Acoustic mate copying: female cowbirds attend to other females' vocalizations to modify their song preferences

Grace Freed-Brown and David J. White*

Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA 19104, USA

We conducted a tutoring experiment to determine whether female brown-headed cowbirds (*Molothrus ater*) would attend to vocalizations of other females and use those cues to influence their own preferences for male courtship songs. We collected recordings of male songs that were unfamiliar to the subject females and paired half of the songs with female chatter vocalizations—vocalizations that females give in response to songs sung by males that are courting the females effectively. Thus, chatter immediately following a song provided a cue indicating that the song was sung by a male who was of high-enough quality to court a female successfully. Using a cross-over design, we tutored two groups of females with song–chatter pairings prior to the breeding season. In the breeding season, we placed the tutored females into sound-attenuating chambers and played them the same songs without the chatter. Females produced significantly more copulation solicitation displays in response to the songs that they had heard paired with chatter than to songs that had not been paired with chatter. This experiment is the first demonstration that females can modify their song preferences by attending to the vocal behaviour of other females.

Keywords: mate-choice copying; public information; female preferences; bird song; cowbirds

1. INTRODUCTION

Public information can have important influences on mating behaviour (White 2004; Valone 2007). Social experiences have been shown to modify mate choices and mate preferences in a variety of species (Westneat *et al.* 2000). Factors that modify females' mate preferences have been of particular interest because any change in preferences can produce a change in assortative mating and can thus influence the intensity of sexual selection (Wade & Pruett-Jones 1990; Gibson & Hoglund 1992; Kirkpatrick & Dugatkin 1994; Jennions & Petrie 1997). Social experiences can modify mate preferences in a number of ways. For example, exposure during development to males with specific characteristics can lead females to imprint on, and establish a preference for, those characteristics (ten Cate & Vos 1999; Payne *et al.* 2000). Also, and of interest to the present work, female preferences can be modified in adulthood by attending to and copying the mate choices of other females ('mate-choice copying'; White 2004).

Females may gain direct and indirect benefits from being able to modify their preferences in response to social information (Freeberg 2000). For example, attending to and copying the mate choices of experienced females may allow naive females to learn about the characteristics of high quality or attractive males. Also, by mating with a male that another female has chosen, a copying female will select a male that is of no lower quality than the choosing female's mate and she will avoid the costs associated with independently searching for and evaluating a mate (Gibson & Hoglund 1992; Pruett-Jones 1992).

Theory thus suggests that malleability in mating preferences can be beneficial. In songbirds, however, there has been limited evidence of malleability in preferences for male courtship song. While there is a large body of literature devoted to understanding the social factors that modify how males learn their songs (Catchpole & Slater 1995), there is comparatively limited evidence available on whether, and how, females learn their preferences. Traditionally, preferences for song have been considered to be consistent and inflexible to social experience. Females in many songbird species, however, have preferences for local song dialects (O'Loughlen & Rothstein 1995), which suggests that some learning must occur. Most work that has been done on learning of preferences has focused on how early experiences hearing song can shape preferences (Payne *et al.* 2000; Riebel 2000, 2003).

Brown-headed cowbirds (*Molothrus ater*) are gregarious songbirds that have been the subject of a large number of examinations of female preferences for male vocalizations (King & West 1983; King *et al.* 1986; Rothstein *et al.* 1988; O'Loughlen & Rothstein 2004). What benefits females gain from having preferences is unclear. Females gain few direct benefits from males; males do not hold territories, nor do they provide females with any resources. Also, since cowbirds are obligate brood parasites, males provide no parental care. It would therefore seem that song preferences provide females with indirect benefits of some sort. It would also seem that cowbirds could be a good system to investigate social influences on mate choice, given that there are few direct costs of copying other females' mate choices, such as no reduction of paternal care, or depletion of resources in a territory.

The development and malleability of female cowbirds' preferences for song have not been well studied (but see

*Author for correspondence (whitedj@psych.upenn.edu).

White *et al.* 2006). Since they are brood parasites, female cowbirds do not have the opportunity to experience and thus imprint on cowbird song early in life. Soon after fledging, however, they flock with other cowbirds. It is therefore possible that their preferences could be shaped by experiencing male song at this time, after they have left the nest and prior to the breeding season. However, experiments exposing females to different types of male song during this time have consistently failed to create any change in females' preferences. In fact, these experiments revealed that it was more likely that the male 'tutor' would change his song to match the female's preference rather than vice versa (West & King 1988).

Recently, evidence of plasticity in female cowbirds' preferences has been discovered (Gros-Louis *et al.* 2003; King *et al.* 2003; West *et al.* 2006). This series of experiments used tutoring preparations where females were exposed to broadcasts of song variants or to live males prior to the breeding season. Results revealed evidence of substantial malleability in song preferences in both young and adult females. The major difference in these experiments compared with the past failures to document malleability was that females were tutored in groups, not in social isolation. For some reason, social housing created substantial variability in females' song preferences. Thus mere exposure to song is not sufficient to modify their preferences; exposure to song must occur with other females present in order to produce malleability. Therefore, it is possible that females may be assessing the preferences of other females and copying them.

Mate-choice copying has not been studied in the context of song preferences in songbirds. It has, however, been a popular area of study in fishes (Dugatkin & Godin 1992; Schlupp *et al.* 1994; Grant & Green 1996; Schlupp & Ryan 1997; Patriquin-Meldrum & Godin 1998; Munger *et al.* 2004; Goulet & Goulet 2006; Widemo 2006; Heubel *et al.* 2008), birds (Hoglund *et al.* 1990; Fiske *et al.* 1996; Slagsvold & Viljugrein 1999; White & Galef 1999a; Doucet *et al.* 2004; Swaddle *et al.* 2005) and some mammals (Clutton-Brock & McComb 1993; Galef *et al.* 2008) including humans (Waynforth 2007). Results of this work have revealed mixed support for mate-choice copying and have shown that there are several mechanisms that can seem like copying, but do not lead to changes in preferences (Pruett-Jones 1992). For example, Clutton-Brock & McComb (1993) found that in fallow deer (*Dama dama*), females are attracted to areas where other females are located, but they do not modify their preferences for the males who happen to be in the area (see also White & Galef 1999c). Male behaviours (Grant & Green 1996) and territories (Jamieson 1995) may change in attractiveness as a consequence of courting or mating with a female, leading other females to be more likely to mate with that male, but again in these cases, females' preferences are not modified. When changes in preferences through mate-choice copying have been documented, it is rarely the case that the nature of the change in females' preferences can be determined. That is, it is usually unclear whether females have gained an enhanced preference for the individual male seen mating or a more general preference for other males with traits in common with the mated male (White & Galef 2000; Godin *et al.* 2005). This distinction is

important in determining how mate-choice copying will influence sexual selection.

The mixed results on how social factors influence preferences are in part due to methodological issues. In the field, it is often impossible to control the many extraneous variables needed to understand how female preferences may be changing (Hoglund *et al.* 1990, 1995), and in the laboratory, most demonstrations rely on using time spent near a male in a preference test as a proxy of the female's likelihood of mating with that male, a relationship that is rarely tested for validity and reliability (White & Galef 1999b).

One advantage in examining preferences in female songbirds is that there is a well-studied assay of preferences for song. King & West (1977) first demonstrated that wild-caught female brown-headed cowbirds housed in sound-attenuation chambers would respond with copulation solicitation displays ('postures') to recordings of variants of male courtship song (see also Searcy 1992). Some songs are more effective at eliciting the posture than others, and by using playbacks, it is possible to get a measure of a song's 'potency' or likelihood of triggering a female's posture. The posture has now been used to test song preferences in a wide variety of female songbirds. It is a clear and unambiguous indicator of a female's preference for a song, and it is a biologically relevant measure because triggering a posture with a song is the only way a male can copulate and reproduce.

Here we conducted an experimental examination of whether females can use mate-choice copying to modify their song preferences. We hypothesized that if females could copy other females' choices, they would need to be able to assess the females' preferences prior to the breeding season in order to take advantage of the time-limited breeding opportunity (approx. two months). In our experiment, we made use of one piece of public information that is a reliable acoustic signal of a female's preference and is available prior to the breeding season. The signal is a chatter vocalization that females produce early in the spring. The vocalization itself shows little developmental or geographical variation (Burnell & Rothstein 1994; see figure 1). Females begin to use it when males begin to court them consistently. Often, when males are successful in courting a female, the female will respond to his song overtures with chatter. The function of chatter is unclear, as it has not been extensively studied. Hauber *et al.* (2001) conducted one of the few studies examining the vocalization. They found that juvenile and adult cowbirds are attracted to broadcasts of chatter, and thus it might play a role in species recognition. This does not explain why females respond to preferred males with the chatter, but given that they do so, it can provide other females with reliable information about a male. Hearing a song immediately followed by chatter indicates that the singer is of high-enough quality to court a female successfully. Females who are not familiar with local males could gain information about the male's attractiveness or quality from attending to these vocal interactions.

We paired recordings of songs with recordings of chatter. We played these song-chatter combinations to two groups of females prior to their breeding season. Each group of females heard a set of songs paired with chatter and another set not paired with chatter. The sets of songs that were

Figure 1. Sound spectrograph recording showing a male's courtship song experimentally paired with female chatter. Spectrogram was made using BSOUND with IGORPRO v. 5.03 (<http://homepage.mac.com/bsnelson/BSound.html>).

paired with chatter were reversed for the two groups of females. We then placed the females into sound-attenuation chambers, played them the songs and measured how effective the songs were at eliciting females' postures. We hypothesized that if females were able to assess other female's mate choices and use them to modify their own song preferences, then songs paired with chatter would be preferred to songs that were not paired with chatter.

2. METHODS

(a) Subjects

Sixteen wild-caught females, trapped in Montgomery County, PA, USA, were used as subjects. Eight of the females were adults; they were at least 1 year of age and had experienced at least one breeding season. The other eight females were juveniles; they were less than 1 year old and had never experienced a breeding season. Prior to the experiment, all females had been living in mixed age and sex flocks in large outdoor aviaries. Aviaries were $18.3 \times 6.1 \times 4$ m and had trees, shrubs, grass and shelters. A mix of millet and canary seed plus a modified Bronx zoo diet for omnivorous birds and vitamin-treated water were provided ad libitum.

(b) Procedure

Beginning on 25 April 2008, we removed subject females from the four aviaries, randomly assigned them to two groups, and housed them in two outdoor $4.26 \times 1.67 \times 2.13$ m flight cages located at opposite ends of the University of Pennsylvania's avian behaviour field station. The two groups were visually and acoustically isolated from each other. Tutoring began on May 5. We broadcast tutoring recordings for 10 days.

(i) Tutoring recordings

Songs. We selected 10 songs from recordings of 10 captive males recorded in Monroe County, IN, USA in 2001. These males and their songs were unfamiliar to the females in the study. We had used these songs in several playback studies in the past and thus had information about other females' preferences for them. We divided these songs into two sets based on past females' preferences, such that both sets had songs of comparable potencies.

Chatter. We recorded chatter from the remaining females housed in the home aviaries. None of the chatter was taken from females that served as subjects in the experiment. We selected for tutoring three chatter vocalizations from each of five females based on recording quality.

We paired songs with chatter such that chatter commenced within 0.1 s of the end of the song (figure 1). This simulates the timing of singing and chattering of courting birds observed in the wild and in aviaries. Group 1 females heard set 1 songs paired with chatter and set 2 songs not paired with chatter. Group 2 females heard set 2 songs paired with chatter and set 1 songs not paired with chatter. Thus all females were exposed to the same songs, but the two groups of females heard a different set of the songs paired with chatter. We were concerned that females would habituate to the tutor songs because they would be hearing the same songs broadcast across a number of days. We attempted to reduce habituation by playing three different pairings of chatter with each song across tutoring sessions. It is possible that chatter can be individually distinct; therefore, we always paired recordings of the same female's chatter with one male's song. Thus across a tutoring session, females would hear an individual male's song paired with three different variants of an individual female's chatter. This is a reasonable simulation of courting birds, since crystallized song does not vary dramatically, but chatter does.

Tutoring sessions were conducted twice each day at approximately 10.00 and 13.00. Each tutoring session comprised a broadcast of the 10 songs played three times each across the session, with 3 min of silence between each song presentation. The tutoring session had approximately 30.5 min duration. The order of the song presentations was counterbalanced across sessions. The order was the same for both groups, and songs were played at the same time; the only difference between groups was in which songs were paired with chatter.

(ii) Evaluation of song preferences

On 15 May 2008, we removed females from the holding cages and placed them into 1 m^3 sound-attenuation chambers. We placed pairs of females into individual chambers because social housing drastically reduces the stress associated with being confined in the small chambers. Past analyses have shown that social housing has no effect on copulatory responses in playback tests (West *et al.* 1996;

Smith *et al.* 2000). Nevertheless, we paired females such that they were from the same tutoring group and they were of the same age class (adult or juvenile). Playbacks commenced the next day.

We conducted two sets of playbacks. First, we played a set of 11 songs from unfamiliar males in order to assess the concordance in preferences among females for a set of untutored songs. This playback set lasted 11 days. We used playback procedures based on published methods (West *et al.* 1996; White *et al.* 2002; King *et al.* 2003). Briefly, songs were played beginning at 6.00 each morning. We broadcast songs from a Compaq Deskpro computer through an LG XDSS amplifier to Bose 161 speakers located in each chamber. The sound pressure levels of the songs were 85 ± 2 dB (a weighted impulse reading at 0.8 m from the speaker—the distance between the females' perch and speaker). We played six songs per day to females with no less than 90 min elapsing between song presentations. Song order was counterbalanced across days such that each song was played equally often early, in the middle and late in the day. Closed circuit video cameras located in each chamber displayed females' responses on a monitor in another room of the laboratory. Three observers, blind to the tutoring condition of the females, recorded whether or not a song elicited a female's copulatory solicitation display. We presented each song six times across the playback session and measured how often each female responded with a posture. Thus, averaging this proportion of presentations receiving postures across females for each song provided a measure of the song's potency that ranged from 0 (no females ever responded to the song) to 1 (all females always responded to the song).

The second playback session commenced 2 days after the end of the first session. It consisted of playing the two sets of the tutor songs for 10 days. Song presentation was randomized, but counterbalanced across days. We did not play any chatter when testing these songs. We used the same procedure to assess females' preferences for the songs as in playback session 1. Here we compared within females how often they produced postures to songs that had been paired with chatter and to songs that had not been paired with chatter during tutoring. Owing to non-normal distributions in the data, we used paired and independent groups non-parametric statistics throughout, but we report means and standard errors for descriptive purposes.

3. RESULTS

In the first playback session of songs from unfamiliar males, females in the two groups showed significant concordance in their preferences for the songs, as measured by the number of postures they produced to the various songs (Kendall's test for concordance, $\chi^2 = 24.9$, d.f. = 9, $p < 0.001$). Thus, for the series of unfamiliar songs where no chatter was added, females in the two groups responded similarly. Six females failed to respond during the first playback session.

In the second playback session when females heard the tutor songs, they produced significantly more solicitation displays for the songs that had been paired with chatter than for the songs not paired with chatter (overall: paired Wilcoxon $T(13) = 1$, $p < 0.005$ (group 1 females: Wilcoxon $T(7) = 0$, $p < 0.02$; group 2 females: Wilcoxon $T(6) = 1$, $p < 0.05$); figure 2). One female from group 1

Figure 2. Mean (± 1 s.e.m.) potency scores for songs paired with chatter and songs not paired with chatter for the two groups of females. Potency was scored as the proportion of times each song elicited a copulation solicitation display from each female out of the six times each song was played during the playback tests. Group 1 females heard set 1 songs paired with chatter, and group 2 females heard set 2 songs paired with chatter. White bars, set 1 songs; black bars, set 2 songs.

(one juvenile) and two females from group 2 (one juvenile and one adult) did not respond with any solicitation displays for the entire playback session and were removed from testing.

We examined whether there was an age effect in responding to song paired with chatter. If copying other females allows inexperienced females to learn from experienced females about high-quality males, then chatter would be more likely to influence inexperienced juvenile females' song preferences than that of experienced adults. This, however, was not the case. For adult and juvenile females, we compared the magnitude of the difference in potency scores between songs paired with chatter and songs not paired with chatter. Juveniles did not show a significantly greater difference in preference for chatter-paired songs over unpaired songs than adult females (mean difference in potency between chatter-paired song and unpaired song: adults, 0.24 ± 0.04 ; juveniles, 0.20 ± 0.06 ; Mann-Whitney U -test = 18.5, $n = 13$, $p > 0.72$). Juvenile females showed overall higher rates of responding with solicitation displays than adults, but this difference did not reach significance (average response rate: adults, 0.54 ± 0.06 ; juveniles, 0.69 ± 0.06 ; $U = 12$, $n = 13$, $p > 0.195$) (figure 3).

Some female subjects were taken from the same holding aviaries in which we recorded chatter; thus they would have been familiar with some of the females who provided chatter. It was possible that chatter from familiar females might influence females differently than chatter from unfamiliar females. Seven of the subject females heard some songs that were paired with chatter from familiar females. For these seven females, we evaluated their rates of responding to songs paired with chatter from familiar females and compared them with the rates of responding to the same songs by females who were not familiar with the females that chattered. We found no effect of familiarity with the chattering female on rates

Figure 3. Mean (± 1 s.e.m.) potency scores for songs paired with chatter and songs not paired with chatter for juvenile and adult females. Black bars, adults; white bars, juveniles.

of responding (4/7 females responded more to the songs if the chattering female was familiar, binomial probability = 0.77, n.s.).

4. DISCUSSION

Females who heard songs followed by chatter in spring showed enhanced preferences for those songs in the breeding season. Females can therefore attend to public information associated with other females' mate choices and can use this information to modify their song preferences. This represents the first experimental manipulation of song preferences based on mate-choice copying. It is also the first time mate-choice copying has been documented using acoustic cues only. This preparation has advantages over other examinations of mate-choice copying because here we are able to control the many confounding variables present in the typical affiliation-time choice test procedure, such as possible changes in the male's behaviour as a consequence of mating or females' tendencies to aggregate with other females (e.g. Galef & White 1998).

Brood parasitic cowbirds would incur few direct costs in mate-choice copying. They would not suffer decreases in male parental care, nor suffer reductions in resources provided from the males. What benefits cowbirds gain by modifying their preferences, however, is unclear at this point. We hypothesized that juvenile females might be able to learn how to identify high quality or attractive males by copying more experienced females, but the results did not show an increased proclivity for juveniles to copy more than adults.

Another possible reason to copy mate choices would be to compete with other females. Copying females do not pay the costs associated with mate search and mate evaluation, and they mate with a male of no worse quality as the choosing female (Pruett-Jones 1992). We have seen some evidence of female competition in captive breeding conditions (unpublished data), but whether this plays any role in assortative mating is unknown. We also do not know whether the costs associated with mate searching in the wild are significant.

One way to investigate the function of mate-choice copying in cowbirds would be to examine what aspects

of females' preferences are being modified by social experiences. Are females gaining a preference for individual males, or are they gaining general preferences for song types? This will be the focus of future experiments, as the answer to the question may help in our understanding of why females copy and help to elucidate what impact copying may have on variance in mating success and sexual selection. For example, if females gain general preferences for song types, it could be that copying allows immigrating females to learn about local song dialects.

While the function and benefit of malleable preferences in cowbirds are unclear at this point, this experiment has revealed that there is in fact pronounced flexibility in song preferences. In the past, we have considered females' preferences to be the stable anchors in the cowbird social system, in contrast to males' songs, which are developmentally plastic; a result of their social experiences with other males and with females, all of which shape the form and quality of the male's final signal (West & King 1996). The results of this work suggest that we should think about females' preferences in the same way that we do males' songs—as a product of a lifetime's social experiences.

All work was done under animal use and care guidelines of the University of Pennsylvania (IACUC #800439).

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REFERENCES

- Burnell, K. & Rothstein, S. I. 1994 Variation in the structure of female brown-headed cowbird vocalizations and its relation to vocal function and development. *Condor* **96**, 703–715. (doi:10.2307/1369473)
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird song: biological themes and variations*. Cambridge, UK: Cambridge University Press.
- Clutton-Brock, T. & McComb, K. 1993 Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behav. Ecol.* **4**, 191–193. (doi:10.1093/beheco/4.3.191)
- Doucet, S. M., Yezerinac, S. M. & Montgomerie, R. 2004 Do female zebra finches (*Taeniopygia guttata*) copy each other's mate preferences? *Can. J. Zool.* **82**, 1–7. (doi:10.1139/z03-210)
- Dugatkin, L. A. & Godin, J. G. J. 1992 Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc. R. Soc. Lond. B* **249**, 179–184. (doi:10.1098/rspb.1992.0101)
- Fiske, P., Kalas, J. A. & Saether, S. A. 1996 Do female great snipe copy each other's mate choice? *Anim. Behav.* **51**, 1355–1362. (doi:10.1006/anbe.1996.0138)
- Freeberg, T. M. 2000 Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. *Behav. Process.* **51**, 177–192. (doi:10.1016/S0376-6357(00)00127-3)
- Galef Jr, B. G. & White, D. J. 1998 Mate-choice copying in Japanese quail *Coturnix coturnix japonica*. *Anim. Behav.* **55**, 545–552. (doi:10.1006/anbe.1997.0616)
- Galef, B. G., Lim, T. C. W. & Gilbert, G. S. 2008 Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. *Anim. Behav.* **75**, 1117–1123. (doi:10.1016/j.anbehav.2007.08.026)

- Gibson, R. M. & Hoglund, J. 1992 Copying and sexual selection. *Trends Ecol. Evol.* **7**, 229–232. (doi:10.1016/0169-5347(92)90050-L)
- Godin, J. G. J., Herdman, E. J. E. & Dugatkin, L. A. 2005 Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim. Behav.* **69**, 999–1005. (doi:10.1016/j.anbehav.2004.07.016)
- Goulet, D. & Goulet, T. L. 2006 Nonindependent mating in a coral reef damselfish: evidence of mate choice copying in the wild. *Behav. Ecol.* **17**, 998–1003. (doi:10.1093/beheco/arl032)
- Grant, J. W. A. & Green, L. D. 1996 Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*). *Behav. Ecol.* **7**, 165–167. (doi:10.1093/beheco/7.2.165)
- Gros-Louis, J., White, D. J., King, A. P. & West, M. J. 2003 Female brown-headed cowbirds' (*Molothrus ater*) social assortment changes in response to male song: a potential source of public information. *Behav. Ecol. Sociobiol.* **53**, 163–173.
- Hauber, M. E., Russo, S. A. & Sherman, P. W. 2001 A password for species recognition in a brood-parasitic bird. *Proc. R. Soc. Lond. B* **268**, 1041–1048. (doi:10.1098/rspb.2001.1617)
- Heubel, K. U., Hornhardt, K., Ollmann, T., Parzefall, J., Ryan, M. J. & Schlupp, I. 2008 Geographic variation in female mate-copying in the species complex of a unisexual fish, *Poecilia formosa*. *Behaviour* **145**, 1041–1064. (doi:10.1163/156853908784474533)
- Hoglund, J., Alatalo, R. V. & Lundberg, A. 1990 Copying the mate choice of others—observations on female Black grouse. *Behaviour* **114**, 221–231. (doi:10.1163/156853990X00130)
- Hoglund, J., Alatalo, R. V., Gibson, R. M. & Lundberg, A. 1995 Mate-choice copying in black grouse. *Anim. Behav.* **49**, 1627–1633. (doi:10.1016/0003-3472(95)90085-3)
- Jamieson, I. 1995 Female fish prefer to spawn in nests with eggs for reasons of mate choice copying or egg survival. *Am. Nat.* **145**, 824–832. (doi:10.1086/285770)
- Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Am. Nat.* **72**, 283–327.
- King, A. P. & West, M. J. 1977 Species identification in the North American cowbird: appropriate responses to abnormal song. *Science* **195**, 1002–1004. (doi:10.1126/science.841321)
- King, A. P. & West, M. J. 1983 Female perception of cowbird song: a closed developmental program. *Dev. Psychobiol.* **16**, 335–342. (doi:10.1002/dev.420160408)
- King, A. P., West, M. J. & Eastzer, D. H. 1986 Female cowbird song perception—evidence for different developmental programs within the same subspecies. *Ethology* **72**, 89–98.
- King, A. P., West, M. J. & White, D. J. 2003 Female cowbird song perception: evidence for plasticity of preference. *Ethology* **109**, 1–13. (doi:10.1046/j.0179-1613.2003.00924.x)
- Kirkpatrick, M. & Dugatkin, L. A. 1994 Sexual selection and the evolutionary effects of copying mate choice. *Behav. Ecol. Sociobiol.* **34**, 443–449. (doi:10.1007/BF00167336)
- Munger, L., Cruz, A. & Applebaum, S. 2004 Mate choice copying in female humpback limia (*Limia nigrofasciata*, family *Poeciliidae*). *Ethology* **110**, 563–573. (doi:10.1111/j.1439-0310.2004.00991.x)
- O'Loughlen, A. L. & Rothstein, S. I. 1995 Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behav. Ecol. Sociobiol.* **36**, 251–259. (doi:10.1007/BF00165834)
- O'Loughlen, A. L. & Rothstein, S. I. 2004 Divergent sexual responses to different categories of foreign courtship songs in female brown-headed cowbirds (*Molothrus ater*). *Auk* **121**, 824–836. (doi:10.1642/0004-8038(2004)121[0824:DSRTDC]2.0.CO;2)
- Patriquin-Meldrum, K. J. & Godin, J. G. J. 1998 Do female three-spined sticklebacks copy the mate choice of others? *Am. Nat.* **151**, 570–577. (doi:10.1086/286142)
- Payne, R. B., Payne, L. L., Woods, J. L. & Sorenson, M. D. 2000 Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Anim. Behav.* **59**, 69–81. (doi:10.1006/anbe.1999.1283)
- Pruett-Jones, S. 1992 Independent versus nonindependent mate choice—do females copy each other. *Am. Nat.* **140**, 1000–1009. (doi:10.1086/285452)
- Riebel, K. 2000 Early exposure leads to repeatable preferences for male song in female zebra finches. *Proc. R. Soc. Lond. B* **267**, 2553–2558. (doi:10.1098/rspb.2000.1320)
- Riebel, K. 2003 The 'mute' sex revisited: vocal production and perception learning in female songbirds. *Adv. Study Behav.* **33**, 49–86. (doi:10.1016/S0065-3454(03)33002-5)
- Rothstein, S. I., Yokel, D. A. & Fleischer, R. C. 1988 The agonistic and sexual functions of vocalizations of male brown-headed cowbirds, *Molothrus ater*. *Anim. Behav.* **36**, 73–86. (doi:10.1016/S0003-3472(88)80251-3)
- Schlupp, I. & Ryan, M. J. 1997 Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behav. Ecol.* **8**, 104–107. (doi:10.1093/beheco/8.1.104)
- Schlupp, I., Marler, C. & Ryan, M. J. 1994 Benefit to male sailfin mollies of mating with heterospecific females. *Science*, 373–374. (doi:10.1126/science.8278809)
- Searcy, W. A. 1992 Measuring responses of female birds to male song. In *Playback and studies of animal communication* (ed. P. K. McGregor), pp. 175–189. New York, NY: Plenum Press.
- Slagsvold, T. & Viljugrein, H. 1999 Mate choice copying versus preference for actively displaying males by female pied flycatchers. *Anim. Behav.* **57**, 679–686. (doi:10.1006/anbe.1998.0996)
- Smith, V. A., King, A. P. & West, M. J. 2000 A role of her own: female cowbirds, *Molothrus ater*, influence the development and outcome of song learning. *Anim. Behav.* **60**, 599–609. (doi:10.1006/anbe.2000.1531)
- Swaddle, J. P., Cathey, M. G., Correll, M. & Hodkinson, B. P. 2005 Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. *Proc. R. Soc. B* **272**, 1053–1058. (doi:10.1098/rspb.2005.3054)
- ten Cate, C. & Vos, D. R. 1999 Sexual imprinting and evolutionary processes in birds: a reassessment. *Adv. Study Behav.* **28**, 1–31. (doi:10.1016/S0065-3454(08)60214-4)
- Valone, T. J. 2007 From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behav. Ecol. Sociobiol.* **62**, 1–14. (doi:10.1007/s00265-007-0439-6)
- Wade, M. J. & Pruett-Jones, S. G. 1990 Female copying increases the variance in male mating success. *Proc. Natl Acad. Sci. USA* **87**, 5749–5753. (doi:10.1073/pnas.87.15.5749)
- Waynforth, D. 2007 Mate choice copying in humans. *Hum. Nat.* **18**, 264–271. (doi:10.1007/s12110-007-9004-2)
- West, M. J. & King, A. P. 1988 Female visual displays affect the development of male song in the cowbird. *Nature* **334**, 244–246. (doi:10.1038/334244a0)
- West, M. J. & King, A. P. 1996 Eco-gen-actics: a systems approach to the ontogeny of avian communication. In

- The evolution and ecology of acoustic communication in birds* (eds D. E. Kroodsma & E. H. Miller), pp. 20–38. Ithaca, NY: Cornell University Press.
- West, M. J., King, A. P. & Freeberg, T. M. 1996 Social malleability in cowbirds: new measures reveal new evidence of plasticity in the eastern subspecies (*Molothrus ater ater*). *J. Comp. Psychol.* **110**, 15–26. (doi:10.1037/0735-7036.110.1.15)
- West, M. J., King, A. P., White, D. J., Gros-Louis, J. & Freed-Brown, G. 2006 The development of local song preferences in female cowbirds (*Molothrus ater*): flock living stimulates learning. *Ethology* **112**, 1095–1107. (doi:10.1111/j.1439-0310.2006.01264.x)
- Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I. & Hein, W. K. 2000 Alternative mechanisms of nonindependent mate choice. *Anim. Behav.* **59**, 467–476. (doi:10.1006/anbe.1999.1341)
- White, D. J. 2004 Influences of social learning on mate-choice decisions. *Learn. Behav.* **32**, 105–113.
- White, D. J. & Galef, B. G. 1999a Mate choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Anim. Behav.* **57**, 465–473. (doi:10.1006/anbe.1998.1015)
- White, D. J. & Galef Jr, B. G. 1999b Affiliative preferences are stable and predict mate choices in both sexes of Japanese quail, *Coturnix japonica*. *Anim. Behav.* **58**, 865–871. (doi:10.1006/anbe.1999.1210)
- White, D. J. & Galef Jr, B. G. 1999c Mate-choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Anim. Behav.* **57**, 465–473. (doi:10.1006/anbe.1998.1015)
- White, D. J. & Galef Jr, B. G. 2000 Culture in quail: social influences on mate choices of female, *Coturnix japonica*. *Anim. Behav.* **59**, 975–979. (doi:10.1006/anbe.1999.1402)
- White, D. J., King, A. P. & West, M. J. 2002 Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). *Behav. Ecol.* **13**, 487–496. (doi:10.1093/beheco/13.4.487)
- White, D. J., Gros-Louis, J., King, A. P. & West, M. J. 2006 A method to measure the development of song preferences in female cowbirds, *Molothrus ater*. *Anim. Behav.* **72**, 181–188. (doi:10.1016/j.anbehav.2006.01.008)
- Widemo, M. S. 2006 Male but not female pipefish copy mate choice. *Behav. Ecol.* **17**, 255–259. (doi:10.1093/beheco/arj021)