Female zebra finches prefer unfamiliar males but not when watching noninteractive video

JOHN P. SWADDLE, LARA MCBRIDE & SABINA MALHOTRA

Institute for Integrative Bird Behavior Studies, Biology Department, College of William and Mary

There is great interest in investigating whether video can be used as an effective stimulus in avian behavioural research. Although there are clear predictions as to the efficacy and limitations of video, there are few empirical tests of whether video stimuli can elicit naturalistic behaviours in birds. Here we assess whether noninteractive digital video presented on flat thin-film transistor (TFT) monitors can be used in zebra finch mate choice studies. Specifically, we tested whether female finches prefer their pair-bonded male over an unfamiliar male when these males are presented as live birds or as noninteractive video images. Our data indicate that, when auditory cues are masked by white noise, female zebra finches strongly prefer to court unfamiliar live males. We hypothesize that the preference for unfamiliar males results from the masking of auditory cues that are crucial to pair-bond maintenance. In video stimulus trials, although females actively courted the video images of males more than they did live males in the live male trials, females did not prefer the unfamiliar males over their pair-bonded males. Therefore, noninteractive digital video presented on TFT screens solicits courtship behaviour from females but also fundamentally changes their mate preferences. We discuss these patterns in light of the possible visual and behavioural differences between the video and live male stimuli and conclude that video displayed on TFT monitors must be used with caution in mate preference studies.

There is substantial interest in investigating the utility of video stimuli in pure and applied avian behavioural research (reviews in D'Eath 1998; Fleishman et al. 1998; Oliveira et al. 2000). For example, digital video editing could be used to perform phenotypic manipulation experiments (Rosenthal 1999; Uetz & Smith 1999), allowing researchers to manipulate subtle aspects of physical appearance and to monitor behavioural responses. Video presentations also have potential in domestic and captive rearing situations to alleviate the stress of isolation cages, to teach birds to feed (Keeling & Hurnik 1993), or to help birds to show appropriate mating preferences and behaviours.

In the past decade researchers have reached a consensus opinion as to the likely limitations of video in avian behavioural research (see discussion in D'Eath 1998; Oliveira et al. 2000). To summarize, traditional cathode-ray tubes (CRT) cause temporal visual problems associated with flicker-fusion rate in avian visual systems. However, this issue can be circumvented by using a thin-film transistor (TFT) video monitor that has constantly illuminated elements (D'Eath 1998; Oliveira et al. 2000). These differences between CRT and TFT monitors appear meaningful because male zebra finches, *Taeniopygia guttata*, and Bengalese finches, *Lonchura striata*, will display vocally to conspecific female images on a TFT but not on a CRT monitor. Therefore, because we decided to study zebra finch responses to video, TFT monitors appear the better choice. Issues of depth perception and visual acuity causing screen pixilation can be reduced by ensuring that subjects do not get too close to the video screen. Similarly, the lack of depth cues in video images can be reduced if the natural image that is videotaped is limited to small variation in the depth axis and if the image is relatively sessile. Sound cues are often not reproduced or synchronized accurately through video playback. Masking sound with white noise or removing sound altogether are viable options for minimizing auditory problems (Oliveira et al. 2000). More insurmountable problems are the lack of behavioural interaction associated with a video image and the fundamental discrepancy in avian colour perception of a natural versus a video stimulus (Oliveira et al. 2000). Importantly, video screens do not emit light in the

ultraviolet (UV) range, yet many bird species perceive light within this range, and UV colours affect important behaviours, including mate preferences (Bennett et al. 1997; Hunt et al. 1997; Hunt et al. 2001). It is important to remember that video is a two-dimensional visual illusion that will never be identical to a live image. However, the illusion may be good enough to solicit appropriate behavioural responses in controlled experimental conditions.

Given the interest in using video stimuli in avian behavioural studies, there are surprisingly few empirical tests of whether video can elicit naturalistic behavioural responses. Under experimental conditions, video can stimulate antipredator (Evans et al. 1993), approach (Clarke & Jones 2001), aggregation (Watanabe 2002) and general sexual behaviours (e.g. Adret 1997; Ikebuchi & Okanoya 1999) in birds. However, to our knowledge, there have been no published tests of how video affects intraspecific mate preferences in any avian species. If we could perform mate choice tests with video stimuli, the power for explaining how phenotypes mediate sexual selection processes will be greatly increased (e.g. Rosenthal 1999; Uetz & Smith 1999).

Here we explore whether video presentation of males can affect mate preferences in the female zebra finch, *Taeniopygia guttata*. The zebra finch is a popular species for mate preference studies (e.g. Miller 1979; Clayton 1990; Swaddle & Cuthill 1994a; Burley et al. 1996; Price 1996; Swaddle 1996; Zann 1996; Cuthill et al. 1997; Birkhead et al. 1998; Adkins-Regan 2002; Royle et al. 2002; Blount et al. 2003). Zebra finches are small monogamous estrildid finches that establish long-term pair bonds (review in Zann 1996). In mate choice tests, paired females show strong preferences for their pair-bonded male over unfamiliar males (Clayton 1990; Zann 1996). We took advantage of these previous observations by testing whether females' preference for their pair-bonded male is influenced by presenting a noninteractive digital video of the same males on a flat TFT screen. In a pilot experiment, we attempted to compare preference for the same males when the live males and video males were behind one-way glass; hence creating noninteractive live males as an experimental treatment of comparison. However, for one-way glass to function there must be a significant illumination difference between the two side of the glass, being significantly darker on the female side so that the live males cannot see the females. Through dozens of trials, we could not successfully adjust the illumination of the apparatus and the total light output of the TFT monitors so that there was sufficient light on the female side of the glass for the females to show active courtship. Therefore, we compared the noninteractive video with interactive live males. In addition, we played white noise throughout the experiment to mask any confounding auditory cues.

We hypothesized that when viewing live males, females would prefer their pair-bonded male over a male they were unfamiliar with (i.e. an extrapair male). However, when viewing the same males by noninteractive video, we hypothesized that females would no longer prefer their pair-bonded male because they would not recognize him. Previous studies with chickens, *Gallus gallus domesticus*, indicate an inability of birds to recognize individuals in video presentations (D'Eath & Dawkins 1996). We also predicted that females would show less overall courtship activity in video trials than in live males trials, because the video stimuli would be less realistic than the live males and also less interactive, therefore excluding reciprocation in courtship activity.

METHODS

Housing Conditions

We arbitrarily paired 24 adult male wild-type zebra finches with 24 adult females. Males and females had previously been kept in single-sex groups and had no previous experience of the opposite sex. Paired birds were also not related to each other. All pairs were housed in wire cages (approximately $50 \times 40 \times 30$ cm) with a nestbox, two perches, and ad libitum access to water, cuttlebone, dry grass nesting material and nutritionally complete seed mix (Volkmann super finch blend). The cages were maintained in a room on a 14:10 h light:dark photoperiod with strip light illumination that had no ultraviolet (UV) wavelength emissions. The rooms were held at approximately $20°C$ and the cages were arranged so that pairs were visually but not acoustically isolated from each other. Birds remained in these cages for at least 5 months before starting mate preference trials and all pairs built nests and attempted to raise a clutch. Therefore, all females were pair-bonded with a male.

Mate Preference Trials

We conducted mate preference trials in a two-chamber mate choice apparatus situated in a different room from that of the housing cages (Fig. 1), but under the same general lighting conditions. In this apparatus, females could display relative preferences for two males. In all preference trials, one of these males was the female's pair-bonded male and the other male was the pair-bonded male of another female (randomly chosen from the pool of available males). Hence, each male appeared as a pair-bonded male for one female and as an unfamiliar male for another female. We conducted mate preference trials in three phases, in which each female chose between the same two males as: (1) live males, (2) noninteractive digital video images on flat TFT monitors, and (3) live males as in the first trial.

For initial live male trials, males were placed in smaller wire stimulus cages with ad libitum food and water (Fig. 1). Males could not see each other but had clear visual access to the female in the choice chamber. Note that females did not experience UV cues because of the overhead lighting conditions in the room. We played white noise at approximately 75 dB through two speakers placed between the male cages and female choice chamber. The speakers did not occlude the view of the males. To our perception, this noise masked most contact calling between the birds. We chose to mask calling to isolate the role of

Male 1   Male 2

Speaker   Speaker

Female

20 cm
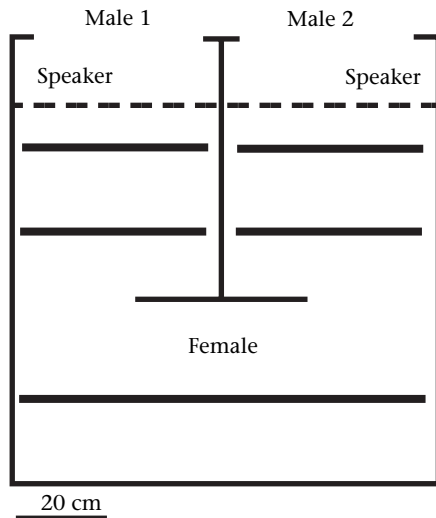
Figure 1. Plan view of the choice chamber. Two males were placed in stimulus cages outside the choice chamber, as indicated. Dark solid bars inside the chamber are perches that the female could display from. The dotted line represents a fine mesh that kept the female 20 cm from the males, or from the video screens. The video screens were placed in the same places as the males during the video stimulus trials. We played white noise through the two small speakers between the female and the stimulus males.

visual information in the females' mate preferences (Oliveira et al. 2000).

To begin each trial, the pair-bonded male of the focal female and a randomly assigned pair-bonded male of another female were placed in their stimulus cages and white barriers were placed between the male cages and the female chamber. The males were randomly assigned to the left or right stimulus cages. The female was released into the chamber and the white barriers were removed. After 30 min, an experimenter returned to the room, replaced the white barriers and switched the two male cages between their left and right positions. This action removed any possible side bias of a female. Once the males had been switched, we removed the white barriers and let the preference trial run for a further 30 min. The behaviour of the female was recorded on a Sony digital video camera for each complete trial. Because of the arrangement of the choice chamber (Fig. 1), we could not always see both males on this video; therefore, we did not quantify male behaviour.

In the analysis stage we ignored the first 10 min of the two 30-min portions of each trial and collected data from the two remaining 20-min periods. We considered the first 10 min to be an acclimation period for the female. From the tapes we calculated the time that each female spent engaged in courtship display activity (hopping between perches, turning, tail flicking and calling) in front of each male. We know from previous studies that this form of assay is a reliable indicator of mate preferences in female zebra finches (Burley et al. 1982; Burley 1988; Swaddle & Cuthill 1994b; Swaddle 1996; Zann 1996).

For the digital video presentation trials, we followed the same basic protocol except that we replaced the male stimulus cages with two identical flat TFT monitors (NEC MultiSync LCD 1720M). Again, females did not experience UV cues and we played white noise in every video preference trial. Before the mate preference trials, we recorded 70 min of digital video of each male used in the experiment. These videos were recorded on professional quality digital mini-dv tapes with a 3-CCD Sony digital video camera approximately 40 cm from the cage front. Males were individually recorded in cages identical to the stimulus cages except that the front bars of the cage were removed and replaced with a transparent Perspex screen to aid focus. Each male was recorded in isolation (i.e. without the presence of a female) and tended not to hop around within his cage or make vocalizations, although the birds did occasionally move laterally on the single perch in their cage. This lateral movement did not result in the bird going in and out of focus on the video. We did not formally quantify movement rates in these videos. We took great care to ensure that the videoed males appeared life-size on the TFT screens. The relative lack of movement of the videoed males also minimized problems of the lack of depth perception cues associated with video, as well as minimizing any possible ghosting or blurring of moving images on the TFT screens. Furthermore, we specifically designed the choice chamber so that the female could not get closer than 20 cm to the video screen, hence minimizing the probability that the visual acuity of the females caused apparent pixilation of the video stimuli and also reducing problems of inaccurate depth cues from a two-dimensional surface (Oliveira et al. 2000).

The digital video of each male was played through a SONY GVD1000 digital video deck connected to each TFT monitor via a Viewsonic VB50 HRTV conversion box. We adjusted the brightness of the TFT screens (approximately 18 foot candles measured with an A. W. Sperry Instruments Incorporated model SLM-110 light meter) to approximately match the ambient lighting in the previous (live) mate choice trials (Oliveira et al. 2000). No sound was played through the video screens; however, the two speakers played white noise in every video trial, as in all the live male trials.

To begin a video trial, we randomly assigned the video of the female's pair-bonded male to one screen (left or right) and assigned the video of the other male to the opposite screen. We started the tapes and lifted the white separation barriers, as for the first phase of the experiment. We also switched the tapes between the two screens after 30 min to control for any female side bias. As before, female behaviour in the video preference trials was recorded on videotape and analysed for the amount of time that each female spent displaying in front of the video display of the two males.

In a third phase of the experiment we repeated the initial live trials, following the protocol described earlier. These additional trials allowed us to compare the change in preference between two live male trials against the change associated with females' viewing a live and a video trial. Hence, we could disentangle repeated viewing from the general effects of video presentation.

For each female, the full sequence of mate preference trials (i.e. live–video–live) was conducted within a 4–5-day

time window. We conducted the experiment in two blocks. We tested 16 pairs of males and females in the first block and eight pairs in the second block. The experimental procedures and housing conditions were approved by our Institutional Animal Care and Use Committee (project approval no. 0311).

Statistical Analyses

To test whether females preferred their pair-bonded male over the unfamiliar male, we conducted paired t tests of the proportion of time spent displaying in front of each male. In this and subsequent analyses, proportional data were arcsine square-root transformed to fit assumptions of normality. To investigate the repeatability of mate preferences between the two live male trials, we conducted a repeated measures ANOVA testing whether the preference for the pair-bonded male changed within individuals over the two tests. We also calculated the coefficient of repeatability r_I, where r_I is calculated as the mean square among males minus the mean square within males, divided by the sum of these two terms (Zar 1999).

To explore whether females' mate preferences changed from the live to the video trials, we calculated the within-individual change in relative preference for the pair-bonded male from (1) the first to second live male trials, and (2) from the first live male to the video trial. We then compared the direction and intensity of these within-individual changes in preferences in a repeated measures ANOVA, comparing the within-female change in her preference associated with observing two live male trials versus a live male and video trial.

We also explored whether the amount of female courtship behaviour was affected by the video stimulus versus the live male stimulus by comparing the amount of time females spent displaying in the average of their two live male trials versus the video trial in a paired t test.

We conducted all analyses using SPSS v11 (Chicago, Illinois, U.S.A.) and used two-tailed tests of probability throughout. Means are reported with associated standard errors, unless otherwise indicated.

RESULTS

In both of the live male trials, females spent significantly more time displaying in front of the unfamiliar male compared with their paired male (paired t test by male (paired versus unfamiliar) of proportion of time spent displaying on nearest perches to live males: first trial: $t_{23} = 4.21$, $P < 0.001$; second trial: $t_{23} = 3.14$, $P = 0.005$; Fig. 2). Therefore, masking auditory cues with white noise during live male mate choice trials appeared to result in a significant preference for unfamiliar males over pair-bonded males.

We calculated the repeatability of mate preferences shown by females from the first to the second live male trials. There was no significant change in mate preference between the two live male trials (ANOVA: $F_{1,23} = 0.446$, $P = 0.511$; observed power = 0.098). Accordingly, mate preferences showed moderately high repeatability ($r_I = 0.61$).
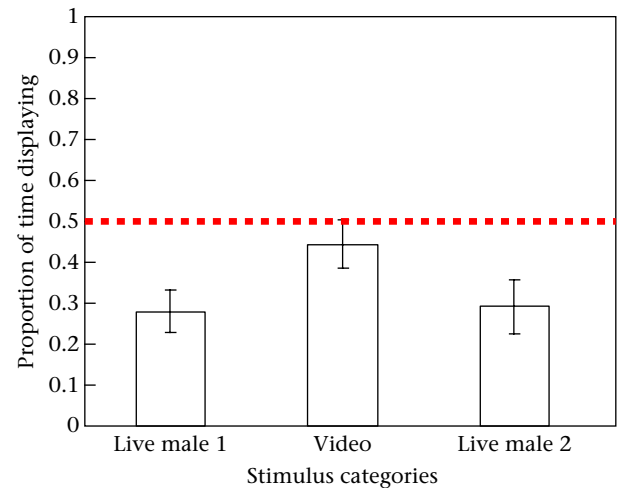

Figure 2. Mean ± SE proportion of time spent by females displaying in front of their pair-bonded male in the three stimulus treatments. The dotted line indicates no preference for either male. Values less than 0.5 indicate a preference for the unfamiliar male. Females consistently preferred the unfamiliar male in the live male trials. Females did not display a preference in the video trials.

When analysing mate preferences in the video trials, we observed a different pattern than in the live male trials. When presented with the video stimulus, females showed no preference for the unfamiliar male over their pair-bonded male (paired t test: $t_{23} = 0.93$, $P = 0.363$; Fig. 2). Consequently, there was a significant change in the females' mate preferences when seeing the males in a video compared with live trials (ANOVA: $F_{1,23} = 6.54$, $P = 0.018$).

Interestingly, females showed slightly more courtship behaviour in front of the video stimuli than in front of the live males (paired t test: $t_{23} = 2.32$, $P = 0.030$; Fig. 3). This pattern is consistent with females responding to the videos as if they were a sexual stimulus.

DISCUSSION

Our results indicate that female zebra finches respond to a noninteractive digital video of males displayed on a flat TFT monitor as if the cue is a sexual stimulus. Females rigorously courted the video presentations (Fig. 3). This result is consistent with those of other studies indicating that video elicits a sexual response in zebra finches (Adret 1997; Ikebuchi & Okanoya 1999) and seemingly naturalistic behavioural responses in birds in general (e.g. Evans et al. 1993; Keeling & Hurnik 1993; Shimizu 1998; Jitsumori et al. 1999; Clarke & Jones 2001; Lundberg & Keeling 2003). Females in our study appeared to court videoed males more actively than live males when audio cues were masked. There were, however, behavioural differences within males between the live and video trials that could help to explain this result. In the video, the males were noninteractive, so females may have increased their display rates in an effort to elicit a reciprocal response from the males. The observation that video elicited increased courtship is somewhat contrary to the accepted
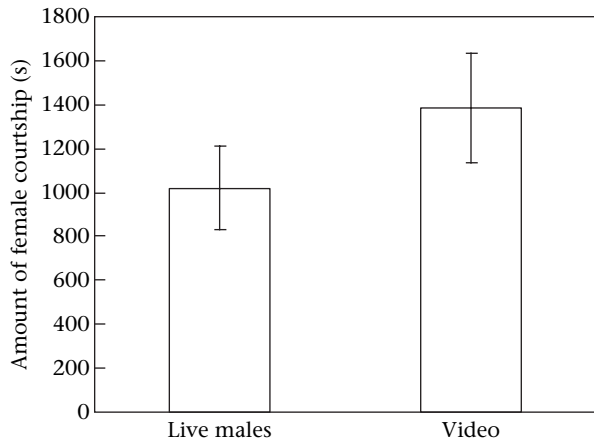
Figure 3. Mean ± SE time (in seconds) spent by females displaying in front of either male in the (average of the) two live male trials and the video trials. Females courted the video stimuli slightly more than the live males.

view that video is not an effective cue in avian visual studies (D'Eath 1998; Lea & Dittrich 1999; Oliveira et al. 2000). Therefore, by minimizing problems of mismatched audio cues, video screen refresh rates, image blurring, pixilation, depth cues and overall illumination differences (as through our methodology), video can be an effective sexual stimulus. If further experiments are performed to take into account interactivity between the observer and video model, better correspondence may be found between video and live trials.

The repeatability of the dichotomous mate preference in the two live male trials in our study is also consistent with that reported for female zebra finches in another study (Forstmeier & Birkhead 2004). Here we show that, even with the masking of audio cues, female zebra finches will show internally consistent mate preferences, further illustrating that female preference, although variable among females, is an inherent trait that can be quantified.

Although female zebra finches showed courtship behaviour in front of TFT video screens, females' mate preferences changed significantly when watching non-interactive video compared with the same live males. Specifically, the preference for unfamiliar males disappeared when choosing between the same males as a video stimulus (Fig. 2). This change (or loss) in preference may be because (1) the video males behaved differently (e.g. a general lack of sexual displays and interactivity), (2) males appeared fundamentally different on the video screen compared to real life, and (3) males behaved consistently differently in the choice chamber when they appeared as a pair-bonded versus an unfamiliar male. These explanations are expanded on below.

Females' preference for unfamiliar males cannot be based on morphological differences because every pair-bonded male appeared as an unfamiliar male in another trial. However, an important difference between our study and previous zebra finch preference trials is that we masked vocalizations by playing white noise in the choice chamber in all live and video trials. We hypothesize that the masked audio cues are important in maintaining pair

bonds and reducing the probability of extrapair behaviour. Audio cues appear to be important in establishing and maintaining such bonds in many bird species, including zebra finches (e.g. Miller 1979; Silcox & Evans 1982; Kellam 2003; Kumar 2004). In zebra finches, a variety of vocalizations and directed song are associated with courtship and nest building (such as kackle calls, arks and whines), all of which appear to be important in establishing a pair bond (Miller 1979; Silcox & Evans 1982; Clayton & Pröve 1989; Zann 1996; Balzer & Williams 1998; Forstmeier & Birkhead 2004). Therefore, it seems logical that these calls could also be important in maintaining the pair bond (Silcox & Evans 1982). In preference tests, females usually prefer the song of their pair-bonded male over the song of an unfamiliar male (Miller 1979).

In the live male trials, female zebra finches may have been actively soliciting extrapair copulations to gain some potential fitness benefit (e.g. Stutchbury 1998; Foerster et al. 2003; Westneat & Stewart 2003). Zebra finches commonly rear few extrapair young (<3%) in natural conditions (Birkhead et al. 1990; Zann 1996). However, Burley et al. (1996) have found much higher frequencies of extrapair young (28%) in a captive colony. Thus, our results may reflect primary female mate choice for extrapair partners in a captive situation. However, this explanation seems unlikely because the predicted frequency of extrapair young (based on rates of female copulation solicitations in this study) would be much greater than 28%. Thus, some feature of our choice chamber may have increased the probability of a female actively preferring the unfamiliar male over her pair-bonded male. The most likely feature is the masking of auditory cues (as discussed above). Therefore, we predict that blocking of auditory cues destabilizes pair bonds in zebra finches. This latter prediction raises the intriguing possibility that sound pollution in nature could increase the probability of extrapair copulations.

An additional explanation for why females' preferences changed when watching video is that females did not recognize either male in the video and, hence, showed no preference when watching the TFT monitors. There is precedent for such a mechanism, because chickens have difficulty recognizing individuals in video (D'Eath & Dawkins 1996).

Another possible explanation for our results is that the behaviour of the males changed when they were paired males versus unfamiliar males (Caryl 1976; Dunn & Zann 1997). Effectively, a male could make himself more attractive when experiencing a novel female than when courting his pair-bonded female (Caryl 1976). This hypothesis is speculative and could not be tested directly because we did not record male behaviour. If males do adjust their behaviour, this hypothesis could account for why female preference for the unfamiliar male occurred only in the live male trials. In the video trials, there should have been no consistent behavioural differences between the two males because we used the same video when the male stimulus was a pair-bonded male or an unfamiliar male. In future experiments it would be interesting to quantify male display rates directly and to control for this statistically in video trial comparisons.

It would also be interesting to control for the level of interactivity between video and live male stimuli. The lack of interactivity could fundamentally alter females' response to videos. Comparing female responses to active and relatively inactive male video stimuli would be a worthwhile follow-up to our initial study.

Overall, we reach mixed conclusions about the further use of noninteractive video stimuli in zebra finch sexual selection studies. If steps are taken to minimize the apparent mismatch of video with live images (e.g. flicker-fusion, pixilation, image blurring, depth cues, as we did in this experiment), video of males can solicit an appropriate sexual response from females (Adret 1997; Ikebuchi & Okanoya 1999). Although video does not replicate a live image (D'Eath 1998; Oliveira et al. 2000), it may appear to be good enough to solicit some natural courtship behaviours. However, the results of our study also indicate that stimulus males looked different enough in video that female mate preferences were eradicated when females chose between noninteractive video males and live males. We cannot say exactly why and how video males looked different to females than did live males (likely candidates are colour and behavioural differences, the latter of which could be minimized in further experiments), but these were not the focal questions of our study. We suggest that our most important result is that although digital video of males presented on TFT monitors can elicit substantial courtship behaviour from females, we also found it can fundamentally alter females' mate preferences. This latter finding has implications for many experimental studies of mate preference; just because an experimental cue (such as video) elicits courtship, we cannot assume that mate preferences have not been altered. Therefore, we conclude that the currently recommended application of video (Oliveira et al. 2000) is a useful research tool for some research questions, but it should be used with caution when exploring questions directly related to mate preferences or individual recognition, at least in zebra finches.

References

Adkins-Regan, E. 2002. Development of sexual partner preference in the zebra finch: a socially monogamous, pair-bonding animal. *Archives of Sexual Behavior*, **31**, 27–33.

Adret, P. 1997. Discrimination of video images by zebra finches (*Taeniopygia guttata*): direct evidence from song performance. *Journal of Comparative Psychology*, **111**, 115–125.

Balzer, A. L. & Williams, T. D. 1998. Do female zebra finches vary primary reproductive effort in relation to mate attractiveness? *Behaviour*, **135**, 297–309.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences, U.S.A.*, **94**, 8618–8621.

Birkhead, T. R., Burke, T., Zann, R. A., Hunter, F. M. & Krupa, A. P. 1990. Extrapair paternity and intraspecific brood parasitism in wild zebra finches, *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology*, **27**, 315–324.

Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1998. Sexual selection in the zebra finch *Taeniopygia guttata*: condition, sex traits and immune capacity. *Behavioral Ecology and Sociobiology*, **44**, 179–191.

Blount, J. D., Metcalfe, N. B., Birkhead, T. R. & Surai, P. F. 2003. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science*, **300**, 125–127.

Burley, N. 1988. Wild zebra finches have band-colour preferences. *Animal Behaviour*, **36**, 1235–1237.

Burley, N., Krantzberg, G. & Radman, P. 1982. Influence of colourbanding on the conspecific preferences of zebra finches. *Animal Behaviour*, **30**, 444–455.

Burley, N. T., Parker, P. G. & Lundy, K. 1996. Sexual selection and extrapair fertilization in a socially monogamous passerine, the zebra finch (*Taeniopygia guttata*). *Behavioral Ecology*, **7**, 218–226.

Caryl, P. G. 1976. Sexual behavior in the zebra finch *Taeniopygia guttata* response to familiar and novel partners. *Animal Behaviour*, **24**, 93–107.

Clarke, C. H. & Jones, R. B. 2001. Domestic chicks' runway responses to video images of conspecifics. *Applied Animal Behaviour Science*, **70**, 285–295.

Clayton, N. S. 1990. Mate choice and pair formation in Timor and Australian mainland zebra finches. *Animal Behaviour*, **39**, 474–480.

Clayton, N. S. & Pröve, E. 1989. Song discrimination in female zebra finches and Bengalese finches. *Animal Behaviour*, **38**, 352–362.

Cuthill, I. C., Hunt, S., Claery, C. & Clark, C. 1997. Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). *Proceedings of the Royal Society of London, Series B*, **264**, 1093–1099.

D'Eath, R. B. 1998. Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews*, **73**, 267–292.

D'Eath, R. B. & Dawkins, M. S. 1996. Laying hens do not discriminate between video images of conspecifics. *Animal Behaviour*, **52**, 903–912.

Dunn, A. M. & Zann, R. A. 1997. Effects of pair bond and presence of conspecifics on singing in captive zebra finches. *Behaviour*, **134**, 127–142.

Evans, C. S., Macedonia, J. M. & Marler, P. 1993. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Animal Behaviour*, **46**, 1–11.

Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainard, D. H. & Endler, J. A. 1998. Colour perception and the use of video playback experiments in animal behaviour. *Animal Behaviour*, **56**, 1035–1040.

Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. T. & Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature*, **425**, 714–717.

Forstmeier, W. & Birkhead, T. R. 2004. Repeatability of mate choice in the zebra finch: consistency within and between females. *Animal Behaviour*, **68**, 1017–1028.

Hunt, S., Cuthill, I. C., Swaddle, J. P. & Bennett, A. T. D. 1997. Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, **54**, 1383–1392.

Hunt, S., Cuthill, I. C., Bennett, A. T. D., Church, S. C. & Partridge, J. C. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? *Journal of Experimental Biology*, **204**, 2499–2507.

Ikebuchi, M. & Okanoya, K. 1999. Male zebra finches and Bengalese finches emit directed songs to the video of conspecific females projected onto a TFT display. *Zoological Science*, **16**, 63–70.

Jitsumori, M., Natori, M. & Okuyama, K. 1999. Recognition of moving video images of conspecifics by pigeons: effects of individuals, static and dynamic motion cues, and movement. *Animal Learning & Behavior*, **27**, 303–315.

Keeling, L. J. & Hurnik, J. F. 1993. Chickens show socially facilitated feeding behaviour in response to a video image of a conspecific. *Applied Animal Behaviour Science*, **36**, 223–231.

Kellam, J. S. 2003. Pair bond maintenance in pileated woodpeckers at roost sites during autumn. *Wilson Bulletin*, **115**, 186–192.

Kumar, A. 2004. Acoustic communication in the red-vented bulbul *Pycnonotus cafer*. *Anais da Academia Brasileira de Ciencias*, **76**, 350–358.

Lea, S. E. G. & Dittrich, W. H. 1999. What do birds see in moving video images? *Current Psychology of Cognition*, **18**, 765–803.

Lundberg, A. S. & Keeling, L. J. 2003. Social effects on dustbathing behaviour in laying hens: using video images to investigate effect of rank. *Applied Animal Behaviour Science*, **81**, 43–57.

Miller, D. B. 1979. The acoustic basis of mate recognition by female zebra finches *Taeniopygia guttata*. *Animal Behaviour*, **27**, 376–380.

Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J. A., Fleishman, L. J., Zeil, J., Barata, E., Burford, F., Gonçalves, D., Haley, M., Jakobsson, S., Jennions, M. D., Körner, K. E., Lindström, L., Peake, T., Pilastro, A., Pope, D. S., Roberts, S. G. B., Rowe, C., Smith, J. & Waas, J. R. 2000. Considerations on the use of video playbacks as visual stimuli: the Lisbon workshop consensus. *Acta Ethologica*, **3**, 61–65.

Price, D. K. 1996. Sexual selection, selection load and quantitative genetics of zebra finch bill colour. *Proceedings of the Royal Society of London, Series B*, **263**, 217–221.

Rosenthal, G. G. 1999. Using video playback to study sexual communication. *Environmental Biology of Fishes*, **56**, 307–316.

Royle, N. J., Hartley, I. R. & Parker, G. A. 2002. Sexual conflict reduces offspring fitness in zebra finches. *Nature*, **416**, 733–736.

Shimizu, T. 1998. Conspecific recognition in pigeons (*Columba livia*) using dynamic video images. *Behaviour*, **135**, 43–53.

Silcox, A. P. & Evans, S. M. 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch *Taeniopygia guttata*. *Animal Behaviour*, **30**, 1237–1243.

Stutchbury, B. J. M. 1998. Female male choice of extra-pair males: breeding synchrony is important. *Behavioral Ecology and Sociobiology*, **43**, 213–215.

Swaddle, J. P. 1996. Reproductive success and symmetry in zebra finches. *Animal Behaviour*, **51**, 203–210.

Swaddle, J. P. & Cuthill, I. C. 1994a. Female zebra finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society of London, Series B*, **258**, 267–271.

Swaddle, J. P. & Cuthill, I. C. 1994b. Preference for symmetric males by female zebra finches. *Nature*, **367**, 165–166.

Uetz, G. W. & Smith, E. I. 1999. Asymmetry in a visual signaling character and sexual selection in a wolf spider. *Behavioral Ecology and Sociobiology*, **45**, 87–93.

Watanabe, S. 2002. Preference for mirror images and video image in Java sparrows (*Padda oryzivora*). *Behavioural Processes*, **60**, 35–39.

Westneat, D. F. & Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology and Systematics*, **34**, 365–396.

Zann, R. A. 1996. *The Zebra Finch: a Synthesis of Field and Laboratory Studies*. Oxford: Oxford University Press.

Zar, J. H. 1999. *Biostatistical Analysis*. Upper Sadle River, New Jersey: Prentice Hall.