Animal Behaviour 97 (2014) 1–12

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Male mate preferences in mutual mate choice: finches modulate their songs across and within male–female interactions

Abbie Heinig, Santosh Pant, Jeffery L. Dunning, Aaron Bass, Zachary Coburn, Jonathan F. Prather*

Neuroscience Program, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, U.S.A.

ARTICLE INFO

Article history:
Received 7 April 2014
Initial acceptance 2 June 2014
Final acceptance 29 July 2014
Published online
MS. number: A14-00289R

Keywords:
Bengalese finch
female mate preference
Lonchura striata domestica
male mate preference
mutual mate choice
song entropy

Male songbirds use song to advertise their attractiveness as potential mates, and the properties of those songs have a powerful influence on female mate preferences. One idea is that males may exert themselves maximally in each song performance, consistent with female evaluation and formation of mate preferences being the primary contributors to mate choice. Alternatively, males may modulate their song behaviour to different degrees in the presence of different females, consistent with both male and female mate preferences contributing to mutual mate choice. Here we consider whether male Bengalese finches, *Lonchura striata domestica*, express mate preferences at the level of individual females, and whether those preferences are manifest as changes in song behaviour that are sufficient to influence female mate choice. We tested this idea by recording songs performed by individual unmated males during a series of 1 h interactions with each of many unmated females. Across recording sessions, males systematically varied both the quantity and the quality of the songs that they performed to different females. Males also varied their song properties throughout the course of each interaction, and behavioural tests using female birds revealed that songs performed at the onset of each interaction were significantly more attractive than songs performed by the same male later during the same interaction. This demonstration of context-specific variation in the properties of male reproductive signals and a role for that variation in shaping female mate preference reveals that male mate preferences play an important role in mutual mate choice in this species. Because these birds thrive so well in the laboratory and are so amenable to observation and experimentation across generations, these results yield a new model system that may prove especially advantageous in disentangling the role of male and female mate preferences in shaping mutual mate choice and its long-term benefits or consequences.

Male song is a primary reproductive signal in songbird mate choice. Many studies have documented the importance of male song in female mate choice (Collins, 2004; MacDougall-Shackleton, 1997; Riebel, 2009; Searcy & Yasukawa, 1996; Tomaszycki & Adkins-Regan, 2005). In some cases, song can have such a profound influence that females will solicit copulation in response to song alone, even if no male is present (Dunning, Pant, Bass, Coburn, & Prather, 2014; Nagle, Kreutzer, & Vallet, 2002; Searcy, 1992; West & King, 1988b). These data have led to the idea that males use song to advertise their attractiveness as potential mates, and females evaluate those songs and use that information to choose their mate. In that light, it is tempting to conclude that the decision of mate choice is made by the female, but it is not only female preferences that contribute to mate choice. Although the importance of female mate preferences has long been appreciated (Darwin, 1871), more recently we have also come to appreciate the importance of male mate preferences in mutual mate choice (reviewed in: Bonduriansky, 2009; Clutton-Brock, 2009; Edward & Chapman, 2011).

Theorists have posited that male mate preferences, evident as systematic differences in the quantity or quality of courtship behaviour that a male uses to court some females more than others, should be most evident in species in which (1) males encounter females simultaneously rather than sequentially, (2) males invest considerable resources in their displays to increase the number of females available for mating, (3) there is variation in female quality and the benefits of mate choice (male mate choice also occurs in species in which males do not make a significant contribution to offspring care; Amundsen, 2000; Amundsen & Forsgren, 2001; Bonduriansky, 2001) and (4) there is variation in the strength and

* Correspondence: J. F. Prather, 1000 East University Avenue, Department 3166, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, U.S.A.
E-mail address: Jonathan.Prather@uwyo.edu (J. F. Prather).

http://dx.doi.org/10.1016/j.anbehav.2014.08.016
0003-3472/

direction of an individual male's mating preferences (reviewed in Edward & Chapman, 2011). Songbirds are excellent subjects for studies of male mate preferences because many species, including the Bengalese finches, *Lonchura striata domestica*, studied here, are highly social and live together in dense colonies. Therefore, males commonly encounter many females simultaneously. Males of those species also sing frequently throughout the day and across many different social contexts, and song is a primary means through which females select their mates (Collins, Hubbard, & Houtman, 1994; Dunning et al., 2014; Woolley & Doupe, 2008). Thus, males invest considerable time and energy in their displays to increase the number of females available for mating. In addition, there can be stark differences in the number of offspring produced by different mated pairs (Godfray, Partridge, & Harvey, 1991; Martin, 1987; Winkler & Walters, 1983), consistent with variation in female quality and the benefits of mate choice. What remains unknown, however, is the degree to which individual males vary in their mate preferences, whether those preferences are of sufficiently high resolution that males express preferences for individual females and whether the behavioural manifestations of such preferences achieve functional significance by influencing female mate choice.

Previous studies of male songbirds reveal at least some contribution of male mate preferences in courtship behaviour. In studies of zebra finches, *Taeniopygia guttata*, another highly social species that lives together in dense colonies, males prefer females that are in especially good condition, reflecting the benefits obtained from a richly supplemented diet and predictive of greater fecundity (Jones, Monaghan, & Nager, 2001; Monaghan, Metcalfe, & Houston, 1996; Wynn & Price, 1993). The male's preference is evident in a greater amount of courtship behaviour directed towards females that are in good condition (e.g. approaching and lingering near the preferred female, etc.; either song was not considered apart from other courtship behaviours (Monaghan et al., 1996), or there was no difference in the amount of song performed to the female of either condition (Wynn & Price, 1993)). These data reveal that males can express a preference between categories of female quality, but they leave open the question of whether males modulate their song behaviour accordingly and whether they express that modulation as a function of individual female identity. In support of the possibility that males may modulate their songs to different degrees in the presence of different females, males of some species, including Bengalese finches, modulate their song properties when they sing directly to a female ('directed song') as opposed to when they sing alone ('undirected song') (Sakata, Hampton, & Brainard, 2008; Sossinka & Bohner, 1980). Females can detect those subtle differences and prefer directed songs more than the undirected songs performed by the same male (Dunning et al., 2014; Woolley & Doupe, 2008). Those data reveal at least some role for male song variation in shaping mate choice, but they do not address the resolution at which males express their mate preferences. It is known that males can modulate their behaviour based on female identity, as males perform greater amounts of song and express less aggression towards mates than they do towards nonmates (Caryl, 1976; Silcox & Evans, 1982) and females prefer their mate's songs (Miller, 1979; O'Loghlen & Beecher, 1996). However, those data do not address the important question of whether male song modulation is also evident at the level of individual females in the premated condition and whether that modulation is sufficient to bias the mate preferences of unmated females. Detection of such changes in male behaviour and a role for those changes in affecting female mate preference would reveal that male mate preferences also greatly influence mutual decisions of mate choice.

Our goals in this study were to determine whether unmated adult male Bengalese finches modulate the quantity and the quality of their songs to different degrees in different pairings with unmated adult females, and to determine whether those song changes achieve functional significance by affecting female mate preferences. To address our hypothesis that males vary their reproductive signalling when singing to each of many different females, we recorded males singing either alone or with each of many different females. We quantified the number of songs performed in each context, and we analysed the properties of those songs by computing their note transition entropy, a measure of note sequence complexity that has been shown previously to change between the directed and undirected conditions (Sakata et al., 2008) and that has been implicated as a possible contributor to female evaluation of song quality (Dunning et al., 2014). Differences in these parameters among songs performed by an individual male in different male–female contexts would support the idea that male Bengalese finches express mate preferences at the level of individual females and manifest those preferences as systematic variation in not only the quantity but also the quality of their reproductive signalling. To test our hypothesis that differences between songs recorded in different contexts are sufficient to affect female mate preferences, we used the songs performed by an individual male in different male–female contexts to test whether females could distinguish between those songs and whether they expressed a systematic preference for one or the other song variant. Detection of a systematic preference would reveal an important role for male mate preferences for individual females as a contributor to mutual mate choice and the control of vocal behaviour.

METHODS

Care and Handling of Experimental Subjects

We performed all experiments using adult (age > 120 days posthatch) male and female Bengalese finches obtained from a commercial breeder or from our breeding colony. Prior to experimentation, we identified males by their song performance and females by the presence of calls but the absence of song over 3 or more days of continuous recording. We housed birds in an aviary colony setting prior to experimentation (15:9 h light:dark photoperiod). During recording, we housed birds in a wire mesh cage ($41 \times 31 \times 24$ cm) inside a sound attenuation chamber (Industrial Acoustics Co., Bronx, NY, U.S.A., model MAC-1).

Ethical Note

We monitored the birds daily and provided seed and water ad libitum. We also minimized the number of times that birds were moved between cages and the duration of handling in each case. These measures ensured that the birds were treated as well as possible given the constraints of the experimental design. Consistent with that goal, all birds remained healthy and robust throughout the study. All procedures were approved by the University of Wyoming Animal Care and Use Committee (protocol number 20140506JP00106-02), were consistent with the ABS Guidelines for the Use of Animals in Research, and were in compliance with all state and federal regulations governing the housing and use of songbirds.

Recording Male Songs Alone or in the Presence of Different Females

Procedures were similar to those reported previously (Dunning et al., 2014). Briefly, we placed a microphone inside the sound-attenuating chamber and recorded continuously (Tchernichovski, Nottebohm, Ho, Pesaran, & Mitra, 2000). We band-pass filtered