The functional role and female perception of male song in Zebra Finches

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Abstract. The song of male Zebra Finches has been the focus of decades of behavioural, developmental, neurobiological and, increasingly, genomic research. Zann was the first to summarise the immense and integrative research effort in a landmark synthesis of field and laboratory studies of Zebra Finches, which paralleled his own championing work on the sociality and vocal behaviour of estrildid finches in the wild and in captivity. The study of the production and perception of Zebra Finch song has driven theoretical, empirical and technological advances in behavioural ecology, endocrinology and neuroethology, and led to a greater understanding of the evolution of animal communication systems in general. A survey of the literature shows that there are still significant gaps in our understanding of the mechanisms underlying the responses of non-singing females to male sexual displays, including song. We focus on recent insights into the features and functions of male song that shape female choice, regarding both behavioural and neurobiological measures of selectivity. This review underscores the need for continued research into the biological mechanisms underlying the perception of male song by female Zebra Finches and confirms this system as a valuable and productive model for research on animal communication.

Additional keywords: Bengalese Finch, female choice, genome, \textit{Lonchura striata} \textit{vars. domestica}, neuroethology, sexual selection, \textit{Taeniopygia guttata}.

Structure and development of Zebra Finch song

The song of the Zebra Finch (\textit{Taeniopygia guttata}), produced solely by males, is a short (1–2 s) vocalisation comprised of harmonic stacks and broadband notes, called syllables, that are produced in stereotyped sequences called motifs. Song motifs are repeated in bouts (Sossinka and Bohner 1980). The number, acoustic features and diversity of syllables that are produced are stereotyped within individuals but vary between individuals (Immelmann 1969). Individual differences allow the songs of male Zebra Finches to be easily distinguished by the human listener and also enable true individual recognition of mates (Miller 1979a) and fathers (Miller 1979b; Slater \textit{et al.} 1988) by females (see below).

Although the female Zebra Finch typically does not sing, masculinisation via oestradiol administration during ontogeny can induce song production, indicating an important role for gonadal hormones in the organisation of sexual dimorphism of vocal displays (Adkins-Regan \textit{et al.} 1994). Genetic determination of sex (Agate \textit{et al.} 2003), coupled with neuroendocrine effects up to the first week after hatching, are most influential for this development of the species-typical sexual differentiation in singing and the neuroanatomical basis of male-only song (Adkins-Regan \textit{et al.} 1994). However, the administration of testosterone to adult females can still induce and increase the frequency of female singing (Adkins-Regan 1999). In parallel, ontogenetic oestradiol treatment causes female Zebra Finches to sing in adulthood, and shows that these songs are learned during development, in parallel to the development of males’ imitative learning of song displays (Simpson and Vicario 1991).

The male Zebra Finch copies his song from an adult tutor during well-defined developmental stages (Slater \textit{et al.} 1988; Zann 1996). Song ontogeny comprises memorising a song template, followed by motor production of subsong and plastic song, until the song becomes crystallised at ~100 days of age. Following the crystallisation, typically only minor adjustments are made in the acoustic characteristics of the song. Such plasticity can include some transient deviations in song pattern, including syllable deletions or alterations, that are likely to reflect changes in the neural motor control pathway in the forebrain (Helekak \textit{et al.} 2000), or amplitude modulation in response to the distance of the intended recipient of the vocal display (Brumm and Slater 2006). But the likelihood and functional relevance of these anatomically and socially induced aspects of acoustic plasticity remain untested in the wild. In parallel with males, female Zebra Finches learn to remember the song of their fathers and familiar brothers during development in captivity (Riebel \textit{et al.} 2002; Riebel 2003), and also learn to recognise the songs of their mates during adulthood (Miller 1979a) but, again, the function of familiarity-based discrimination of songs by females in nature remains unclear.

Zebra Finches of both sexes are able to learn about conspecific song from playbacks of vocalisations (Bolhuis \textit{et al.} 1999), although males will more thoroughly and accurately imitate songs of tutors with whom they can vocally and visually
interact (Eales 1989). Evidence from blindfolded juvenile males has further shown that physical interaction itself, even in the absence of vision, enhances the learning of song (Adret 2004). This is in contrast to the social inhibition of song imitation by several brothers in the same cage (Tchernichovski and Nottebohm 1998) and presents a strong case for further investigations into the role that the sex and numbers of siblings might play during development in both male imitation of, and female preference for, tutor songs.

In the absence of a live song tutor, a male Zebra Finch will develop a rudimentary version of the adult species-typical song that is characterised by abnormally high frequencies and long syllables, often repeated in bouts that lack the normal stereotypy in syllable order of adults (Williams et al. 1993). This type of song is referred to as isolate song. Previously untutored adult Zebra Finches have also been shown to copy new syllables from tutors or exemplars to which they are exposed at an age that is beyond the typical sensitive period of song learning in this species (Eales 1985; Morrison and Nottebohm 1993). Imitation and improvisation occur in each generation of males to produce normal (social) adult song. A recent experiment tracked the change in features of male song across multiple generations, but started with males that sang isolate songs as tutors (Fehér et al. 2009). The results were unexpected in that normal, species-typical song structure re-established themselves within approximately four generations in a closed microcosm where males of the previous generation served as song tutors for the next generation of males.

Such novel experimental paradigms and surprising findings also have critical implications and require new theory to explain the evolutionary benefit and cost of investment into the neural substrates of imprinting, copying and learning to generate song cultures. For example, pinpointing the relative roles of species identity versus tutoring experience in shaping generational cultural shifts could involve documenting the process of cultural evolution of song, and the impacts on female perception, across generations, starting with male Zebra Finch tutors singing heterospecific songs (e.g. through cross-fostering with Bengalese Munias (or Bengalese Finches, Lonchura striata var. domestica) as parents; Clayton 1989; Campbell and Hauber 2009a). Using cross-fostered males as initial tutors would be especially valuable because male Zebra Finches are imperfect mimics of Bengalese Munia songs: whereas they copy syllable structure closely, they retain some syntax and rhythm of Zebra Finch songs (e.g. Woolley et al. 2010). In turn, the neurophysiological basis of preferences in female Zebra Finches between normal songs and Bengalese Munia-like songs of conspecific males is still unresolved (Campbell and Hauber 2010b). Such new manipulations would thus both inform and challenge traditional hypotheses for the roles and consequences of early experience and learning in shaping species specificity in female choice for conspecific songs (see below).

**Song and female mate-choice**

Male song is one of the important cues for mate-choice in female Zebra Finches. Field and laboratory observations indicate that males readily approach single females, whereas females are more discriminating in their spatial approaches (Zann 1996; Campbell and Hauber 2009b). This is in concordance with general predictions of intersexual differences in the thresholds of mate-discrimination, as females bear a greater reproductive cost of erroneous mate-choice than do males, even in biparental species (Hauber and Lacey 2005). Choosing a suitable social partner and, eventually, a mate is essential in Zebra Finches in general, and for females in particular, because the pair-bond is lasting; separation apparently occurs only with the death of one partner (Zann 1996), and new research has confirmed that extra-pair fertilisations are rare in natural populations (Birkhead 2010; Griffith et al. 2010). Additionally, in the wild, the probability of offspring survival to sexual maturity is estimated to be as low as one in four (Zann 1996) and so a female’s choice of a mate, who is to provide parental care and genetic contributions to her offspring, has a critical impact on her own reproductive success, through both the physical condition and the genetic quality of the male.

Zebra Finches are not territorial and males sing to females at close range, within loose breeding colonies and large flocks (Zann 1996). Song is thus typically accompanied by other sensory and social cues, including colour of plumage and bill, body size and courtship dance. Several male morphological traits serve as visual cues for female Zebra Finches, signalling information that is relevant to mate-choice. Immelmann (1959), working on captive birds, initially identified bill-colour, eye-stripe, and tail-bands in male Zebra Finches as visual conspecific recognition signals for females. Since then, studies that tapped into the natural variation of vocal and visual sexual cues, and the experimental alteration of these traits, repeatedly demonstrated that hearing male vocalisations and perceiving other sensory cues, including colour of plumage and bill, interact to influence female attraction to potential mates (Campbell and Hauber 2009c, 2010b). The relative salience and role of these cues in female choice within natural populations, however, remain unclear, as does their developmental trajectory, with Richard Zann’s own last study on wild-caught birds demonstrating opposing effects of nutritional constraint during development in reducing the complexity of song displays, but not the accuracy of song copying, of male Zebra Finches (Zann and Cash 2008).

Although multimodal sensory cues are clearly involved in female mate-choice, including the synergistic effects of vision and hearing (Campbell and Hauber 2010a), many laboratory studies have shown that song alone can direct the choice behaviour of a female and predict which males are attractive (Miller 1979a, 1979b; Clayton 1990; Riebel et al. 2002; Tomaszycki and Adkins-Regan 2005; Holveck and Riebel 2007; Vignal et al. 2008; Campbell and Hauber 2009a; Vyas et al. 2009). Next, we discuss the role of male song in female mate-selection and how song preferences of females are related to pairing, mating and reproductive behaviours.

**Female behaviours that predict mate-preference**

To understand the role of male song in mate-choice by females, it is critical to describe and quantify female displays of social discrimination, sexual preferences, male attraction and mating decisions. Mate-choice-related behaviours in female Zebra Finches can be broadly grouped into three major classes. First,
females may display preference for particular songs or categories of songs (e.g. conspecific songs over heterospecific songs, familiar songs of the father over unfamiliar conspecific songs). This has been shown experimentally through spatial proximity to the source of song (Miller 1979b) or by active elicitation of song playback by females (Braaten and Reynolds 1999; Riebel 2009), or both. In these experimental paradigms, female Zebra Finches may approach or stay close to speakers that are playing particular songs more so than speakers playing other songs (Miller 1979b; Campbell et al. 2009a; Campbell and Hauber 2010b). Females may also hop on perches or peck keys that elicit the playback of particular songs more than they hop on perches or peck keys that elicit playback of other songs (Braaten and Reynolds 1999; Riebel 2000). These behaviours are typically interpreted in experimental reports as indicating attraction, although spatial proximity or key-pecking may or may not indicate sexual attraction and mate-choice (ten Cate and Mug 1984; see below). For example, spatial approach and elicitation of playback preferences can occur towards the songs of males that are unsuitable mates (e.g. fathers; Miller 1979b; Riebel 2000). Furthermore, both adult males and pre-reproductive juveniles show these types of song preferences (Braaten and Reynolds 1999). Therefore, female mate-choice may not be the only context that attracts Zebra Finches to particular songs.

Nevertheless, in many cases, spatial proximity to and elicitation of playback of specific songs are clearly related to female sexual attraction. For example, female Zebra Finches show spatial proximity preferences for conspecific songs over heterospecific songs (Clayton and Prove 1989; Braaten and Reynolds 1999; Lauay et al. 2004; Campbell et al. 2009a) and for the songs of their own mates (Miller 1979b; Clayton 1988; Woolley and Doupe 2008). The avoidance of the costs of hybridisation (Hauber et al. 2001) and delays in re-establishing the pair-bond (Adkins-Regan and Tomaszyczi 2007) is adaptive in systems with social monogamy, such as that of the Zebra Finch. Experimental work with playback of song or mate-choice has also shown that spatial proximity preferences of females towards particular classes of stimuli are consistent across trials and over time (Forstmeier and Birkhead 2004; Campbell et al. 2009a), and predict the rate of copulation solicitation displays (Witte 2006; Holveck and Riebel 2007) and pair-formation (Clayton 1990; Tomaszyczi and Adkins-Regan 2005; Campbell and Hauber 2010a). Therefore, spatial proximity and song-elicitation behaviours appear to indicate reliably sexual attraction in domesticated stocks of female Zebra Finches, although not consistently so in wild-caught stocks (Rutstein et al. 2007).

A second and more clearly identifiable class of female attraction behaviours to specific male songs is the production of social and sexual displays by females. These include ritualised hops on perches, tail-queriing (i.e. copulation solicitation displays; Morris 1954), body shakes, bill-wipes and the production of calls (Zann 1996). With the exception of calls, these behaviours typically do not occur in the absence of hearing male song (Zann 1996; Rutstein et al. 2007), and can be elicited by song alone (Clayton and Prove 1989; Campbell and Hauber 2009a; Vyas et al. 2009). Although there is increasing use of multiple attraction behaviours in assessing preferences (Campbell and Hauber 2009a, 2010b), the interpretation of behavioural responses by females could benefit from more detailed and multivariate analyses. Measuring additional features such as displacement behaviours (e.g. preening or feeding) could enhance understanding of, potentially, not just the absence of a preference, but an aversion to the male stimuli presented.

A third, and most committed, class of mate-choice behaviours for female Zebra Finches is pair-bonding and breeding. Stages of pair-bonding can be measured by observing clumping (sitting close together), allopreening, and nest-building. Successful breeding progresses from a female laying eggs, followed by both sexes incubating the eggs and ultimately, provisioning the hatchlings. Although studies measuring breeding-related behaviours require the use of live males, the role of male song per se in eliciting and maintaining female pair-bonding and mating behaviour can be studied using experimental manipulations. Examples of such manipulations with live stimuli include surgically muting the male to prevent him from singing (Tomaszyczi and Adkins-Regan 2006), raising juveniles in isolation from adult males to cause males to produce less-attractive, isolate songs (Lauay et al. 2004), and cross-fostering juveniles to broods of other species of finches to produce heterospecific-like songs (Woolley et al. 2010). Female nest-building, breeding-like hormonal states, and egg laying can be induced by playback of song alone, although combining playbacks with exposure to finch-like models of males or video playback of behaving males enhances female responsiveness (Tchernichovski et al. 1998; Campbell and Hauber 2010a).

The Zebra Finch has served as a prominent model system for the behavioural and developmental basis of mate-choice in vertebrates (Zann 1996), and several recent studies have examined in more detail the relationships between the characteristics of male songs and the adaptive consequences of female-choice (Forstmeier and Birkhead 2004; Holveck and Riebel 2007, 2010). One clear conclusion is that mate-choice is performed by both sexes, and involves more than just the discrimination of male song by females. This is likely because male choice for fecund and responsive females, and the resulting mutual mate-choice, benefits both sexes during their long-term social and genetic partnership (Wynn and Price 1993; Griffith et al. 2010; Holveck and Riebel 2010). We next discuss the aspects of song that appear to be attractive to females, some of the evolutionary explanations for why these features may be attractive, and several potential proximate mechanisms of how these features have an impact on the ontogeny and mechanisms of neural processes underlying female mate-choice.

**Aspects of song that attract females**

**Familiarity**

Female Zebra Finches prefer to hear familiar songs; they show preferential spatial proximity and peck at keys more often to hear songs that they have heard before. The two clearest examples of this effect are preferences for the songs of fathers and mates. Father-song preferences have been found using several methods of assessing female discrimination, including spatial proximity and playback elicitation (Miller 1979b; Clayton 1988, 1990; Riebel 2000; Riebel et al. 2002). Miller (1979b) found that exposure to fathers up until only 35 days of age was sufficient...
to acquire a memory of, and preference for, father song up to several months into adulthood, suggesting that early exposure is sufficient for long-term storage of acoustic memories. Social interactions between fathers and daughters are likely to be involved in the development of these preferences, but are not required; females that are exposed to male songs, but not live fathers, during development also show preferences for those same songs as adults (Riebel 2000). Therefore, familiarity with a song that was experienced during a critical stage of development, rather than the association of a song with the father, may cue a female’s recognition of her father’s song (Riebel 2003). The relevance of this effect for the dynamics of families and mating has yet to be tested in the wild, given that Zebra Finches disperse from their natal colonies after independence (Zann 1996).

The preferences of a female for hearing her mate’s songs have also been demonstrated using spatial proximity measures (Immelmann 1959; Miller 1979b; Clayton 1988; Woolley and Doupe 2008). Miller (1979a) showed that nearly all mated females preferred to perch near a speaker playing the songs of their mates, and some even preferred the songs of their prior mates after separation and forced re-pairing with a different mate, again suggesting long-term memory for a specific class of songs. The behavioural preferences of females for the song of their fathers and their mates imply attraction to familiar songs in social contexts that can be either sexual or non-sexual. Further understanding of the relative role of familiarity in female song-preference could examine the interplay between experience and male quality (as discussed below). For example, would females raised with exposure to low-quality song, upon reaching maturity, select low-quality songs that share acoustic features with the father’s songs over high-quality but unfamiliar songs?

Kin identity

As described above, male Zebra Finches learn to mimic the songs of their tutors, typically those of their fathers (Forstmeier et al. 2009), and female Zebra Finches show behavioural preferences that are consistent with long-term memory of the familiar songs of their fathers and male siblings (Miller 1979a; Riebel and Smallegange 2003). Therefore, song also has the potential to be used for kin-recognition (Burley et al. 1990; Zann 1997). Such familiarity-based kin-recognition was demonstrated in cooperatively breeding birds (Sharp et al. 2005), and could also be reliable for kin-recognition in a colonial, highly social system, such as that of Zebra Finches, if young male siblings were to learn songs exclusively from their genetic and social fathers in the wild as predictably as they do in captivity (Slater and Mann 1990; Zann 1996).

In contrast, the potential for familiarity-independent kin-recognition using song is weakened by recent investigations into the genetic basis of Zebra Finch vocalisations. Specifically, studies on the heritability of some song features, including length and repertoire size, showed heritability to be low when using an experiment-wide partial cross-fostering paradigm that disassociated genetic influences from parental effects into eggs and during early development (Forstmeier et al. 2009). The results imply that unfamiliar songs are less likely to carry predictably kin-relevant information. However, other song features may be influenced by more heritable aspects of morphology that are also known to influence acoustic features of vocal displays, including body size and bill-shape, through their impacts on frequency, tonality (timbre) and rate of production of syllables of male songs (Forstmeier et al. 2009).

Overall, it appears that irrespective of the relative salience of non-heritable versus heritable components of song features, female preference for kin vocalisations is extensively based on familiarity with the individual singing that song. Accordingly, adult females did not show consistent preferences in an operant task for the songs of their unfamiliar brothers despite the acoustical similarity of these songs to the familiar songs of their fathers (Riebel and Smallegange 2003; but see Miller 1979a). It is unlikely that the lack of such an effect was a result of small samples sizes in this recent study, because the same sample of female subjects was observed to display consistent preferences for familiar songs of relatives over unfamiliar songs of unrelated individuals in the same operant choice paradigm (Riebel et al. 2002). Further research is needed to confirm the degree to which specific characteristics of male songs can be and are used for recognising genetic relatedness in Zebra Finches in the wild, perhaps in the context to avoid costly inbreeding (Fetherston and Burley 1990) with unfamiliar relatives following natal dispersal (Zann 1996).

Species identity

To understand the role of song features other than familiarity in female preferences, it is necessary to decouple familiarity from other aspects of songs. Song-playback experiments using only unfamiliar (never before heard) stimuli have shown that female Zebra Finches are more attracted to conspecific songs than to heterospecific songs (ten Cate and Mug 1984; Clayton and Prove 1989; Clayton 1990; Braaten and Reynolds 1999; Riebel 2000; Brazas and Shimizu 2002; Lauay et al. 2004; Campbell and Hauber 2009a, 2010a). Clayton (1990) also demonstrated that females show preferences for the unfamiliar songs of their own subspecies (T. g. castanotis from mainland Australia v. T. g. guttata from the Lesser Sunda Islands). The physiological bases of conspecific song-preferences in female Zebra Finches are still unknown. Studies that investigate species differences in peripheral and central song processing and perception in female Zebra Finches are needed to understand the proximate mechanisms of behaviours that imply memory and recognition of vocal signals of species-identity (Hauber et al. 2007a, 2007b).

Several isolation-rearing and cross-fostering studies have addressed how developmental experience influences behavioural aspects of female conspecific song preferences. In isolation-rearing studies, females are raised without exposure to adult males (Hauber et al. 2007a). In cross-fostering studies, females are raised by adults of another species (usually Bengalese Munias; Campbell and Hauber 2009a; Woolley et al. 2010) or subspecies (Clayton 1987). The intent of both types of manipulations is to determine whether female song preferences are learned and, if so, to describe the effects of early auditory and social experience on song preferences and, presumably, mate-choice.
Females show behavioural discrimination between conspecific songs and songs of other species of bird that are phylogenetically and geographically distant from Zebra Finches; for example, females raised in isolation from singing males preferentially listen to playbacks of Zebra Finch songs over songs of Common Starlings (*Sturnus vulgaris*) and Common Canaries (*Serinus canaria*) (Braithen and Reynolds 1999; Lauay et al. 2004). This preference for conspecific song is shown by both sexes of juvenile and adult Zebra Finches (Braithen and Reynolds 1999; Campbell and Hauber 2010b), suggesting that the developmental origin of own-species song-preferences is a more general phenomenon and not limited to female mate-choice. Recent work has demonstrated that preferences of socially raised females for conspecific songs over songs of heterospecific African, Asian, and Australian estrildid finches do not depend on phylogenetic distance or geographical sympatry (Campbell et al. 2009a). Future work, however, should assess the strength of such conspecific song-preferences in the wild, as well as identifying the potential role of phylogeny and sympatry in preferences of females (and males) reared in isolation for conspecific songs over heterospecific songs (Campbell and Hauber 2009b).

Females that are cross-fostered show a developmental duality in species recognition: there is evidence of both an own-species bias and the role of early experience (Campbell and Hauber 2009a). For example, females that have been raised by Bengalese Munias are more likely to spend time perching near male Bengalese Munias than are females that have been raised by Zebra Finches, but overall spatial proximity and sexual display preferences are shown for male Zebra Finches (ten Cate and Mug 1984). When spatial proximity preferences for only the songs of different species were quantified for females that had been raised by Zebra Finches or Bengalese Munias, females that were raised by Zebra Finches preferred Zebra Finch song while the cross-fostered females did not discriminate among the songs of three different species (Campbell and Hauber 2009a). Yet, intraspecifically, females that are raised by adults of another subspecies show preferences for the foster-subspecies songs as adult Zebra Finches (Clayton 1990). These studies indicate that the social experiences of juveniles guide adult song preferences and that a juvenile’s experience with parental adults can be considered to be a form of sexual imprinting (ten Cate et al. 2006). The adaptive significance of sexual imprinting in directing female attraction to paternal-like songs is that it serves as a mechanism for matching a female with a conspecific male for mating (Irwin and Price 1999).

The neurophysiological mechanisms of sexual imprinting on parental songs are unknown in females. Further, the neural pathways that are involved in attending to, and that are shaped by, the perception of salient sexual signals during imprinting need to be identified. Another important topic for exploration is the neural basis of how auditory cues of species identity direct female attraction and sexual display behaviours to conspecific song. Subsequently, as with all model species, it also needs to be explored how the neural circuits that mediate song-processing and sexual attraction differ between Zebra Finches and other acoustically oriented species. Such neurophysiological work has only just begun to be conducted (e.g. Woolley et al. 2010) on comparing neuronal information coding in male Zebra Finches and Bengalese Munias). Important clues and future discoveries may come from understanding what acoustic aspects of conspecific songs serve as behavioural cues for female attraction (discussed in the next section below).

**Song-type**

The Zebra Finch song is not territorial in function and has been considered traditionally to serve in attracting and stimulating females (Morris 1954). However, the male sings two different song-types: directed and undirected songs. The production of either type is determined by immediate social cues, including proximity to female and male conspecifics (reviewed in Zann 1996). The presence of a female for example, elicits directed song that is typically sung at a faster rate, with more introductory elements and song phrases per bout, and is characteristically accompanied by the male courtship dance (Williams 2004). The undirected song, in contrast, is typically performed by a male in isolation or without a specifically intended receiver, although it too may serve as a general display to attract females and to advertise quality for potential extra-pair copulations (Dunn and Zann 1996; Holleck and Riebel 2010).

Numerous experiments have assessed female choice for conspecific males based on song (most recently extensively reviewed by Riebel 2009) and it appears that the directed song is what listening females approach preferentially (Woolley and Doupe 2008). This preference for an individual male’s directed song is strengthened by mating experience, with the strongest preference shown for the directed song of the female’s mate. This is consistent with the roles that directed song play in courtship and individual recognition of mates (Woolley and Doupe 2008). Once a pair-bond is formed, however, continued production of attractive songs (e.g. high rate, large repertoire of vocalisations; see below) is not required for pair-bond maintenance in Zebra Finches, as shown by the continued paired status between females and surgically muted or song-altered males (Tomaszczyki and Adkins-Regan 2006).

**Song-rate and repertoire size**

Features of the normal male song that appear to be particularly attractive to females are high rates of song output (ten Cate and Mug 1984; Collins et al. 1994) and high numbers of different syllables, also known as repertoire size (Clayton and Prove 1989; Holleck and Riebel 2007; Vyas et al. 2009). Playback of male Zebra Finch songs with more and different syllables, whether comprised of elements sung by the same male or combined from the songs of different males, are more attractive than repeated playback of the same syllables (Collins 1999). The length of syllables has also been found to be attractive to females, but this feature of song is often confounded with the presence of more song-elements in motifs (reviewed in Riebel 2009). Vyas et al. (2009) specifically tested whether females showed preferences, as indicated by more body shakes and calling, for complex songs or long simple songs (those that were long in duration but had relatively few song-elements) over shorter simple songs, and found that complex songs were preferred.

For females raised hearing normal adult vocalisations, songs produced by socially tutored males are preferred over the more poorly structured, less consistent, and higher pitched isolate songs
of males that have not been tutored (Lauay et al. 2004). Females are also sensitive to whether males sing acoustically intact songs; surgically altered males that sing abnormal songs are less attractive as indicated by female spatial proximity and pair-bond formation (Tomaszycki and Adkins-Regan 2005). Hearing male song during development is critical not only for the development of preferences for complex over simple songs or conspecific over heterospecific songs (Campbell and Hauber 2009a), but also for the development of consistent preference behaviours for the songs of the same individual males (Riebel 2009). This has been reported in both females (Riebel et al. 2002) and males (Pytte and Suthers 1999).

Female attraction to males that sing a more structured song composed of a larger repertoire of syllables may be adaptive, by directing females to males whose progeny are also likely to perform attractive songs. This is because the neural circuitry that controls song learning by, and vocal performance of, males (Airey et al. 2000) and the amount of paternal care contributing to predictable variation in neural, morphological and vocal traits, or both, may have considerably heritable components (Freeman-Gallant and Rothstein 1999). Future work aimed at estimating the true heritability of the genomic, anatomical, physiological and social basis of song behaviour will require cross-fostering paradigms aimed at estimating the contributions of shared genes (Forstmeier et al. 2009) from shared ontogenies (Ward et al. 2001).

There is also conflicting evidence on the role of the condition and social context of male chicks during early development on imitative learning and the structure of song in adulthood (Buchanan et al. 2004; Gil et al. 2006; Zann and Cash 2008). Male Zebra Finches that sing frequently must also maintain increased rates of oxygen and energy consumption to keep up this singing behaviour. Specifically, males must manage physiologically demanding rapid shifts during singing between the many vocal and silent intervals characteristic of Zebra Finch songs. This in turn, may modulate the overall cost of fast, transition-rich, song-production typical in this species (Franz and Goller 2003), and thus serve as both honest indicator and a constraint on the evolution of costly song display behaviour in male Zebra Finches.

Attributes of song, such as the number of elements per motif and rates of singing, are also correlated with morphological measures of male sexual displays (Holbeck and Riebel 2007) and with general learning ability, as assayed using a laboratory test of foraging problem-solving (Boogert et al. 2008). Furthermore, increased developmental stress is correlated with male songs that have fewer song-elements and are less attractive to females in adulthood (Spencer et al. 2005). Therefore, high-quality songs, in terms of acoustic repertoire and rate of output, signal a high-quality male. As discussed above, females that are attracted to these types of songs may benefit from selecting reliably high-quality mates regardless both genetic (Forstmeier et al. 2009) and parental contributions (Freeman-Gallant and Rothstein 1999). Further interpretation of female preferences and the role of the developmental environment might require investigations of whether exposure to typical high-quality male song while being reared in a nutritionally poor environment, and vice versa, might influence song preferences in adulthood. Correspondingly, recent studies have suggested that females may modulate their mate-choice criteria regarding male quality in response to their own perceived quality (e.g. through self-referenced phenotype matching; Hauber and Sherman 2001). For example, poor-condition females may benefit from being less choosy overall to avoid a prolonged search for a mate (Burley and Foster 2006). Alternatively, females in poor condition may even benefit from choosing males of low rather than high quality if less time and effort are required to compete for a high-quality male who may, in turn, opt to pair with a different, higher quality female (Holbeck and Riebel 2010). Assortative mating by quality is consistent with the patterns of mutual mate-choice by both sexes reported in captive Zebra Finches (Wynn and Price 1993). These recent studies on assortative mating based on self-perceived quality also call for a new way of theorising about how song may function in female mate-choice and raises several questions about how males and females pair in nature. For example, what range of quality is there among the potential breeders in wild Zebra Finch colonies, given the role of predation and other ecological constraints acting on reducing initial recruitment into the breeder pool? Also, do low-quality birds attempt to pair and breed or trade-off to increase condition until they reach a threshold at which pair-bonding and breeding are likely to succeed? If assortative and mutual-quality matching occurs in wild Zebra Finches, then the role of directional selection on male sexual signals, including song, in female mate-choice will have to be re-thought.

**Proximate mechanisms of female attraction to song**

*Hormones*

There is likely to be a dynamic interplay between behavioural interactions and hormone levels influencing selectivity in social species. For example, there is increasing evidence of behavioural and physiological feedback following manipulations of male traits relevant for female mate-prefeferences in Zebra Finches (Pariser et al. 2010), as well as in other species of bird (Rubensteins and Hauber 2008; Safran et al. 2008). For example, sex steroid hormones modulate female Zebra Finch reproductive behaviours, and may have an impact on female perception, discrimination and attraction to song (Adkins-Regan 2009). Yet, the activational role of oestrogen in female attraction to song requires further scrutiny. Historically, females, in which displays of sexual attraction, such as tail-quivers, are measured, have been treated with oestriadiol before playbacks, suggesting that higher oestriadiol levels promote sexual receptivity and display rate (e.g. Clayton and Prove 1989). Recent work using acute inhibition of oestrogen production in the auditory forebrain confirms a short time-scale at which oestrogen can act on neuronal and behavioural responses to male song (Remage-Healey et al. 2010) Specifically, Vyas et al. (2008, 2009) found that females preferred complex songs when they were treated with oestriadiol, but not when they had naturally low circulating levels of oestriadiol that were induced by isolating females from exposure to males. Taken together, the results of these studies suggest that higher oestrogen levels may modulate female responses to specific aspects of sexual attractiveness of male song. Accordingly, new data on the effects of oestrogen manipulations on gene expression and on the electrophysiological responses of neurons that are important for song processing (Tremere et al.
preference of female Zebra Finches. Nonetheless, it remains to be tested whether repeated playbacks of the same syllables cause neural habituation in the auditory nuclei of females, in parallel with the reduced behavioural preferences for less variable songs (Collins 1999). Progress is ongoing, however, as Tremere et al. (2009) recently found that acute, direct administration of oestradiol into NCM resulted in greatly increased firing rates of single neurons responding to song, thus providing a potential link between hormonal state and the neural processing of specific acoustic features of male song in the female brain.

Advancing the role of the Zebra Finch as a model species

The Zebra Finch has been a model species for diverse, insightful, surprising, technologically advancing, and controversial studies on the ultimate and proximate bases of reproductive vocal behaviour (Zann 1996; Zeigler and Marler 2008). There is a continuing need to follow the tradition of Richard Zann to test critical theory with observations and experiments in wild populations of Zebra Finches or, lacking experimental feasibility, strive for more specific comparisons between data collected from both wild-caught and domesticated strains of Zebra Finches (Rutstein et al. 2007). This research will also benefit from the application of rapidly advancing genomic and imaging technologies in the study of Zebra Finches in captivity as a model species (Boumans et al. 2007; Voss et al. 2007; Campbell et al. 2009b; Warren et al. 2010). The Zebra Finch is well positioned to maintain this driving role for research in the near future, as its full genome is only the second avian species genome to be sequenced (Hauber et al. 2008; Balakrishnan et al. 2010). More discoveries are surely to be gained from the ongoing advances of imaging-based and other in vivo and chronic neurobiological data-acquisition methods (Fee and Leonardo 2001; Maul et al. 2010). The research investment made to date combined with new technological advances will ensure that the Zebra Finch remains an important and productive model system for future work, including studies of the function and the theory of acoustic communication, species recognition and reproductive behaviours highlighted here.

Acknowledgements

This article is dedicated to Richard Zann’s memorable visit and departmental seminar at the School of Biological Sciences of the University of Auckland in late 2008 when M. E. Hauber and D. L. M. Campbell were based in New Zealand. We thank the referees and editors for their comments on draft manuscripts. For funding, we thank the Searle Scholars Fund, the US National Science Foundation and National Institutes of Health (to S. M. N. Woolley), and the Provost’s Office of Hunter College and the Research Foundation of the City University of New York (to M. E. Hauber).

References


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Manuscript received 24 January 2010, accepted 20 April 2010

http://www.publish.csiro.au/journals/emu