Effects of singing on copulation success and egg production in brown-headed cowbirds, *Molothrus ater*

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Abstract: We examined the relationship between singing and reproductive success in
cowbirds. We amassed data from 17 captive flocks (164 males, 167 females) that we
have studied over four years. For each flock, we conducted extensive observations on
social interactions as the birds competed, courted, and reproduced. We collected and
incubated all eggs laid during the breeding season and performed parentage analyses on
the seven flocks with the highest levels of egg production. Finally, we measured males’
song quality in playback tests. Here we assessed what aspects of singing were associated
with (1) copulation success and (2) offspring production. Results differed for these two
measures of reproductive success because of high variance in egg production within and
across groups. The overall amount of songs males directed to females, a measure of
courtship persistence, was the one variable strongly associated with males’ copulation
success. For offspring production, there was significant between-flock variability that
was more pronounced than the within-group variability. The one variable that was found
to be strongly associated with eggs laid within and across groups was the amount of
countersinging males produced; a measure of male-male singing competition. Song
attractiveness did not predict any unique variance in either measure of reproductive
success. The relationship between female egg production and male competition suggests
that females may be trading off current versus future reproduction based on the
opportunities available in groups to evaluate males’ competitive abilities.

**Key words:** birdsong, social behavior, egg production, cowbird, reproductive success
In communication research, much interest has centered on the relationship between signals and reproductive success. Examining the characteristics of signals that lead to enhanced mating success can provide a means to determine how a communication system may have evolved (Searcy and Nowicki, 2005) and how sexual selection may operate on signals and signaling (Andersson, 1994).

Bird song has been a particularly effective model for studying how signals relate to reproductive success. In many species, male birds sing to attract females, and courtship songs elicit females’ copulation solicitation displays (Catchpole, 1987). Thus having an attractive signal is a necessary component of a male’s reproductive success. Males also use song in interactions with other males and these interactions can influence who is ultimately able to reproduce (Nowicki and Searcy, 2005; Searcy and Andersson, 1986).

Evidence of song’s contribution to reproductive success comes from extensive studies: (1) in the field, where characteristics of song and mating success can be measured (Alatalo et al., 1990; Baker and Boylan, 1999; MacDougall-Shackleton et al., 2002; Otter et al., 2001; Payne and Payne, 1993; Rehsteiner et al., 1998; Searcy, 1984), and (2) in the lab where controlled investigations of females’ song preferences can be assessed (Holveck and Riebel, 2007; King and West, 1977a; O’Loghlen and Beecher, 1997; O’Loghlen and Rothstein, 1995; Pasteau et al., 2009; Searcy, 1981; Searcy, 1984; Searcy, 1992). This body of research has provided a wealth of data on the wide variety of song and singing characteristics that may be important to reproductive success, such as song quality, song complexity, repertoire size, amplitude, singing effort, song matching and sharing (Catchpole and Slater, 1995; Howard, 1974; Kroodsma and Byers, 1991;
Kroodsma and Miller, 1996; Marler and Slabbekoorn, 2004; Nordby et al., 1999; Searcy and Andersson, 1986; Smith, 1977). Song can be an indicator of a male’s: resource holding potential, health, learning ability, developmental resilience to stress, attentiveness to females, or social skills.

One challenge in examining the link between song characteristics and reproductive success has been in tying together lab examinations of female preferences with mating patterns seen in the wild. Often, the relationship between mate preferences and mate choice is not a simple one. The lab preparation, removed from the context in which mating occurs, fails to incorporate many aspects of social life. Male or female competition, for example can influence reproductive success and change the relationships between traits females prefer and traits that are ultimately selected (Beecher, 1996; Nordby et al., 2000; Searcy, 1984). Alternatively, research in the wild often lacks the control necessary to be able to isolate the important aspects of singing from many of the other covarying factors that may influence mating success.

The goal of this work was to examine the relationship between characteristics of song and reproductive success in a controlled lab environment, but in a context that provided individuals enough freedom to live and breed in groups. We studied brown-headed cowbirds, a gregarious songbird. The cowbird serves as an excellent model for studying relationships between social behavior and reproductive success because wild-caught individuals will breed in large outdoor aviaries. There are of course many differences between flocks in captivity and in the wild (food availability, shelter, range size, and safety from predation for example). Thus, captive flocks cannot be considered
analogous to populations in the wild. They do, however, offer a powerful means to
control aspects of social systems that cannot be controlled in the field. In our captive
flocks, birds court, copulate, and lay eggs in mock nests. These patterns of behavior do
resemble the seasonal patterns of singing, courting and mating reported in the wild
(Friedmann, 1929; Ortega, 1998; Smith et al., 2000). There is, however, wide variation in
field reports of cowbird social demographics and in social behavior (Brainard, 1998). In
the lab, we can have some control over aspects of the social and physical environment,
providing a means to assess how social interactions may influence reproductive success.

We are also able to examine female preferences for male courtship song by
measuring copulation solicitation displays given by females in response to recordings of
songs played in sound attenuation chambers (King and West, 1977). Thus we can have
controlled measures of females' preferences for songs and we can also measure actual
mating patterns of birds in groups. Observations of birds during the breeding season
provide us with measures of song use; as males use song to compete with other males, to
court, and to copulate. Past work has revealed that song use can vary dramatically across
males and can be influenced by social experiences during development. For example,
juvenile males who had experience with adult males learn to engage in more social
singing (to both males and females) than juveniles who do not have social experiences
with adult males (White et al., 2007; White et al., 2002b). Experienced juveniles also
engage in countersinging bouts more often than naive juveniles (White et al., 2007).

Cowbird countersinging differs from what is typically considered under this term, which
usually refers to males matching song types with neighbors across long distances
Male cowbirds are not territorial, so countersinging takes place at very close distances (often within inches). Countersingers alternate songs and can sing flurries of songs rapidly (routinely singing 10 or more songs per minute). Singing to other males is related to dominance (Dufty, 1986; Rothstein et al., 1988), but countersinging also seems to have an influence on females. In groups producing high levels of countersinging, females more frequently approach and spend time near the males (King et al., 2003; West et al., 2002).

Cowbirds are obligate brood parasites and are therefore not constrained in their reproduction by the burden of parental care. They thus have the potential to lay more eggs than species that must care for their young. In our captive conditions we are able to collect and incubate all eggs laid in the breeding season to get measures of reproductive output. In the past we have been struck by the wide variation in egg production we have found across different groups (King et al., 2003; West et al., 2002), but we have never, until now, had a sample size of independent groups large enough to examine this variability in detail. We have not been able, for example, to determine whether the across-group variability was due to a few extremely fecund females, or whether females as a group were stimulated to lay eggs as a consequence of overall aspects of the social group. Either way, if females have control over their egg production and vary reproductive output in response to the qualities of the males present, then this could have an effect on reproductive success and on selection. Given a large enough sample size we should be able to assess what characteristics of males may be associated with reproductive stimulation.
Here we report on the patterns and relationships among social behavior and reproductive success in captive flocks of cowbirds, using extensive datasets of the social and singing behavior of 331 birds (164 males, 167 females), the complete egg production of females spanning four years for 17 captive flocks, microsatellite parentage analysis on seven of the flocks with highest egg production, and finally, results of song playback tests examining female preferences for recordings of songs from the majority of the males in the groups.

Methods

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

Measures

For all groups, three observers took extensive measures of social behavior prior to, and during the breeding season. We used a speech-recognition data collection system to record the timing of behavioral events continuously (White et al., 2002a). We report data from samples during the time that eggs were collected (May 1 – June 10).
**Song use:** We noted patterns and amount of male vocalizations in 15-min censuses (White et al., 2002b). Within each census, we noted the individual who sang or whistled, whether it was directed to another bird (sung within 60 cm and oriented toward another individual), or was undirected. We programmed our database to determine whether or not song occurred in a countersinging bout. A vocalization occurred in a countersinging bout if the recipient of a directed vocalization responded to the singer with a directed vocalization within 15 sec. Past work has suggested that countersinging is a more sensitive measure of male singing competition than is male directed singing alone (King et al., 2003; White et al., 2007). We also recorded all observed copulations. The automated speech recognition system provided us with high levels of interobserver reliability in song censuses (song per male; r = .98, p < .001). Since we collected different numbers of censuses across the groups, we controlled for this by transforming all measures to be per 15-min data collection block (each individual’s measures divided by the total number of censuses taken on the group).

**Song playbacks:** We made breeding season audio recordings of songs of males within the flocks and played them to females in sound attenuating chambers. The 64 female subjects used for playbacks were unfamiliar with the males whose songs were being tested. They were of the same age range as the females in the rest of the study and had been housed in aviaries with males prior to being placed in sound attenuation chambers. We measured each song’s ‘potency’, or effectiveness at eliciting females’ copulatory postures (see West et al., 2002; White et al., 2002b for details of playback procedure). We played back songs from males from ten of the flocks. We selected one song from each male based on
recording quality for playback. Time did not permit us to test multiple songs from each 

male. Potency scores from different songs of the same male typically do not vary 

substantially (unpublished observations). We conducted playbacks of pairs of aviaries 

over the course of four breeding seasons. Each song was played six times in total to 

females and we scored for each song how often females responded to the playback with a 

copulation solicitation display.

Egg collection: At approximately 0530 h each morning in the breeding season we 

collected all eggs laid in all groups. We incubated eggs for 10 days to determine whether 

they were fertile. Mock nests in the aviaries contained grass clippings and yogurt-covered 

peanuts that served as false eggs. For further details of sampling procedures, refer to the 

within-year studies (King et al., 2003; West et al., 2002; White et al., 2002a; White et al., 

2002b; White et al., 2002c).

Microsatellite analysis. We conducted a parentage analysis on a sample of seven of the 

aviaries (* groups in Table 1). The seven aviaries chosen were ones that produced enough 

eggs to allow us the possibility of detecting patterns of successful reproduction among 

individuals within groups. We used microsatellite markers to assign maternity and 

paternity to each fertile egg. We collected blood samples (50 – 100 µl) from all putative 

parents by puncture of the brachial vein and we stored the blood at -20°C until needed for 

analysis. Whole embryos were harvested on day 10 of incubation and also stored at - 

20°C. We extracted DNA from both blood and embryo using standard organic solvent 
purification (Sambrook and Russel, 2001).
We determined parentage using four pairs of nuclear microsatellite markers \((M\mu 20, M\mu 25, M\mu 29, \text{and} D\mu 16)\) either developed specifically for brown-headed cowbirds (Alderson et al., 1999) or for yellow warblers \((Dendroica petechia)\) (Dawson et al., 1997). We followed Alderson et al. (Alderson et al., 1999) for PCR reaction conditions for all primers. We analyzed amplification products on an ABI PRISM 310 Genetic Analyzer (Applied Biosystems). We then further analyzed the resulting data with the Genescan® Analysis 2.0.2 and Genotyper® 2.0 software packages. All microsatellite loci were highly variable and averaged 21 alleles/locus. The observed number of heterozygotes did not differ from the expected number of heterozygotes for all four loci. Furthermore, the estimated occurrence of null alleles was also correspondingly low. In addition, we were able to genotype another female at only one of the four loci. All other adults were typed completely.

Data Analysis

First we used Generalized Linear Mixed Models (GLMM) testing copulation success as the dependent variable. Copulation success was a continuous variable scored for each bird based on the number of copulations they attained across the duration of the breeding season. Because groups had different total numbers of observations taken, individual’s copulation success was calculated per number of song census blocks taken on each group. We ran models for male and female copulation success separately, using a dummy code for group (aviaries 1-7) as a random factor, and song characteristics as covariates. Although we have a large assortment of different measures of song, for these analyses we focused on a subset of the song measures in order to reduce the levels of
multicollinearity. Thus we selected song measures that past work have revealed to assess
different aspects of social interactions and not to be highly inter-correlated (King et al.
2003; White et al. 2002b). As a measure of courtship effort, we used amount of female-
directed song males produced per census block taken on the group. To measure male-
male singing competition, we used the amount of countersinging males produced per
census block. We also entered a measure of song potency for the males from whom we
had playback results. This score was the potency score averaged across the playback
females. We had song potency measures for 53 of the 68 males in the seven groups.
(Inter-correlation coefficients for female directed song, countersinging, and potency
averaged r=0.21). For models testing female copulation success, we used the amount of
female-directed song females heard from males per census block, the song potency, and
amount of countersinging per census block produced by the male with whom the female
copulated. Females only ever copulated with one male, thus each female had only one
value for the dependent variable in the analysis. Some of the males copulated with
multiple partners. We entered their results with each of their females as repeated
measures and entered individual as a random variable.

Next we ran GLMMs with number of offspring produced as the dependent
variable. Offspring produced was a continuous variable calculated as the number of
fertile eggs each individual sired across the entire breeding season. Across years, the
number of days that we collected eggs varied (between 33 and 37 days). We controlled
for this by transforming eggs collected to be per day of egg collection (total eggs
collected for each female divided by number of days collecting eggs). We square-root
transformed offspring produced per day in order to maintain homogeneity of variance
across groups. We again ran separate models for males and females. We entered the same
factors and covariates in the offspring production models as in the copulation success
models above.

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

Results

Overall, across the 17 aviaries, there was wide variation in eggs collected, ranging from
13 to 79 fertile eggs. Among the groups selected for parentage analyses, we were able to
measure the parentage of 373 eggs. There was substantial variation in egg laying both
within and across these groups. Figure 1a illustrates the number of fertile eggs produced
per female in each of the seven groups. Each line represents one group with the order of
females sorted from highest egg producer to lowest for each group. Figure 1b illustrates
the number of offspring sired per male across the seven groups. Both males and females
had pronounced variation in reproductive success, with males exhibiting more, but not
significantly more skew (mean variance in reproductive success for males = 0.17 ± 0.08,
females = 0.05 ± 0.02, paired t test, $t(6) = 1.88$, $p > .10$). Males had on average 1.60 ± 0.11 partners, females never mated with more than one male in a breeding season.

**Copulation Success.** No variable in the model significantly accounted for variation in male or female copulation success. For males, the amount of female-directed song produced was not significant in the model when each female partner was entered individually. However, total female-directed song produced by males (collapsing across all females with whom a male copulated) was significantly related to copulation success. Within the groups, the amount of males’ female-directed song produced had on average a .77 (±0.07) correlation with copulation success (6/7 groups had significant correlations).

Countersinging and song potency were not significantly associated with copulation success within groups. Figure 2 illustrates the relationship between males’ copulation success and total female-directed song they produced seen in the seven groups. This difference between the results of the model for female-directed song (per partner) compared to total female-directed song (for all partners), indicates that males who can invest in singing to more females are more successful in copulating.

**Offspring Produced.** Both models using offspring produced as the dependent variable revealed that countersinging was significantly related to offspring produced (male model, $F(1, 49) = 8.15$, $P < .01$; female model, $F(1,47) = 6.31$, $p < .02$). Also, in both models there was a significant variance associated with group (male model, $F(6,42) = 4.36$, $p < .005$; female model, $F(6,47) = 3.62$, $p < .005$). Female-directed song and song potency failed to predict any unique variance in offspring produced.
The significant effect of group in the models for offspring produced suggests that some variance in egg production found across groups was not explained by the variables tested within groups. The subset of groups we used for parentage testing (a restricted range of only the highest egg producing groups) would have grossly underestimated the size of this group effect. We therefore examined egg production across all 17 aviaries.

**Across Groups: Egg Production.** The multiple regression model was significant (F(4,6) = 4.98, p<.05) and explained 61.4 percent of the variance (adjusted) in egg production across groups. Countersinging was the only variable that significantly predicted egg production across groups (Beta = .812, t = 3.48, p<.02). Figure 3a illustrates the relationship between countersinging and egg production. We then removed countersinging from the model. Once countersinging was removed, the regression model was no longer significant (F(3,7) = 1.01, p>.44), explaining only .3% of the variance (adjusted) and no other variables came close to predicting egg production (all Beta t values < 1.6, all ps>.14). In contrast to countersinging, figure 3b illustrates the (lack of) relationship between female-directed song and egg production.

**Discussion**

The analysis of the relationships between singing and reproductive success in cowbirds revealed three notable results: (1) copulation success and offspring production were very different measures of reproductive success owing to the striking variability in egg production within and across conditions; (2) aspects of song use, but not song potency, were important contributors to reproductive success; and (3) the only significant predictor of female egg production between and across groups was countersinging.
Copulation success: The one characteristic of singing that related to copulation success for males was the overall amount of female-directed song they produced. This is a pattern we have seen in past groups of cowbirds (Freeberg, 1996), and reports in other species have found that courtship persistence and effort relates to mating success (Shamble et al. 2009; Vinnedge and Verrell, 1998). The effect could only be found when grouping all of a male’s partners together, thus males’ copulation success is increased by courting multiple partners.

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

Offspring Produced: Surprisingly, it was the amount of countersinging – male singing interactions with other males – that best predicted offspring production. The pronounced across-group variance in egg production was also a surprise. The significant amount of variance associated with the group factor in the GLMM models suggested that variability in egg production across groups could not be accounted for in its entirety by the singing interactions of the females’ partners. Also, the differences across aviaries could not be attributed to a few females, as there were significant numbers of females in some groups producing more eggs than females in other groups (Figure 1a). This pattern was found even in the restricted range of the highest egg producing aviaries. The multiple
regression analysis provided suggestive evidence that it may be the ambient amount of
countersinging in the group that stimulates female egg production. Experiments,
however, will be needed to elucidate the mechanism of countersinging’s effect on egg
production. It could be the temporal patterns of countersinging or the visual displays
males produce when countersinging that stimulate females’ reproductive hormones
(sensu Lehrman, 1965). It is also possible that countersinging co-varies with some other
unmeasured variable that is critical in driving changes in egg production.

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

The lack of a relationship between either measure of reproductive success and
song potency was unexpected. Having a song a female prefers is necessary for a male to
copulate. Also, there is evidence in many species that song quality can serve a
stimulatory function for egg production (Brockway, 1965; Kroodsma, 1976; Leboucher et
al., 1998). That song preferences did not correspond to copulation success or
reproductive stimulation suggests that something occurring in social contexts may lead
females to (a) mate with males whose songs do not correspond to their preferences, (b)
assess males based on characteristics other than song potency, (c) change their song preferences in some way (Freed-Brown and White, 2009; King et al. 2003), or (d) use different criteria for selecting mates in different social contexts. In support for this last possibility, past work has revealed that there have been some social groups where song potency has indeed correlated strongly with mating success (West et al., 1981; White et al., 2002c). How preferences may vary with social context is at this point unknown. It could be that there are many different characteristics of males that females use for mate selection and that the characteristics that are most important to females in any particular group depend on the assortment of males and the frequency or variance of traits within a group that are being compared.

The results suggest that reproductive success for males depends on singing persistently to females and also engaging in male-male singing bouts; two song-use behaviors that past work has found to be highly influenced by social learning during development. In past studies we have found that males can vary dramatically in their propensities for both types of directed singing, and groups of males can be influenced to be more male- or female-directed by other males in their flock (Freeberg et al. 1995; White et al. 2002b, 2007, in press). In the past we have described different groups as ‘cultures’ where different social compositions lead to variation in social behavior and singing patterns (White et al. 2007). In some groups, allocating more time to courtship may account for reproductive success, whereas in other groups, engaging in more male competition may be a more successful strategy. It remains unclear what effect these cultures may have on selection. For example, do different cultures lead specialist males to
be more successful in one type of condition and less successful in another, or are the most successful males the ones who are flexible and can change their behavior to match the culture in which they find themselves? To answer these questions, longitudinal studies are necessary where subjects live and breed in different cultures across years.

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

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

One focus of studies of communication systems has been on signal honesty (Bradbury and Vehrencamp, 1998; Searcy and Nowicki, 2005). Signals are only useful to
receivers if they provide reliable information. From this perspective, countersinging may be a more honest indicator of a male’s quality than his song potency. Males can copy songs and can develop high potency song as a consequence of certain developmental experiences (King and West, 1977b; West and King, 1988; White et al., 2002b). Thus whereas any male can develop a high potency song, not every male can defend singing one in a context with other males. Other males react aggressively to high potency song, so countersinging provides valuable information about the ability of a male to engage with other males. Thus in conditions where there is an abundance of countersinging, there would be an abundance of reliable information about males for females to evaluate. Thus if females experience multiple groups in a season or in their lifetimes (if over wintering mortality is not substantial; but see Darley, 1971), it could be that females manage tradeoffs in future versus current reproductive success based on the amount of information available in groups to assess male social quality.

It could be that the dramatic variation shown here in clutch size may only be found in a brood parasite that does not face increases in parental care resulting from laying high numbers of eggs. Social control of reproduction may be a phenomenon that generalizes beyond brood parasites, however. At the individual level, females in many species have been shown to have control over egg production in response to various types of environmental stimuli (Carey, 1996). Also, at the group level, intraspecific variation exists in reports of clutch sizes across populations of several social bird species (Baicich and Harrison, 1997; Gill, 1994). Furthermore, changing egg production is only one example of a way in which a social context could influence reproductive success.
The current work implies that understanding how selection acts on an individual of a social species requires measuring two types of processes, (1) processes that lead to assortative mating at the individual level, and (2), group-dependent processes that create the social context in which the individual must reproduce.

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Figure Legends

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.

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.

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.
Table 1. Flock composition for 17 aviaries

<table>
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<th>Aviary</th>
<th>Year</th>
<th>Total Birds</th>
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<th>Number of females</th>
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* indicates groups included in microsatellite analysis.
a. $R^2 = 0.718$

b. $R^2 = 0.007$

189x253mm (600 x 600 DPI)
In birdsong research there has been much interest placed on the relationship between vocal signals and reproductive success. We have studied seventeen captive flocks of brown-headed cowbirds across four years. Here we combine social behavior and singing data with measures of copulation success and egg production to assess what aspects of song related to reproductive success. We found two important measures. First, the one variable that related to copulation success was the overall amount of songs males directed to females – a measure of courtship effort. The one variable that was found to be strongly associated with eggs laid within and across groups was the amount of countersinging males produced; a measure of male-male singing competition. Song attractiveness did not predict any unique variance in either measure of reproductive success. The relationship between female egg production and male competition suggests that females may be trading off current versus future reproduction based on the opportunities available in groups to evaluate males’ competitive abilities.