Robust Fall Social Displays Predict Spring Reproductive Behavior in Brown-Headed Cowbirds (*Molothrus ater ater*)

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Abstract

The ability to engage others in close proximity may be an essential component of social life and shapes the development of social skills. Variation in the willingness to initiate and sustain close interaction with conspecifics is known as sociability. The Brown-headed Cowbird (*Molothrus ater*) uses an affiliative display called the head-down to bring individuals into close proximity. During fall 2009, we manipulated a large flock of cowbirds in a fission–fusion perturbation and recorded the frequency of head-downs and social approaches. During the fission–fusion perturbation, the rate of head-downs remained both correlated and repeatable across perturbations. In spring 2010, we separated individuals into three aviaries, a high, intermediate, and low aviary, based on the frequency of head-down displays they initiated during the previous fall 2009. When breeding, males in the high flock produced a higher number of songs within counter-singing matches, and females laid more eggs in comparison with the other aviaries. These findings suggest that head-down displays performed outside the breeding season may contribute to the development and maintenance of reproductive competence by providing intimate social interactions with others.
highly sociable human females often have multiple sexual partners and are more likely to become pregnant in comparison with less sociable individuals (Jokela et al. 2009). In common lizards (*Lacerta vivipara*), females who were more sociable, or tolerant of another’s odor after hatching, were more likely to become pregnant and produced more offspring than less tolerant females (Cote et al. 2008). In baboons (*Papio cynocephalus*), females who initiate close social contact with other females exhibit higher rates of offspring survival (Silk et al. 2003). These studies suggest that variation in sociability may be an important component in an individual’s reproductive performance.

How individuals engage, interact, and form relationships with conspecifics is a major determinant of reproductive success. From courtship, to pair bond formation, to successful copulation, reproduction requires individuals to initiate and sustain close social contact with conspecifics. Previous research has documented that affiliative displays, or behaviors used to initiate and sustain close contact with conspecifics while minimizing aggression, are widespread across a range of social species. In birds and primates, affiliative displays are used to establish and maintain pair bonds with others, increase group cohesion, manage stress, and reduce agonistic interactions (Carter et al. 1999; Sapolsky & Share 2004; Stöwe et al. 2008). For example, allogrooming in many mammals has been shown to assist in the formation of coalitions, solidify social ranks, and facilitate the survival of offspring (Silk et al. 2003; Silk 2007), while allopreening in birds has also been shown to facilitate offspring survival (Emery et al. 2007; Lewis et al. 2007). Individual differences in affiliative behaviors are often used to assess an individual’s sociability (Silk et al. 2010; Koski 2011). Nevertheless, few studies have explicitly looked at the consistency and repeatability of affiliative behaviors across different social contexts and their relationship to later reproductive behaviors.

Brown-headed cowbirds engage in an affiliative display known as the head-down. During a head-down, an individual freezes in a low crouched position with its head pointed downwards so that the back of the head and neck are positioned in close proximity, if not touching, a neighboring individual for at least one-second. Reports of head-down displays in both wild and captive populations of brown-headed (Webber 1983; Hunter 1994), bronzed (*Molothrus aeneus*) (Garrett & Molina 2005), shiny (*Molothrus bonariensis*) (Post & Wiley 1992), giant (*Molothrus oryzivorus*) (Payne 1969) and bay-winged (*Molothrus badius*) (Selander 1964) cowbirds suggest it has a widespread social role. Repeated use of the behavior has been shown to facilitate close proximity between individuals (Stevenson 1969), integrate others into the flock (Rothstein 1977, 1980), and have appeasing influence on others (Robertson & Norman 1976; Scott & Grumstrup-Scott 1983). Head-down displays are very seasonal with nearly all displays occurring during the fall and winter when cowbirds assemble into large flocks (Ortega 1998). Some have suggested that the display functions to sustain close proximity while reducing aggressive behavior during periods when social cohesion is necessary (Ortega 1998). Head-down displays can also be reciprocated, when individuals respond to another’s head-down with a matching display Fig. 1. Most displays last for a few seconds, but we have observed head-downs that have lasted for upwards of 10 min. Head-down displays emerge early in development (Lowther & Rothstein 1980), with reciprocated displays observed in 43-day-old hand-reared birds housed without adult contact (J. L. Miller, unpublished data).

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**Fig. 1:** Sequential progression of a head-down display. The display starts with two male cowbirds facing different directions (1: start). The individual on the right initiates (2: initiated) a reciprocated display (3: reciprocated) and then moves (while maintaining the head-down posture) in close proximity to the individual on the left until the crest of their heads touch (4: touching). After maintaining the display for around a minute, the individual on the left goes out of the display (5: end 1), pecks lightly at the individual on the left right (not shown) until he goes out of the display. The individual on the left then adopts an alert posture, while the individual on the right adopts a raised head posture with crest feathers raised (6: end 2).
The head-down shares many postural and functional similarities with affiliative behaviors seen in other bird species (Selander & LaRue 1961; Selander 1964). In this study, we used the frequency that individuals engage in head-downs as a proxy for their sociability.

Cowbirds are obligate brood parasites and therefore lack experience with their own species during early development. This has led some researchers to consider cowbird reproductive behavior as being relatively inflexible (Mayr 1974). Nonetheless, many studies have shown that social experience before the breeding season influences and individual’s reproductive behavior. For instance, White et al. (2002) and Gersick et al. (2012) found that adult cowbirds who interacted with a more diverse range of individuals before the breeding season are more reproductively successful than cowbirds that experienced more stable conditions prior to breeding season. Female mate preferences are also shaped by social experience before the breeding season. For instance, females with previously established song preferences will modify their song preference after interacting with males prior to the breeding season (West et al. 2006). Here, females exposed to males for 4 days switched to prefer the songs of the males they interacted over previously tutored songs using play backs. These results suggest that social interaction before breeding season can shape an individual’s later reproductive behavior.

An individual’s sociability will influence how often and how closely they interact with conspecifics. Already variation in fall social approach tendencies remains correlated across social contexts and over time (Kohn et al. 2011). Both adult and juvenile females and adult males initiated comparable rates of approaches with others across changes in group size and composition. Nonetheless, this study did not look to see if individuals initiated close social contact through head-down displays when interacting with others. Here, cowbirds that consistently engage in more head-down displays are considered more sociable than individuals who consistently initiate fewer head-downs across contexts. Individuals that consistently utilize more head-down displays may have more experience in engaging others in close proximity, which may reflect how they interact, court, and mate (King et al. 2003). Because of the importance of social experience for the expression of reproductive skills, we hypothesize that consistent patterns of sociability during the fall may predict reproductive behavior during the breeding season.

All cowbird courtship revolves around directed song. During a directed song, a male orients toward another individual typically within 50 cm and performs a song while bowing (Friedmann 1929). Male cowbirds require extensive socialization with experienced males for the development of proper song use (White et al. 2002b), and female social interaction shapes both female song preferences (West et al. 2006) and male song quality. Males sing within inches of other individuals, and all song interactions require close spatial proximity to accurately assess song quality (King et al. 1981; West et al. 1981). An important aspect of cowbird courtship is counter-singing. During counter-singing matches, two males exchange directed songs in a tit-for-tat manner. Increased levels of counter-singing stimulates female egg production and correlates with male reproductive success (White et al. 2010b). Counter-singing requires significant social skills as males must interpret and respond appropriately to another male in close proximity without withdrawing. Yearling males housed without access to experienced adults develop poor counter-singing skills (White et al. 2002b; Gros-Louis et al. 2006). Thus, variation in sociability may shape the expression of counter-singing by facilitating interaction skills with conspecifics. We hypothesize that birds who initiate more head-downs during the fall will counter-sing more during the spring breeding season and consequently stimulate females to lay more eggs.

In this study, our first objective was to document the consistency and repeatability of the head-down rates across multiple social contexts. Consistency captures the stability in the rank-ordered behavioral distribution of individuals across contexts, while repeatability estimates the proportion of the behavioral variance that is due to differences between individuals. During the fall, we subjected a large flock to a fission–fusion perturbation to investigate if rates of head-downs remain correlated across changes in social context. Our second objective was to investigate the relationship between these tendencies and reproductive performance. In the spring, we separated individuals into high, intermediate, or low flocks based on their frequencies of head-downs during the fall. Within each flock, we recorded male courtship behavior and female egg production to document if variation in fall head-down displays predicts variation in spring reproductive behavior.

Methods

Subjects
We used 21 adult female and 17 adult male cowbirds. Birds were originally captured in Philadelphia County, Pennsylvania, or Monroe County, Indiana, and housed...
in aviaries in Monroe County, Indiana. Birds ranged in age from 3 to 11 yrs with an average age of 6 yrs. Previous studies have shown no differences in the song or social behavior between the Pennsylvania and Indiana populations (Freeberg & White 2006). All individuals had been housed together for a year prior to the present study. Each bird was marked with uniquely colored leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin (Aquavite, Nutritional Research, Keighley, West Yorkshire, UK) treated water, red and white millet, canary seed, and a modified Bronx Zoo diet for blackbirds.

Aviaries

We used the aviary complex described in detail in Smith et al. (2002). In the present study, we used three aviaries within the complex, each with identical dimensions (9.1 x 21.4 x 3.4 meters). Aviaries 1 and 2 were separated by an indoor enclosure, and aviaries 2 and 3 were separated by wire mesh that permitted visual contact. Ecological conditions were similar throughout all aviaries with shrubs, trees, grass, a covered feeding station, and access to an indoor enclosure. All aviaries allowed birds to be exposed to ambient climatic conditions, wild cowbirds, and the sight and occasional interaction with predators.

Behavioral Observations

To record behavior during the fall and the spring, we utilized a scan sampling procedure: the entire flock was scanned and behaviors were recorded as they were observed. During scan sampling blocks in fall of 2009, we recorded approach interactions and head-down displays. An approach was scored when one individual approached a conspecific within a radius of 30 cm around its body. During both approaches and head-downs, the identity of the individual who initiated the behavior and the individual who was the recipient were recorded. A reciprocated head-down was scored when a recipient of a head-down concurrently returned the display. Fall observation blocks were seven minutes long. During scan sampling blocks in spring of 2010, we primarily recorded male vocal behavior. In particular, we recorded the identities of the male singing and the individuals receiving the song. A directed song was recorded when one individual oriented on a 45 degree angle from a neighboring individual and performed a song display that included fluffing up and bowing while singing a song. Males could direct songs toward males or females singly or use directed songs within counter-singing matches with another male. A counter-singing match consists of two males exchanging directed songs in a tit-for-tat manner. A counter-singing match was recorded when a recipient of a directed song reciprocated with his own directed song within at least 15 s. An undirected song was recorded when an individual sang a song while not oriented toward any neighboring individual. Outside of song we also recorded male copulations. All observations were conducted between 7:00 and 10:30 in the morning when cowbirds are most active. Spring observation blocks were 15 min long.

All scan sampling blocks were conducted using voice recognition technology. When used in combination with voice recognition technology scan sampling can accurately acquire a more comprehensive dataset than focal sampling (White & Smith 2007). We used the procedure and equipment described in detail by White et al. (2002a). All behaviors were recorded using IBM (International Business Machines Corp, White Plains, NY, USA) ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500-MHz IBM compatible computer. Behavioral observations were spoken into a Telex FMR 150 (Telex Communications, Inc, Lincoln, NE, USA) wireless microphone, transcribed into Microsoft Word 2004, edited for voice recognition errors, and then imported into a database (4th Dimension 2004.8; ACI Inc). Observer reliability was tested using intraclass correlation coefficients between the two observers (GMK and APK) for the fall and spring and revealed a high level of agreement (fall: ICC = 0.86, p < 0.0001, spring: ICC = 0.87, p < 0.0001).

Fall Baseline Data Collection

On Sept. 2, 2009, all individuals were moved into aviary 1. From Sept. 3–18, two observers conducted daily counterbalanced observations, each recording approach behaviors and head-downs. Observers collected a total of 126 seven-minute observation blocks.

Fall Fission Perturbation

On Sept. 18, 2009, we separated the birds into two aviaries based on their frequency of approaches during the baseline period so that both flocks contained a similar distribution of approaches. Aviary 1 contained 11 females and nine males, and aviary 2 contained 10 females and eight males. From Sept. 19 to Nov. 20, 2009, two observers conducted daily counterbalanced observations and each collecting a total of 286 seven-minute observation blocks, recording approach behaviors and head-downs.
Fall Fusion Perturbation
On Nov. 21, 2009, the partition separating the two aviaries was opened and both flocks were allowed to interact. From Nov. 21 to Dec. 4, two observers recorded approach behaviors and head-downs in both aviaries. Observers collected a total of 108 seven-minute observation blocks during the fusion stage.

Spring Breeding Season Head-Down Segregation
Individuals were ranked by the total amount of head-downs they initiated during the baseline, fission, and fusion periods in the fall. On Apr. 4, 2010, each individual was assigned to one of three new aviaries based on the frequency of head-downs they performed during the fall. The high aviary contained the birds that initiated the most head-downs (six females and five males, head-down range: females = 68–193, males = 175–270), birds in the intermediate aviary initiated a moderate number of head-downs (seven females and six males, head-down range: females = 34–68, males = 106–158), and birds in the low aviary initiated the lowest number of head-downs (seven females and six males, head-down range: females = 0–28, males = 27–95). From Apr. 5 until Jun. 13, two observers, working concomitantly, recorded a total of 411 fifteen-minute observation blocks. From Apr. 29 to Jun. 13 we collected all eggs laid.

Egg Collection
From Apr. 28 to Jun. 13, 2010, each aviary was supplied with eight prefabricated nests. White yogurt covered raisins were used as decoy eggs, previous studies have shown that cowbirds readily remove yogurt covered raisins from nests and treat them as they would host eggs (White et al. 2010b; Kohn et al. 2011). One decoy egg was added to each nest daily for 5 d to simulate the normal laying pattern seen in many passerines. Nests were moved to different locations every 10 d. At 7:00 am, each morning, all cowbird eggs were collected and replaced with a decoy egg. All eggs were then placed in a Petersime Model 1 incubator (Petersime Incubator Company, Gettysburg, Ohio). After eight days of incubation, eggs were removed and candled to determine if they were fertile.

Data Analysis
Given the low numbers of individuals and non-normality of data, we primarily used non-parametric tests (using two-tailed p-values). Freidman and Wilcoxon signed-rank tests were used to investigate the differences in the rates of head-downs (number of head-downs per observation block for each individual) between males and females during the baseline, fission, and fusion periods. Spearman’s correlations were used to look at the relationship between the rates of head-downs across the three periods and between individual approach behavior and rates of head-downs. Repeatability of rates of head-downs across periods was assessed using two-way random intraclass correlation coefficients.

Generalized linear models (GLM) were used to look at differences in the rate and proportion of counter-singing bouts between the spring aviaries. Our GLM for the rate of counter-singing utilized a quasi-Poisson distribution to control for overdispersion with a log link function, with the rate of songs in counter-singing bouts per observation block as the dependent variable. Our GLM for the proportion for songs in counter-singing matches used a binomial distribution with a logit link function with the proportion of total songs within counter-singing matches as the dependent variable. For both models, the explanatory factors were the spring aviary, the rate per block of male directed songs, and undirected songs as explanatory variables. Each model was simplified in a stepwise procedure by removing non-significant variables and comparing simplified models with a chi-square log likelihood test (Crawley 2005). We used variance inflation factors to assess potential multicollinearity in out explanatory factors for each model. A variance inflation factor of 10 or above indicates potential multicollinearity and makes model interpretation difficult (Chatterjee et al. 2000). In all of our models the variance inflation factor remained below two demonstrating no effects of multicollinearity. Further post hoc analysis was conducted using Kruskal–Wallis and Mann–Whitney U-tests. Chi-square goodness-of-fit tests were used to look at the differences in egg production across the aviaries.

Results
Fall Head-Downs
We observed a total of 3499 head-downs during the fall of 2009. There was a total of 598 female to female (FF: median = 21, IQR = 22), 773 female to male (FM: median = 30, IQR = 35), 886 male to male (MM: median = 29, IQR = 69), and 1242 male to female head-downs (MF: median = 77, IQR = 56).
Males exhibited higher rates of head-downs than females \( (U = 83.5, n_1 = 21, n_2 = 17, p = 0.006) \). Neither males nor females displayed any significant sex bias in their head-down rates \( (rate\ FF vs. rate\ FM: t = 70.5, n = 21, p = 0.33, rate\ MF vs. rate\ MM: t = 106, n = 17, p = 0.17) \). Our fission–fusion perturbation significantly influenced the overall rates of head-downs \( (X^2 = 39.07, n = 21, p < 0.001, \text{males: } X^2 = 32.12, n = 17, p < 0.001) \) with the highest rates of head-downs observed during the fission period for both sexes Fig. 2. During the fission period, we uncovered no significant differences in rates of head-downs across aviaries for both males \( (n = 17, \text{male: } X^2 = 25, p = 0.17) \) and females \( (n = 21, \text{female: } X^2 = 30, p = 0.12) \). We found that rates of head-down displays were significantly repeatable across the baseline, fission, and fusion periods for both females \( (ICC = 0.46, f = 3.56, p = 0.003) \) and males \( (ICC = 0.40, f = 2.96, p = 0.004) \). Furthermore, we found significant correlations in the rates of head-downs across all periods for both males and females (Table 1). Thus, head-down rates were both consistent and repeatable across the fall.

**Social Approach and Head-Downs**

The frequency that females engaged in head-downs reflected their overall social approach tendencies. Females who performed a higher number of head-downs both initiated and received more approaches from others than females who performed fewer head-downs \( (approaches\ initiated\ vs.\ head-downs: r = 0.81, n = 21, p < 0.0001, \text{approaches\ received\ vs.\ total\ head-downs}: r = 0.66, n = 21, p < 0.001) \). Within each period, female approach numbers correlated positively with the rates of head-downs (Table 2), and therefore, female head-down frequencies reflected their propensity to approach conspecifics. The number of head-downs a male initiated did not correlate with how frequently they approached others and how frequently others approached them \( (approaches\ initiated\ vs.\ head-downs: r = 0.29, n = 17, p = 0.26, \text{approaches\ received\ vs.\ head-downs}: r = 0.08, n = 17, p = 0.77) \). Therefore, male head-down frequencies did not significantly reflect their propensity to approach conspecifics.

**Spring Singing Behavior**

We recorded a total of 29 551 songs during the spring, with a total of 15 100 songs directed toward males and 9186 songs directed toward females and 5265 undirected songs (Table 3). In each aviary, males directed more songs toward males than toward females \( (low\ aviary: t = 2.201, n = 6, p = 0.03, \text{intermediate\ aviary: } t = 1.992, n = 6, p = 0.046, \text{high\ aviary: } t = 2.023, n = 5, p = 0.043) \). We uncovered no difference in the number or proportion of female (number: \( H_2 = 0.5739, p = 0.75 \); proportion: \( H_3 = 0.5739, p = 0.75 \)).
Table 1: Spearman’s rho correlations in the rates of head-downs for males and females over the three periods of the social perturbation experiment

<table>
<thead>
<tr>
<th>Head-down</th>
<th>Baseline–fission</th>
<th>Fission–fusion</th>
<th>Baseline–fusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>0.81***</td>
<td>0.89***</td>
<td>0.76**</td>
</tr>
<tr>
<td>Male</td>
<td>0.64**</td>
<td>0.81***</td>
<td>0.68**</td>
</tr>
</tbody>
</table>

Significant correlations are noted with asterisks. ***p < 0.005, **p < 0.05, *p < 0.05.

Table 2: Spearman’s correlations between the rates of head-downs and social approaches for males and females over the three periods of the social perturbation experiment

<table>
<thead>
<tr>
<th>Sex</th>
<th>Degree</th>
<th>Baseline</th>
<th>Fission</th>
<th>Fusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Initiated</td>
<td>0.58*</td>
<td>0.80***</td>
<td>0.76***</td>
</tr>
<tr>
<td></td>
<td>Received</td>
<td>0.62*</td>
<td>0.58*</td>
<td>0.60**</td>
</tr>
<tr>
<td>Males</td>
<td>Initiated</td>
<td>0.41</td>
<td>0.44</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>Received</td>
<td>-0.18</td>
<td>0.18</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

Significant correlations are noted with asterisks. ***p < 0.005, **p < 0.05, *p < 0.05.

H₂ = 1.1634, p = 0.559) or male directed song (number: H₂ = 5.119, p = 0.08; proportion: H₂ = 0.4875, p = 0.7837) across the three aviaries.

Flocks exhibited a progressive increase in the amount of counter-singing from the low to high flocks. Our GLM indicated a significant influence of both aviary (t = 5.810, df = 16, p < 0.0001) and the rate of songs sung to males outside counter-singing bouts (t = 5.368, df = 16, p = 0.0001) on the rate of songs in counter-singing matches. We observed a total of 6965 directed songs within counter-singing matches, with 1741 songs (median = 286, IQR = 151) in the low aviary, 2093 (median = 389, IQR = 227) songs in the intermediate aviary, and 3131 songs in the high aviary (median = 633, IQR = 608, Table 3).

Males in the high flock placed more emphasis on counter-singing in contrast to the males in the intermediate and low flocks. Our GLM on the proportion of songs within counter-singing matches indicated a significant influence of aviary (t = 7.566, df = 16, p < 0.0001). There were significant differences between the three aviaries in the proportion of songs within counter-singing matches (H₂ = 6.9477, p = 0.031, Fig 3) with the high aviary displaying a higher proportion of songs in counter-singing matches than the low and intermediate aviaries (low vs. high aviary: U = 2, n1 = 6, n2 = 5, p = 0.02, intermediate vs. high aviary: U = 3, n1 = 6, n2 = 5, p = 0.03).

Males who initiated more head-downs during the fall had a higher proportion of songs in counter-singing matches than other males. Across all aviaries, we discovered a significant correlation between the number fall head-downs and the proportion of songs within counter-singing matches during the spring (r = 0.48, p = 0.05). We uncovered no relationship between the number of fall head-downs and the proportion of undirected (r = −0.35, p = 0.17), male directed (r = 0.17, p = 0.51), and female directed song (r = −0.22, p = 0.38).

Egg Production and Copulations

Females in the spring aviaries produced significantly different numbers of eggs, with 76 eggs in the low aviary, 107 eggs in the intermediate aviary, and 138 in the high aviary (chi-square goodness-of-fit test: X² = 17.96, p < 0.0001, Fig 4). The low aviary produced 29 fertile eggs, the fewest of the three aviaries (38% fertilization rate), followed by the intermediate aviary that produced 38 (36% fertilization rate) fertile eggs, and the high aviary that produced 60 fertile eggs (43%, fertilization rate). While the number of fertilized egg laid differed across the three aviaries (chi-square goodness-of-fit test: X² = 17.96, df = 2, p < 0.0001) the proportion of fertilized eggs laid did not differ across the three aviaries (chi-square goodness-of-fit test: X² = 0.67, df = 2, p = 0.72). We observed no differences in the number of copulations across aviaries (H₂ = 0.14, p = 0.93), although the observed instances of copulation were low, with an average of three for the high, 3.17 for the intermediate, and 1.7 for the low aviaries.

Discussion

Our findings demonstrate that the head-down display is a robust component of the behavioral repertoire of cowbirds. Head-down rates remained correlated and
repeatable across multiple social contexts and over time for both males and females. Females who initiated more head-down displays were more likely both to approach and to be approached by others. Most individuals participated in reciprocated displays, but females were more likely to reciprocate head-downs from males than from females. During the spring, flocks composed of high frequency head-downers displayed higher rates and proportions of songs within counter-singing matches and exhibited higher egg production in comparison to other flocks. Across all flocks, males who initiated more head-downs in the fall had a higher proportion of their songs within counter-singing matches. Thus, fall head-down displays recorded in Sept., Oct., and Nov. were predictive of competent social behavior 6 mo later during May. and Jun. of the following year.

Male approach rates did not correlate with their head-down rates, and male cowbirds are more likely to use head-down displays in contrast to females. Previous studies have shown that repeated head-down use facilitates closer proximity between conspecifics (Selander & LaRue 1961; Stevenson 1969) and appeases aggressive tendencies in others (Scott & Grumstrup-Scott 1983). If the head-down provides a cue that subsequent interactions will not be aggressive (Ortega 1998), it will shape how males and females engage conspecifics. Unlike females, male cowbirds form strong dominance relationships with conspecifics, and this will lead to male approaches being perceived as more agonistic than female approaches. Many studies have shown that male approaches are used to displace others (Rothstein et al. 1986), and thus, higher males approach rates may not reflect an increased willingness to initiate close social contact. Therefore, more sociable males may use head-down displays more frequently than females as a means of minimizing withdrawal of conspecifics that may interpret their close proximity as agonistic. Furthermore, as males are more dominant, females may perceive close male proximity as more agonistic and therefore be more likely reciprocate head-down initiated by males than females.

The robustness of head-down rates across contexts demonstrates that cowbirds show consistent individual variation in their sociability. While the mean frequency of head-downs changed across the different contexts, both males and females maintained correlated and repeatable rates of head-down displays throughout the fall. Furthermore, neither males nor females exhibited any sex bias in the head-downs they initiated, demonstrating that head-downs are used generally to initiate close contact with all conspecifics. Consistent variation in affiliative behaviors may reflect underlying differences in an individual’s...
willingness to engage in close social interaction. Outside of fighting and copulations, the head-down is the only behavior that brings individuals into physical contact and sustains that contact for extended periods of time. During the fall, cowbirds converge into large flocks and the head-down display is used to navigate an increasingly complex social environment. Some have suggested that the display may be particularly advantageous during roosting, obtaining food while group foraging (Scott & Grumstrup-Scott 1983), structuring social order (Rothstein 1980), and assessing new individuals (Rothstein 1977). While the current study did not address the functional benefits of head-down displays, it’s individual consistency suggests that certain individuals may reliably seek out closer social interactions than others and therefore are more sociable than others.

By bringing individuals closer together, sociability will shape opportunities for learning social skills or the appropriate behavioral responses to others. Here, we demonstrated that sociability during the fall predicted reproductive behavior months later. In cowbirds, social experiences with others before the breeding season can influence later reproductive skills (White et al. 2002b, 2010a). The head-down display disappears during the breeding season and thus cannot play a direct role in structuring breeding opportunities. Nonetheless, the use of head-down displays during the fall may facilitate the close interactions needed to learn social skills and have cascading influence on reproductive performance. The ontogeny of social skills requires individuals to seek out, engage, and learn from others. Different social experiences can shape the expression of later social skills. For instance, cichlid fish (Neolamprologus pulcher) raised with adults exhibited more appropriate behavioral responses when competing with others (Taborsky et al. 2012), and male cowbirds who experienced a more varied social environment outcompeted others for access to mates (White et al. 2010a). Head-down displays, by fostering close social interaction, will be important determinants of an individual’s experience and access to social learning opportunities. While the current study did not investigate the developmental or proximate mechanisms linking head-down displays with reproductive behavior, it is the first demonstration in birds that affiliative displays can predict reproductive skills across contexts and over long periods of time.

Counter-singing is an essential component of male courtship behavior. Flocks composed of the most sociable males exhibited significantly higher proportion of songs within counter-singing matches. Furthermore, male sociability during the fall correlated with the proportion of songs in counter-singing matches, but not the proportion of female, male, or undirected songs. Counter-singing is a predictor of male reproductive success, stimulates egg production in females, and is learned through close interaction with others (White et al. 2010b). White et al. (2002b) found that juvenile males who interacted with adults prior to the breeding season engaged in more frequent and longer counter-singing matches than juveniles who did not interact with adults. To counter-sing effectively, males must remain in close proximity with other males and respond appropriately without withdrawing or escalating to aggression. Thus, a male’s sociability may shape their ability to counter-sing, as more sociable males may be more willing to remain in close proximity to another singing male than less sociable individuals. This study suggests that a male’s sociability during the fall is an important predictor of their later reproductive skills during the breeding season.

Females in flocks composed of more sociable cowbirds produced more eggs than flocks with less sociable cowbirds. While male counter-singing has been shown to reflect increased female egg production, previous studies have also demonstrated that exposure to highly interactive females can also increase levels of counter-singing (King et al. 2003). Therefore, flocks containing more sociable females may stimulate more counter-singing and egg production than other flocks. The design of this study does not address whether male counter-singing stimulates females to lay more eggs or if more reproductively competent and sociable females stimulate males to engage in more counter-singing. Furthermore, the identities of the laying females were not known in the present study, and therefore, it is unknown if more sociable females within each flock also produced more eggs. Future studies that independently manipulate male and female affiliative behavior while identifying laying females are needed to understand the direction of effects. Nonetheless, these results do suggest that sociability can create opportunities to acquire social engagement skills and that, taken as a whole, the ability to confidently engage others in close proximity is essential for cowbird courtship and reproduction.

All functions of social life require individuals to manage, control, and construct spatial relations between conspecifics (Byrne & Whiten 1988). The ability to sustain close proximity with others is one of the most basic skills individuals must master, and creates a foundation where other behaviors arise. From protection from predators, to play (Burghardt 2005), to social bonding (Stöwe et al. 2008), affiliative
behaviors are used to managing proximity between individuals. Despite this, very little is known about the evolutionary and developmental consequences of variation in sociability. Our study demonstrates that consistent variation in affiliative behavior predicts basic reproductive competence. This suggests that selection may act on underlying affiliative tendencies that, by shaping how individuals engage each other, determine the expression of behavior across contexts.

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Literature Cited


