distribution of overlaps was random and affected each male equally, we believe that there was no net effect on the female's perception of the male. To ensure that no song from the stimulus males would compete with the playback songs that were the object of

the female's choice, we temporarily muted the males using a surgical technique described by McDonald (1989). Although muted males were unable to sing for 3–4 days, they could still make nonsong vocalizations (chirps), fly, perch, and in all other ways behave normally. Test males stayed in the same cage throughout the 2–3 days of trials, but we alternated the treatments between cages after each trial. For example, if a given male's loudspeaker played a long song in one trial, it would play a short song in the next trial. We used a total of 13 males as stimuli for the females in each of our three experiments, and used a hand-held spectrophotometer (Hill 1998) to ensure that plumage colour of the test males in a given trial was the same. We also assessed male body size by measuring the beak and tarsus, and used only pairs of males that were of similar size overall (i.e. <10% difference in each of the two measurements). However, because captive female house finches do not use male body size as a criterion in mate choice (Hill 1990), slight differences in size between our stimulus males should not have affected our results.

During a trial, a test female was held in an adjoining cage (the fifth lane mentioned above) that was divided into two chambers by a partition that began 1.2 m above the ground and continued up to the ceiling. The female could remain in the outer chamber, where she had access to food and water but could not view the males, or she could fly under the partition into the inner chamber and view males individually from perches in front of their cages. Before beginning any trials for the year, we placed each flock of females into the mate choice cage for 1 week to allow them to adjust to the set-up. We videotaped all trials for later analysis to minimize disturbance of the female that might be caused by the nearby presence of an observer.

Playback Tapes

To prepare each playback tape, we began by selecting a high-quality recording of one male recorded in the field and entering the best two to three songs into a Macintosh computer, using the built-in analogue-to-digital converter sampling at 22 kHz. We then made two identical copies of those songs so that the first copy could be manipulated in one direction, and the second copy could be manipulated in the opposite direction (Fig. 1). For instance, songs in one copy were lengthened and songs in the other copy were shortened. Thus, each pair of songs used in a particular playback trial (i.e. short versus long songs, large versus small song element repertoire size, high versus low song rate) was made from the same initial recording. This approach controlled for any unknown or unquantified differences that might arise when simultaneously presenting recordings from different males.

More specifically, songs were shortened by identifying song elements that occurred in a repeated series within the song, and then deleting some of those repeats. Songs were lengthened by inserting additional copies of elements that the bird had sung in a repeated series. Each of these techniques was modelled on patterns seen in our analysis of naturally occurring house finch song, and no

song parameters were altered beyond the species' natural range of variation (Fig. 2). We were also careful not to alter other parameters that might be important as signals. For instance, long and short songs were presented at the same song rate (number of songs per min), and the number of unique elements in each song was held constant. To manipulate song element repertoire size while holding song length constant, we added or removed several unique elements from a song and then maintained the length by inserting or deleting copies of elements that the bird had already used in a repeated series. We began with songs that contained 15 unique song elements, then removed three elements from the first copy of the song and added three elements to the second copy of the song. The two resultant songs were identical, except that one had 12 unique song elements and the other had 18 (Fig. 2). Finally, we manipulated song rate by presenting identical copies of a song at either five songs/min (low rate) or 10 songs/min (high rate), with intervals of silence between the playback songs.

Presenting multiple females with a choice between the same exemplars created trials within an experiment that were not completely independent. To minimize pseudoreplication, we used four different exemplars of each treatment. We presented each female with only one exemplar of a given treatment, and repeated the use of that exemplar only for every fourth female. Furthermore, we used songs from four different males to construct playback tapes for each of the three experiments. Thus, we used songs from a total of 12 males to construct our playback tapes.

Assessing Choice

From the 90-min videotaped record of a trial, we recorded the female's location every 30 s. We considered any time she spent on the perch in front of a male's cage to be time spent in association with that male, and we considered that female's choice to be for the male with which she spent more of her time (Hill 1990; Enstrom 1993; Johnson et al. 1993; Swaddle & Cuthill 1994; Tobias & Hill 1998). If the female spent less than a total of 15 min interacting with the males, that trial was not used in further analyses.

In addition to recording the amount of time a female spent in association with the males, we recorded any other behavioural interactions she had with them. We were particularly interested in noting any copulation solicitations, which in the wild typically precede mating. Female house finches also displayed a circular flight pattern in front of males that appeared to serve as a courtship solicitation signal. After females interacted with a singing male, they launched themselves from their perch while simultaneously looking back at the male. When the male's attempt to follow the female was barred by the wire mesh of the mate choice pen, the female circled back immediately to perch in front of the male and then repeated the cycle. We scored performance of copulation solicitations and circular flights as secondary confirmation of a female's preference for a particular male. In each case, the copulation solicitations and circular flights were directed at the

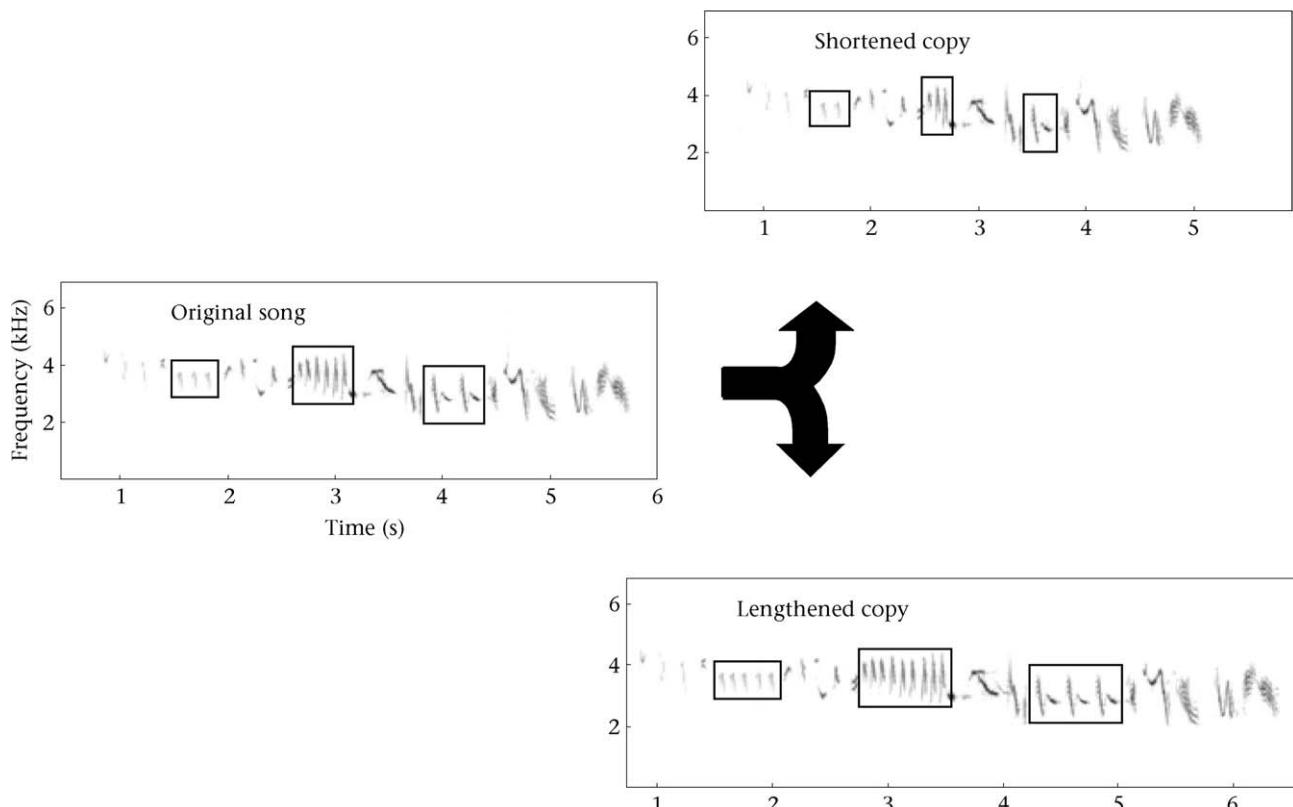


Figure 1. Construction of playback tapes. Identical copies of a source tape were manipulated to yield tapes played to females in a mate choice arena. In the example shown here, we manipulated song length by identifying elements that were used repetitively (enclosed in boxes for illustration purposes), then we either deleted or inserted copies of those elements to produce short and long exemplars, respectively.

male with which the female had spent the majority of her time.

Statistical Analysis

We compared the strength of female preferences for the two choices using chi-square analysis. We considered the expected number of trials in which a given treatment was preferred to be one-half the total number of trials in which females made a choice. For example, in the test of preferences for repertoire size, 37 females chose one of the males, so our expected value was 18.5. To examine whether one of the four exemplars in a given experiment (i.e. long versus short songs) might have a unique quality that would cause females to choose differently from females in the population as a whole, we analysed the proportion of time that each female spent near the loudspeaker broadcasting exemplars from each category, then performed an ANOVA on the mean proportions for each exemplar. A power analysis (Cohen 1992) revealed that we had a greater than an 80% likelihood of detecting large effect if one existed.

RESULTS

Each flock of females adapted quickly to the mate choice arena during the 1-week habituation period before the

start of experiments. Females moved freely throughout the fifth lane of the arena (described above), used all perches and showed no distinct preferences for one section relative to another. These behaviours continued when females were returned individually to the mate choice arena for experimental trials. House finches that are injured or ill typically remain stationary and eat very little; none of the birds used in our experiments showed these behaviours. All males in our experiments also moved freely throughout their cages during trials and interacted frequently with the females, suggesting that muting had no adverse impact. All males recovered their ability to sing within 1 week after surgery.

Male house finches in Alabama showed substantial variation in the length, rate and elemental repertoire size of their songs (Fig. 2). Although variation was not normally distributed for song length (Shapiro-Wilks test: $W = 0.89$, $P < 0.05$) or song element repertoire size ($W = 0.93$, $P < 0.05$), we failed to detect a significant deviation from normality for song rate ($W = 0.95$, $P = 0.10$). The mean \pm SE song length of wild male house finches was 2.93 ± 0.09 s (range 0.5–11.6 s; $N = 900$; 20 songs from each of 45 males). The mean \pm SE number of unique song elements used/song was 12.25 ± 0.63 (range 4–39 unique elements/song; $N = 300$; 20 songs from each of 15 males). Mean \pm SE song rate was 6.06 ± 0.18 songs/min (range 4–10 songs/min; $N = 900$; 20 songs from each of 45 males).

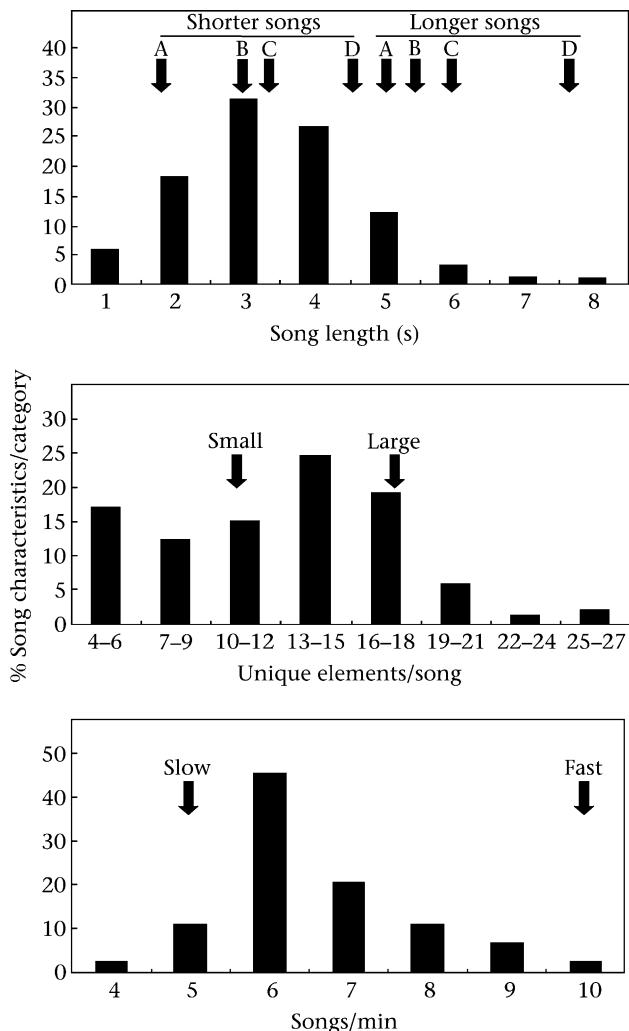


Figure 2. Frequency distribution of song characteristics of house finches in Auburn, Alabama, U.S.A. Arrows indicate the values offered as choices to female finches in a mate choice arena (see text). In the tests of song length preference, corresponding letters above arrows indicate the two song lengths that were offered as choices in a given trial (e.g. one-fourth of the females chose between short song A and long song A, and one-fourth chose between short song B and long song B, etc.).

Females showed no significant preference for either of the lanes in which the males were kept during the trial (chi-square test: $\chi^2_1 = 1.20$, $P = 0.28$) and displayed no significant preference for individual males ($\chi^2_{12} = 15.01$, $P = 0.24$). The proportion of time that females associated with the longer song in a given exemplar did not differ between the four exemplars used in the song length experiment (ANOVA: $F_{1,3} = 0.98$, $P = 0.41$). Similarly, we detected no effect of individual exemplars in the song rate ($F_{1,3} = 1.21$, $P = 0.33$) or song complexity experiments ($F_{1,3} = 0.73$, $P = 0.40$), suggesting that any effects of pseudoreplication in our analysis were minimal. Females showed significant preferences for long songs ($\chi^2_1 = 6.74$, $P < 0.01$) and for fast song rates ($\chi^2_1 = 5.12$, $P = 0.02$), making clear choices in 38 of 40 trials and 33 of 40 trials, respectively. Although females made a choice relative to

the repertoire size of song elements in 37 of 40 trials, they showed no significant preference for either a large or small repertoire ($\chi^2_1 = 0.68$, $P = 0.41$; Fig. 3). In 11 of the 38 cases in which females made a choice relative to song length, the females also performed copulation solicitation displays (10 cases) or circular flights (1 case), providing a secondary confirmation of their preference in each case. In 17 of the 33 cases in which females made a choice relative to song rate, the females also performed copulation solicitation displays (15 cases) or circular flights (2 cases), providing a secondary confirmation of their preference in each case. Finally, in 20 of the 37 cases in which females made a choice relative to song element repertoire size, the females also performed copulation solicitation displays (13 cases) or circular flights (7 cases), providing a secondary confirmation of their preference in each case.

DISCUSSION

The conspicuous song so typical of passerines can function in male–male competition to maintain territories, or it can increase a male's attractiveness to potential mates. House finches are not territorial (Hill 1993, 2002), minimizing the intrasexual role for song and making it likely that their song functions primarily in mate choice. In support of that hypothesis, we found that female house finches assess and respond to the song of conspecifics. In our study, most females preferred male songs that were longer and that were produced at a higher rate. Females did not show a consistent preference for the repertoire size of song elements, which is a measure of song complexity.

Increased song complexity has consistently been shown to be the object of female choice in studies of both captive and wild birds (for a review see Searcy & Yasukawa 1996). Therefore, our results are surprising in that female house finches showed no preference for songs containing higher numbers of unique song elements. However, it is worth noting that nearly all females made a choice relative to element repertoire size, and performed copulation solicitations and circular flights at higher rates in those trials than in either of our other experiments. Thus, like females

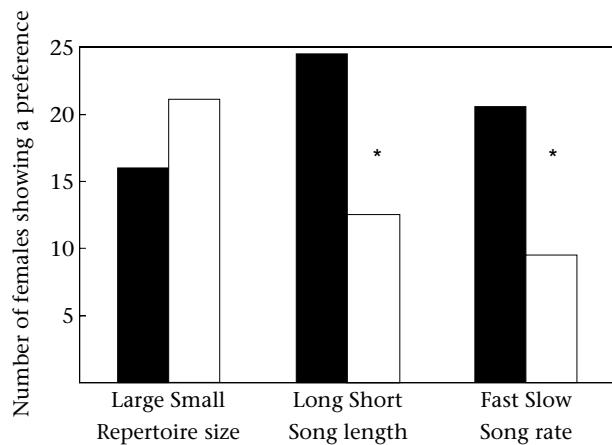


Figure 3. Preferences for song characteristics shown by female house finches. Asterisks indicate significant differences in the number of females showing a preference for a particular song characteristic.

of other species, female house finches seem interested in song complexity but the preferred degree of complexity appears to be specific to individual females.

Previous researchers suggested that song complexity has been selected to signal information about the genetic quality (Hasselquist et al. 1996) or developmental history (Nowicki et al. 1998) of an individual. However, those are longer-term characteristics that can also be revealed by morphological features, such as plumage colour or degree of bilateral symmetry (Møller & Swaddle 1997). Because the plumage colour of male house finches is condition dependent (Hill 2002), females can gain a substantial amount of information about a male's long-term condition by assessing a trait other than song complexity. Thus, when choosing a social mate, female house finches may focus on those characteristics of song that indicate a male's current condition, with information gained in that way being complementary to anything learned by assessing plumage colour (Nolan 2002). An alternative possibility is that some traits may be important in choosing a social mate, while others play a role in choosing an extrapair mate. For example, female great reed warblers, *Acrocephalus arundinaceus*, assess territory quality and song element repertoire size when choosing a social mate, but any extrapair mate chosen always has a larger repertoire size than the social mate (Hasselquist et al. 1996). In other words, female house finches may use information encoded in song length and song rate when choosing a social mate, and assess song complexity when choosing an extrapair mate.

Our failure to demonstrate a female preference for song complexity may lie in methodological differences between our study and those conducted previously. Much of the previous research on this topic involved species with song repertoires as opposed to syllable or element repertoires, and defined song complexity as the total number of song types that a given bird sings. We focused on the individual elements comprising those songs. Therefore, we offered females, in effect, a choice between simple versus complex versions of the same song type; our changes in the elemental composition of the songs were not sufficient to consider them truly different song types. Even if they were, the number of song types in each category (simple or complex) would be equal. Therefore, if females are more responsive to song type diversity (i.e. to differences in the repertoire size of song types a male sings), rather than song element diversity, our test would not detect the female preference.

Trainer & McDonald (1995) suggested that longtailed manakins, *Chiroxiphia linearis*, attract females by highly synchronous and consistent song production. Precise reproduction of a variety of song elements may be a valid measure of a male's neuromuscular ability to sing complex songs. Singing complex elements or songs might require the same tight control of the syrinx and its associated nerves and muscles as is required to produce a learned song in a consistent manner. Therefore, song precision or stereotypy may be preferred by female house finches in the wild (Nolan 2002). In our mate choice experiments, however, we constructed playback songs from the same source, so the songs offered to females were identical in the degree of element precision. The consequence of

controlling for all differences in our playback songs except for those in element repertoire size was that we increased our ability to detect preferences for song element diversity but limited our ability to detect preferences for other measures of song complexity.

Finally, it is possible that we found no preference for a large or small repertoire of song elements because the choices we offered females failed to encompass the natural range of variability as well as the choices for song length or song rate. For those two parameters, females were offered choices representing the extremes of what they would hear from wild birds, but the repertoire sizes used in our playback tapes were each relatively close to the modal repertoire size for males in this population. We consider this final possibility unlikely, however, given that the song with a large repertoire (18 unique song elements) was 50% larger than that with a small repertoire (12 unique elements); if song element diversity is important in female choice, a 50% difference in its elaboration would seem likely to be sufficient as the basis for choice when all other factors are held equal.

The preference of female house finches for increased song length and song rate fits a general cross-species pattern of female choice for males with the most elaborate expression of a preferred trait, particularly in morphological characteristics (Andersson 1994). Selection has also been demonstrated for extreme expression of other behavioural traits. For example, intense courtship and high levels of attentiveness (Sorenson & Derrickson 1994), large song repertoires (Howard 1974) and long vocalizations (Wasserman & Cigliano 1991; Sullivan & Hinschaw 1993) are chosen by females of a variety of avian species. All of these preferences, including those of female house finches for long songs and high song rates, make sense when viewed as female choices for mates willing or able to invest more in their current reproductive effort than as choices for males displaying less elaborated traits.

Behavioural traits used as cues in female mate choice often appear to require an investment of valuable resources and, therefore, may indicate a male's condition and ability to bear the high energetic costs of nesting. Reviews of the daily energy expenditure of a wide variety of birds (Drent & Daan 1980; Masman et al. 1989) indicate that small passerines operate at 3.5–4.0 times their basal metabolic rate during nesting, so assessment of a potential mate's ability to bear this burden could play a significant role in determining a female's fitness. For example, the fitness of a female house finch is heavily dependent on her mate's ability to feed her and their offspring. Male house finches provide nearly all of a female's food while she is incubating (Hill 1993), then provide slightly more than half of the food required by their nestlings (McGraw et al. 2002), and finally perform all provisioning of the fledglings (Hill 1993). This role of the male as a food provider is sufficiently important to nest success that females may abandon their nest if male provisioning rate is insufficient (Hill 1991). Therefore, selection should favour females that are able to judge a male's foraging ability before they invest in a nesting attempt, and should favour evolution of male signals that honestly signal success at acquiring food.

Song may serve as one such honest signal. In a variety of species, increases in song output are directly related to food supplementation (Gottlander 1987; Alatalo et al. 1990; Cucco & Malacarne 1997; Thomas 1999) and territory quality (Galeotti 1998), while performance of physically demanding activities results in a decrease in the amount of song produced (Nyström 1997; Martin-Vivaldi et al. 1998). Thus, the amount of song produced by a male, as measured by both song length and song rate, may provide an index to his foraging ability and may help to explain our finding that female house finches preferred longer songs and higher song rates. Consistent with that idea, Nolan (2002) found that longer songs are typical of the youngest male house finches, and McGraw et al. (2001) found that the youngest male house finches provide more food to their offspring than do the oldest males.

Although short songs and low song rates were less preferred, they were still chosen by a substantial number of females. Roughly 30% of the females chose shorter songs and slower song rates. Similarly, red plumage was consistently preferred over dull plumage in Hill's (1990) study of female preferences for plumage colour, yet 15% of females chose males other than the reddest one available. This variance in female strategies of mate choice is almost entirely unstudied. It may represent error in the measures of female choice that were employed, or it may represent real variation in the mate preferences of females within the population (Kokko 2000). This raises the interesting possibility that female mate choice is a condition-dependent strategy (Badyaev & Qvarnström 2002). For example, female house finches can compensate for lowered male provisioning rates (Stoehr et al. 2001), but it seems costly for them to do so. Those females less able to make that compensation may choose males signalling their ability or willingness to provide food. This is consistent with Nolan's (2002) finding that the preferred song length is typical of young males, which also bring more food to the nest (McGraw et al. 2001). At the same time, those females able to compensate for decreased male provisioning have the option of selecting a mate based on characteristics other than those signalling her likelihood of receiving direct benefits. For example, older male house finches, which sing the nonpreferred short songs and provide less food, also begin nesting earlier in the season (Hill 2002) and thereby fledge more chicks than males nesting later (McGraw et al. 2001). Therefore, future research may focus productively on tests of the variance in female mate choice relative to the female's age, health and other measures of her body condition.

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