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Effects of singing on copulation success and egg production

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in brown-headed cowbirds, *Molothrus ater*

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5 1 Effects of singing on copulation success and egg production6  
7 2 in brown-headed cowbirds, *Molothrus ater*8  
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10 3 Abstract: We examined the relationship between singing and reproductive success in  
11 4 cowbirds. We amassed data from 17 captive flocks (164 males, 167 females) that we  
12 5 have studied over four years. For each flock, we conducted extensive observations on  
13 6 social interactions as the birds competed, courted, and reproduced. We collected and  
14 7 incubated all eggs laid during the breeding season and performed parentage analyses on  
15 8 the seven flocks with the highest levels of egg production. Finally, we measured males'  
16 9 song quality in playback tests. Here we assessed what aspects of singing were associated  
17 10 with (1) copulation success and (2) offspring production. Results differed for these two  
18 11 measures of reproductive success because of high variance in egg production within and  
19 12 across groups. The overall amount of songs males directed to females, a measure of  
20 13 courtship persistence, was the one variable strongly associated with males' copulation  
21 14 success. For offspring production, there was significant between-flock variability that  
22 15 was more pronounced than the within-group variability. The one variable that was found  
23 16 to be strongly associated with eggs laid within and across groups was the amount of  
24 17 countersinging males produced; a measure of male-male singing competition. Song  
25 18 attractiveness did not predict any unique variance in either measure of reproductive  
26 19 success. The relationship between female egg production and male competition suggests  
27 20 that females may be trading off current versus future reproduction based on the  
28 21 opportunities available in groups to evaluate males' competitive abilities.29  
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54 22 **Key words:** birdsong, social behavior, egg production, cowbird, reproductive success  
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5 1 In communication research, much interest has centered on the relationship between  
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7 2 signals and reproductive success. Examining the characteristics of signals that lead to  
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10 3 enhanced mating success can provide a means to determine how a communication system  
11  
12 4 may have evolved (Searcy and Nowicki, 2005) and how sexual selection may operate on  
13  
14 5 signals and signaling (Andersson, 1994).

16  
17 6 Bird song has been a particularly effective model for studying how signals relate  
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19 7 to reproductive success. In many species, male birds sing to attract females, and courtship  
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21 8 songs elicit females' copulation solicitation displays (Catchpole, 1987). Thus having an  
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23 9 attractive signal is a necessary component of a male's reproductive success. Males also  
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26 10 use song in interactions with other males and these interactions can influence who is  
27  
28 11 ultimately able to reproduce (Nowicki and Searcy, 2005; Searcy and Andersson, 1986).  
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31 12 Evidence of song's contribution to reproductive success comes from extensive studies:  
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33 13 (1) in the field, where characteristics of song and mating success can be measured  
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35 14 (Alatalo et al., 1990; Baker and Boylan, 1999; MacDougall-Shackleton et al., 2002; Otter  
36  
37 15 et al., 2001; Payne and Payne, 1993; Rehsteiner et al., 1998; Searcy, 1984), and (2) in the  
38  
39 16 lab where controlled investigations of females' song preferences can be assessed  
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42 17 (Holveck and Riebel, 2007; King and West, 1977a; O'Loughlen and Beecher, 1997;  
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44 18 O'Loughlen and Rothstein, 1995; Pasteau et al., 2009; Searcy, 1981; Searcy, 1984; Searcy,  
45  
46 19 1992). This body of research has provided a wealth of data on the wide variety of song  
47  
48 20 and singing characteristics that may be important to reproductive success, such as song  
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50 21 quality, song complexity, repertoire size, amplitude, singing effort, song matching and  
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52 22 sharing (Catchpole and Slater, 1995; Howard, 1974; Kroodsma and Byers, 1991;  
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5 1 Kroodsma and Miller, 1996; Marler and Slabbekoorn, 2004; Nordby et al., 1999; Searcy  
6  
7 2 and Andersson, 1986; Smith, 1977). Song can be an indicator of a male's: resource  
8  
9 3 holding potential, health, learning ability, developmental resilience to stress, attentiveness  
10  
11 4 to females, or social skills.  
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14 5 One challenge in examining the link between song characteristics and  
15  
16 6 reproductive success has been in tying together lab examinations of female preferences  
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18 7 with mating patterns seen in the wild. Often, the relationship between mate preferences  
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20 8 and mate choice is not a simple one. The lab preparation, removed from the context in  
21  
22 9 which mating occurs, fails to incorporate many aspects of social life. Male or female  
23  
24 10 competition, for example can influence reproductive success and change the relationships  
25  
26 11 between traits females prefer and traits that are ultimately selected (Beecher, 1996;  
27  
28 12 Nordby et al., 2000; Searcy, 1984). Alternatively, research in the wild often lacks the  
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30 13 control necessary to be able to isolate the important aspects of singing from many of the  
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32 14 other covarying factors that may influence mating success.  
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38 15 The goal of this work was to examine the relationship between characteristics of  
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40 16 song and reproductive success in a controlled lab environment, but in a context that  
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42 17 provided individuals enough freedom to live and breed in groups. We studied brown-  
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44 18 headed cowbirds, a gregarious songbird. The cowbird serves as an excellent model for  
45  
46 19 studying relationships between social behavior and reproductive success because wild-  
47  
48 20 caught individuals will breed in large outdoor aviaries. There are of course many  
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50 21 differences between flocks in captivity and in the wild (food availability, shelter, range  
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52 22 size, and safety from predation for example). Thus, captive flocks cannot be considered  
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5 1 analogous to populations in the wild. They do, however, offer a powerful means to  
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7 2 control aspects of social systems that cannot be controlled in the field. In our captive  
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9 3 flocks, birds court, copulate, and lay eggs in mock nests. These patterns of behavior do  
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11 4 resemble the seasonal patterns of singing, courting and mating reported in the wild  
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13 5 (Friedmann, 1929; Ortega, 1998; Smith et al., 2000). There is, however, wide variation in  
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15 6 field reports of cowbird social demographics and in social behavior (Brainard, 1998). In  
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17 7 the lab, we can have some control over aspects of the social and physical environment,  
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19 8 providing a means to assess how social interactions may influence reproductive success.  
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24 9 We are also able to examine female preferences for male courtship song by  
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26 10 measuring copulation solicitation displays given by females in response to recordings of  
27  
28 11 songs played in sound attenuation chambers (King and West, 1977). Thus we can have  
29  
30 12 controlled measures of females' preferences for songs and we can also measure actual  
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32 13 mating patterns of birds in groups. Observations of birds during the breeding season  
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34 14 provide us with measures of song use; as males use song to compete with other males, to  
35  
36 15 court, and to copulate. Past work has revealed that song use can vary dramatically across  
37  
38 16 males and can be influenced by social experiences during development. For example,  
39  
40 17 juvenile males who had experience with adult males learn to engage in more social  
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42 18 singing (to both males and females) than juveniles who do not have social experiences  
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44 19 with adult males (White et al., 2007; White et al., 2002b). Experienced juveniles also  
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46 20 engage in countersinging bouts more often than naive juveniles (White et al., 2007).  
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48 21 Cowbird countersinging differs from what is typically considered under this term, which  
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50 22 usually refers to males matching song types with neighbors across long distances  
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1 (Beecher et al., 2000). Male cowbirds are not territorial, so countersinging takes place at  
2 very close distances (often within inches). Countersingers alternate songs and can sing  
3 flurries of songs rapidly (routinely singing 10 or more songs per minute). Singing to other  
4 males is related to dominance (Dufty, 1986; Rothstein et al., 1988), but countersinging  
5 also seems to have an influence on females. In groups producing high levels of  
6 countersinging, females more frequently approach and spend time near the males (King  
7 et al., 2003; West et al., 2002).

8           Cowbirds are obligate brood parasites and are therefore not constrained in their  
9 reproduction by the burden of parental care. They thus have the potential to lay more  
10 eggs than species that must care for their young. In our captive conditions we are able to  
11 collect and incubate all eggs laid in the breeding season to get measures of reproductive  
12 output. In the past we have been struck by the wide variation in egg production we have  
13 found across different groups (King et al., 2003; West et al., 2002), but we have never,  
14 until now, had a sample size of independent groups large enough to examine this  
15 variability in detail. We have not been able, for example, to determine whether the  
16 across-group variability was due to a few extremely fecund females, or whether females  
17 as a group were stimulated to lay eggs as a consequence of overall aspects of the social  
18 group. Either way, if females have control over their egg production and vary  
19 reproductive output in response to the qualities of the males present, then this could have  
20 an effect on reproductive success and on selection. Given a large enough sample size we  
21 should be able to assess what characteristics of males may be associated with  
22 reproductive stimulation.

1 Here we report on the patterns and relationships among social behavior and  
2 reproductive success in captive flocks of cowbirds, using extensive datasets of the social  
3 and singing behavior of 331 birds (164 males, 167 females), the complete egg production  
4 of females spanning four years for 17 captive flocks, microsatellite parentage analysis on  
5 seven of the flocks with highest egg production, and finally, results of song playback tests  
6 examining female preferences for recordings of songs from the majority of the males in  
7 the groups.

## 8 Methods

9 Subjects. We caught all birds in Monroe County, IN from 1999-2004, and housed them in  
10 9.1 x 21.4 x 3.4 m aviaries (see table 1). Aviaries contained trees, perches, ground cover,  
11 and indoor shelters. Birds had *ad libitum* access to water and a modified Bronx zoo diet  
12 for omnivorous birds plus canary seed and red and white millet. In the breeding season,  
13 we supplemented the diet with 1/4-cup crushed oyster shell per aviary. These flocks have  
14 been the subject of several studies in the past. In all cases, the only difference across the  
15 groups was in their age class composition (see table 1). For more details about the social  
16 compositions of the flocks, refer to the individual studies (King et al., 2003; West et al.,  
17 2002; White et al., 2002b; White et al., 2002c)

## 18 Measures

19 For all groups, three observers took extensive measures of social behavior prior  
20 to, and during the breeding season. We used a speech-recognition data collection system  
21 to record the timing of behavioral events continuously (White et al., 2002a). We report  
22 data from samples during the time that eggs were collected (May 1 – June 10).

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5 1 Song use: We noted patterns and amount of male vocalizations in 15-min censuses  
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7 2 (White et al., 2002b). Within each census, we noted the individual who sang or whistled,  
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9 3 whether it was directed to another bird (sung within 60 cm and oriented toward another  
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11 4 individual), or was undirected. We programmed our database to determine whether or not  
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13 5 song occurred in a countersinging bout. A vocalization occurred in a countersinging bout  
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15 6 if the recipient of a directed vocalization responded to the singer with a directed  
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17 7 vocalization within 15 sec. Past work has suggested that countersinging is a more  
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19 8 sensitive measure of male singing competition than is male directed singing alone (King  
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21 9 et al., 2003; White et al., 2007). We also recorded all observed copulations. The  
22  
23 10 automated speech recognition system provided us with high levels of interobserver  
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25 11 reliability in song censuses (song per male;  $r = .98$ ,  $p < .001$ ). Since we collected different  
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27 12 numbers of censuses across the groups, we controlled for this by transforming all  
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29 13 measures to be per 15-min data collection block (each individual's measures divided by  
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31 14 the total number of censuses taken on the group).

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33 15 Song playbacks: We made breeding season audio recordings of songs of males within the  
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35 16 flocks and played them to females in sound attenuating chambers. The 64 female subjects  
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37 17 used for playbacks were unfamiliar with the males whose songs were being tested. They  
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39 18 were of the same age range as the females in the rest of the study and had been housed in  
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41 19 aviaries with males prior to being placed in sound attenuation chambers. We measured  
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43 20 each song's 'potency', or effectiveness at eliciting females' copulatory postures (see  
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45 21 West et al., 2002; White et al., 2002b for details of playback procedure). We played back  
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47 22 songs from males from ten of the flocks. We selected one song from each male based on  
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1 recording quality for playback. Time did not permit us to test multiple songs from each  
2 male. Potency scores from different songs of the same male typically do not vary  
3 substantially (unpublished observations). We conducted playbacks of pairs of aviaries  
4 over the course of four breeding seasons. Each song was played six times in total to  
5 females and we scored for each song how often females responded to the playback with a  
6 copulation solicitation display.

7 Egg collection: At approximately 0530 h each morning in the breeding season we  
8 collected all eggs laid in all groups. We incubated eggs for 10 days to determine whether  
9 they were fertile. Mock nests in the aviaries contained grass clippings and yogurt-covered  
10 peanuts that served as false eggs. For further details of sampling procedures, refer to the  
11 within-year studies (King et al., 2003; West et al., 2002; White et al., 2002a; White et al.,  
12 2002b; White et al., 2002c).

13 Microsatellite analysis. We conducted a parentage analysis on a sample of seven of the  
14 aviaries (\* groups in Table 1). The seven aviaries chosen were ones that produced enough  
15 eggs to allow us the possibility of detecting patterns of successful reproduction among  
16 individuals within groups. We used microsatellite markers to assign maternity and  
17 paternity to each fertile egg. We collected blood samples (50 – 100  $\mu$ l) from all putative  
18 parents by puncture of the brachial vein and we stored the blood at -20°C until needed for  
19 analysis. Whole embryos were harvested on day 10 of incubation and also stored at -  
20 20°C. We extracted DNA from both blood and embryo using standard organic solvent  
21 purification (Sambrook and Russel, 2001).

1 We determined parentage using four pairs of nuclear microsatellite markers  
2 (*Maμ20*, *Maμ25*, *Maμ29*, and *Dpμ16*) either developed specifically for brown-headed  
3 cowbirds (Alderson et al., 1999) or for yellow warblers (*Dendroica petechia*) (Dawson et  
4 al., 1997). We followed Alderson et al. (Alderson et al., 1999) for PCR reaction  
5 conditions for all primers. We analyzed amplification products on an ABI PRISM 310  
6 Genetic Analyzer (Applied Biosystems). We then further analyzed the resulting data with  
7 the Genescan® Analysis 2.0.2 and Genotyper® 2.0 software packages. All microsatellite  
8 loci were highly variable and averaged 21 alleles/locus. The observed number of  
9 heterozygotes did not differ from the expected number of heterozygotes for all four loci.  
10 Furthermore, the estimated occurrence of null alleles was also correspondingly low. In  
11 addition, we were able to genotype another female at only one of the four loci. All other  
12 adults were typed completely.

### 13 Data Analysis

14 First we used Generalized Linear Mixed Models (GLMM) testing copulation  
15 success as the dependent variable. Copulation success was a continuous variable scored  
16 for each bird based on the number of copulations they attained across the duration of the  
17 breeding season. Because groups had different total numbers of observations taken,  
18 individual's copulation success was calculated per number of song census blocks taken  
19 on each group. We ran models for male and female copulation success separately, using a  
20 dummy code for group (aviaries 1-7) as a random factor, and song characteristics as  
21 covariates. Although we have a large assortment of different measures of song, for these  
22 analyses we focused on a subset of the song measures in order to reduce the levels of

1 multicollinearity. Thus we selected song measures that past work have revealed to assess  
2 different aspects of social interactions and not to be highly inter-correlated (King et al.  
3 2003; White et al. 2002b). As a measure of courtship effort, we used amount of female-  
4 directed song males produced per census block taken on the group. To measure male-  
5 male singing competition, we used the amount of countersinging males produced per  
6 census block. We also entered a measure of song potency for the males from whom we  
7 had playback results. This score was the potency score averaged across the playback  
8 females. We had song potency measures for 53 of the 68 males in the seven groups.  
9 (Inter-correlation coefficients for female directed song, countersinging, and potency  
10 averaged  $r=0.21$ ). For models testing female copulation success, we used the amount of  
11 female-directed song females heard from males per census block, the song potency, and  
12 amount of countersinging per census block produced by the male with whom the female  
13 copulated. Females only ever copulated with one male, thus each female had only one  
14 value for the dependent variable in the analysis. Some of the males copulated with  
15 multiple partners. We entered their results with each of their females as repeated  
16 measures and entered individual as a random variable.

17       Next we ran GLMMs with number of offspring produced as the dependent  
18 variable. Offspring produced was a continuous variable calculated as the number of  
19 fertile eggs each individual sired across the entire breeding season. Across years, the  
20 number of days that we collected eggs varied (between 33 and 37 days). We controlled  
21 for this by transforming eggs collected to be per day of egg collection (total eggs  
22 collected for each female divided by number of days collecting eggs). We square-root

1 transformed offspring produced per day in order to maintain homogeneity of variance  
2 across groups. We again ran separate models for males and females. We entered the same  
3 factors and covariates in the offspring production models as in the copulation success  
4 models above.

5 Finally, we incorporated all 17 aviaries into a multiple regression using total  
6 number of fertile eggs produced per aviary per female as the dependent variable, and the  
7 per census block totals of female-directed song, countersinging, copulations, and average  
8 potency of all the males in the group as predictors. Thus although we did not have  
9 information on the within-group variation in maternity and paternity in all of the groups,  
10 this test was run to examine whether overall characteristics of groups played a role in  
11 stimulating the reproductive condition of the females in those groups (using each group  
12 as an independent datapoint).

### 13 Results

14 Overall, across the 17 aviaries, there was wide variation in eggs collected, ranging from  
15 13 to 79 fertile eggs. Among the groups selected for parentage analyses, we were able to  
16 measure the parentage of 373 eggs. There was substantial variation in egg laying both  
17 within and across these groups. Figure 1a illustrates the number of fertile eggs produced  
18 per female in each of the seven groups. Each line represents one group with the order of  
19 females sorted from highest egg producer to lowest for each group. Figure 1b illustrates  
20 the number of offspring sired per male across the seven groups. Both males and females  
21 had pronounced variation in reproductive success, with males exhibiting more, but not  
22 significantly more skew (mean variance in reproductive success for males =  $0.17 \pm 0.08$ ,

1 females =  $0.05 \pm 0.02$ , paired t test,  $t(6) = 1.88$ ,  $p > .10$ ). Males had on average  $1.60 \pm 0.11$   
2 partners, females never mated with more than one male in a breeding season.

3           **Copulation Success.** No variable in the model significantly accounted for  
4 variation in male or female copulation success. For males, the amount of female-directed  
5 song produced was not significant in the model when each female partner was entered  
6 individually. However, total female-directed song produced by males (collapsing across  
7 all females with whom a male copulated) was significantly related to copulation success.  
8 Within the groups, the amount of males' female-directed song produced had on average a  
9  $.77 (\pm 0.07)$  correlation with copulation success (6/7 groups had significant correlations).  
10 Countersinging and song potency were not significantly associated with copulation  
11 success within groups. Figure 2 illustrates the relationship between males' copulation  
12 success and total female-directed song they produced seen in the seven groups. This  
13 difference between the results of the model for female-directed song (per partner)  
14 compared to total female-directed song (for all partners), indicates that males who can  
15 invest in singing to more females are more successful in copulating.

16           **Offspring Produced.** Both models using offspring produced as the dependent  
17 variable revealed that countersinging was significantly related to offspring produced  
18 (male model,  $F(1, 49) = 8.15$ ,  $P < .01$ ; female model,  $F(1, 47) = 6.31$ ,  $p < .02$ ). Also, in both  
19 models there was a significant variance associated with group (male model,  $F(6, 42) =$   
20  $4.36$ ,  $p < .005$ ; female model,  $F(6, 47) = 3.62$ ,  $p < .005$ ). Female-directed song and song  
21 potency failed to predict any unique variance in offspring produced.



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1           **Copulation success:** The one characteristic of singing that related to copulation  
2 success for males was the overall amount of female-directed song they produced. This is  
3 a pattern we have seen in past groups of cowbirds (Freeberg, 1996), and reports in other  
4 species have found that courtship persistence and effort relates to mating success  
5 (Shamble et al. 2009; Vinnedge and Verrell, 1998). The effect could only be found when  
6 grouping all of a male's partners together, thus males' copulation success is increased by  
7 courting multiple partners.

8           None of our measures proved effective in predicting numbers of copulations  
9 achieved by females, suggesting that either we have not measured the characteristics of  
10 social interactions important to explain female copulation rates, or else the interactions  
11 that predict copulations for females occur earlier in the spring. The focus of current work  
12 is in determining whether females who are courted early in spring pair bond earlier and  
13 copulate more with their partners.

14           **Offspring Produced:** Surprisingly, it was the amount of countersinging – male  
15 singing interactions with other males – that best predicted offspring production. The  
16 pronounced across-group variance in egg production was also a surprise. The significant  
17 amount of variance associated with the group factor in the GLMM models suggested that  
18 variability in egg production across groups could not be accounted for in its entirety by  
19 the singing interactions of the females' partners. Also, the differences across aviaries  
20 could not be attributed to a few females, as there were significant numbers of females in  
21 some groups producing more eggs than females in other groups (Figure 1a). This pattern  
22 was found even in the restricted range of the highest egg producing aviaries. The multiple

1 regression analysis provided suggestive evidence that it may be the ambient amount of  
2 countersinging in the group that stimulates female egg production. Experiments,  
3 however, will be needed to elucidate the mechanism of countersinging's effect on egg  
4 production. It could be the temporal patterns of countersinging or the visual displays  
5 males produce when countersinging that stimulate females' reproductive hormones  
6 (sensu Lehrman, 1965). It is also possible that countersinging co-varies with some other  
7 unmeasured variable that is critical in driving changes in egg production.

8         The two measures of reproductive success – copulation success and egg  
9 production – were remarkably disassociated in their relationships with singing. Females  
10 have some control over copulation success because females must produce solicitation  
11 displays in order for males to copulate successfully (Yokel and Rothstein, 1991). The  
12 variation in egg production, however, did not relate to copulation success; it was related  
13 to male competition and not to courtship persistence. This suggests that females have  
14 two levels of control over reproduction; one based on copulation success, and the other  
15 related to regulating egg production.

16         The lack of a relationship between either measure of reproductive success and  
17 song potency was unexpected. Having a song a female prefers is necessary for a male to  
18 copulate. Also, there is evidence in many species that song quality can serve a  
19 stimulatory function for egg production (Brockway, 1965; Kroodsma, 1976; Leboucher et  
20 al., 1998). That song preferences did not correspond to copulation success or  
21 reproductive stimulation suggests that something occurring in social contexts may lead  
22 females to (a) mate with males whose songs do not correspond to their preferences, (b)

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5 1 assess males based on characteristics other than song potency, (c) change their song  
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7 2 preferences in some way (Freed-Brown and White, 2009; King et al. 2003), or (d) use  
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9 3 different criteria for selecting mates in different social contexts. In support for this last  
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11 4 possibility, past work has revealed that there have been some social groups where song  
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13 5 potency has indeed correlated strongly with mating success (West et al., 1981; White et  
14  
15 6 al., 2002c). How preferences may vary with social context is at this point unknown. It  
16  
17 7 could be that there are many different characteristics of males that females use for mate  
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19 8 selection and that the characteristics that are most important to females in any particular  
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21 9 group depend on the assortment of males and the frequency or variance of traits within a  
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23 10 group that are being compared.  
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29 11 The results suggest that reproductive success for males depends on singing  
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31 12 persistently to females and also engaging in male-male singing bouts; two song-use  
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33 13 behaviors that past work has found to be highly influenced by social learning during  
34  
35 14 development. In past studies we have found that males can vary dramatically in their  
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37 15 propensities for both types of directed singing, and groups of males can be influenced to  
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39 16 be more male- or female-directed by other males in their flock (Freeberg et al. 1995;  
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41 17 White et al. 2002b, 2007, in press). In the past we have described different groups as  
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43 18 'cultures' where different social compositions lead to variation in social behavior and  
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45 19 singing patterns (White et al. 2007). In some groups, allocating more time to courtship  
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47 20 may account for reproductive success, whereas in other groups, engaging in more male  
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49 21 competition may be a more successful strategy. It remains unclear what effect these  
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51 22 cultures may have on selection. For example, do different cultures lead specialist males to  
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5 1 be more successful in one type of condition and less successful in another, or are the most  
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7 2 successful males the ones who are flexible and can change their behavior to match the  
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9 3 culture in which they find themselves? To answer these questions, longitudinal studies  
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11 4 are necessary where subjects live and breed in different cultures across years.

14 5       There are two points of caution to be noted in interpreting these results: First, as is  
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16 6 always a risk with lab research, there is the possibility that the characteristics of our  
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18 7 captive system are not representative of the characteristics of groups in the wild. Other  
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20 8 than knowing that female-directed song and countersinging exist in the wild, there is little  
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22 9 information from the wild bearing on the patterns of reproductive success found in this  
23  
24 10 work. It is extremely difficult to assess a female brood parasite's reproductive success in  
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26 11 the wild, and impossible to have enough control over the social and physical ecology to  
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28 12 determine how social environments may influence reproductive success in the wild. Even  
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30 13 if the overall effects differ between the lab and the wild, the captive studies provide  
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32 14 information about the plasticity in female reproductive behaviors and male abilities. Such  
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34 15 plasticity could allow for the potential for different cultures to develop and be maintained  
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36 16 in the wild (Freeberg et al., 2001).

42 17       Second, the associations found here are only correlations, and it is therefore  
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44 18 possible that other unmeasured variables account for the relationships found in the  
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46 19 analysis. Future experiments under more controlled conditions will allow us to extend the  
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48 20 discoveries found here and to move toward statements of causation.

52 21       One focus of studies of communication systems has been on signal honesty  
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54 22 (Bradbury and Vehrencamp, 1998; Searcy and Nowicki, 2005). Signals are only useful to  
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5 1 receivers if they provide reliable information. From this perspective, countersinging may  
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7 2 be a more honest indicator of a male's quality than his song potency. Males can copy  
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9 3 songs and can develop high potency song as a consequence of certain developmental  
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11 4 experiences (King and West, 1977b; West and King, 1988; White et al., 2002b). Thus  
12  
13 5 whereas any male can develop a high potency song, not every male can defend singing  
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15 6 one in a context with other males. Other males react aggressively to high potency song,  
16  
17 7 so countersinging provides valuable information about the ability of a male to engage  
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19 8 with other males. Thus in conditions where there is an abundance of countersinging, there  
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21 9 would be an abundance of reliable information about males for females to evaluate. Thus  
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23 10 if females experience multiple groups in a season or in their lifetimes (if over wintering  
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25 11 mortality is not substantial; but see Darley, 1971), it could be that females manage  
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27 12 tradeoffs in future versus current reproductive success based on the amount of  
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29 13 information available in groups to assess male social quality.  
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35 14 It could be that the dramatic variation shown here in clutch size may only be  
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37 15 found in a brood parasite that does not face increases in parental care resulting from  
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39 16 laying high numbers of eggs. Social control of reproduction may be a phenomenon that  
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41 17 generalizes beyond brood parasites, however. At the individual level, females in many  
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43 18 species have been shown to have control over egg production in response to various types  
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45 19 of environmental stimuli (Carey, 1996). Also, at the group level, intraspecific variation  
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47 20 exists in reports of clutch sizes across populations of several social bird species (Baicich  
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49 21 and Harrison, 1997; Gill, 1994). Furthermore, changing egg production is only one  
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51 22 example of a way in which a social context could influence reproductive success  
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1 (Adkins-Regan and Mackillop, 2003; Mazuc et al., 2003; Silk et al., 2003, in press). The  
2 current work implies that understanding how selection acts on an individual of a social  
3 species requires measuring two types of processes, (1) processes that lead to assortative  
4 mating at the individual level, and (2), group-dependent processes that create the social  
5 context in which the individual must reproduce.

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Figure 1. Variance in reproductive success for (a) females and (b) males in the seven groups for which we had parentage information. Reproductive success was measured by the number of offspring produced per day of egg collection. Across conditions, total days of egg collection ranged between 33 – 37 days. Individuals within each group are sorted in descending order based on number of offspring produced.

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Figure 2. Scatterplot depicting the relationship between each male's amount of female-directed song produced per block of data collection and his copulation success. Each regression line represents one of the seven flocks.

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Figure 3. Scatterplots depicting the relationship across 17 groups between (a) countersinging (CS), and (b) female-directed singing produced in the group per block of data collection with numbers of eggs produced in the groups.

1 Table 1. Flock composition for 17 aviaries

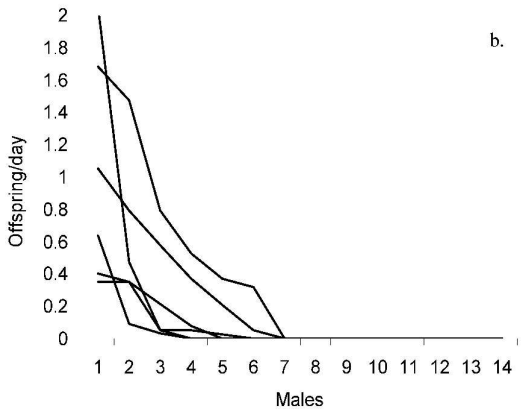
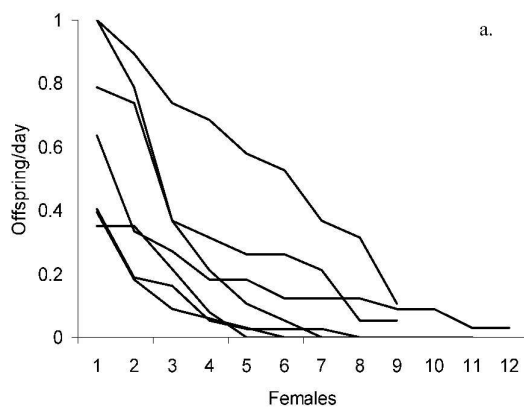
Aviary	Year	Total	Number of males		Number of females	
	Studied	Birds	Adult	Juvenile	Adult	Juvenile
1	2000	22	0	12	6	4
2	2000	19	0	9	6	4
3	2000	20	6	4	6	4
4*	2001	20	0	10	6	4
5*	2001	20	0	10	6	4
6	2001	20	0	10	6	4
7	2001	20	0	10	6	4
8	2001	21	11	0	6	4
9	2001	20	10	0	10	0
10	2002	16	0	6	10	0
11	2002	17	0	7	10	0
12*	2002	25	14	0	12	0
13*	2002	24	7	7	10	0
14	2004	16	0	8	8	0
15*	2004	17	7	0	10	0
16*	2004	17	8	0	9	0
17*	2004	17	8	0	9	0

2 \* indicates groups included in microsatellite analysis.

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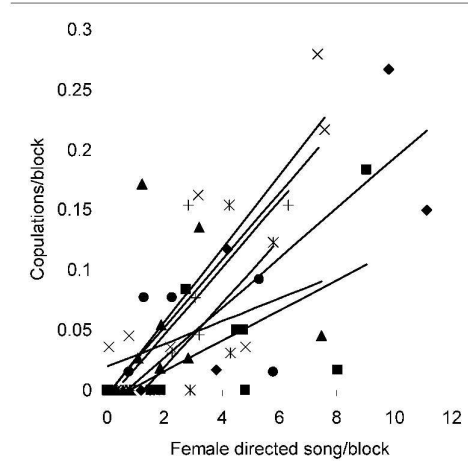
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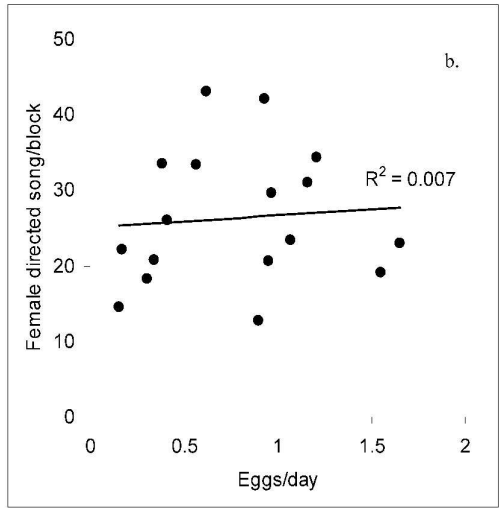
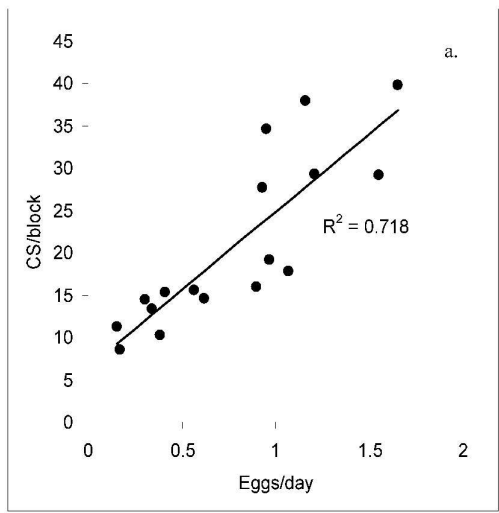
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1 In birdsong research there has been much interest placed on the relationship between vocal signals and  
2 reproductive success. We have studied seventeen captive flocks of brown-headed cowbirds across four  
3 years. Here we combine social behavior and singing data with measures of copulation success and egg  
4 production to assess what aspects of song related to reproductive success. We found two important  
5 measures. First, the one variable that related to copulation success was the overall amount of songs males  
6 directed to females – a measure of courtship effort. The one variable that was found to be strongly  
7 associated with eggs laid within and across groups was the amount of countersinging males produced; a  
8 measure of male-male singing competition. Song attractiveness did not predict any unique variance in either  
9 measure of reproductive success. The relationship between female egg production and male competition  
10 suggests that females may be trading off current versus future reproduction based on the opportunities  
11 available in groups to evaluate males' competitive abilities.  
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