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2    Female vocalizations predict reproductive output in Brown-headed

3    Cowbirds (*Molothrus ater*)

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24    ABSTRACT:

25        Pair bonds are often maintained through the reciprocal and coordinated exchange

26    of communicative signals. The ability to recognize and appropriately respond to a

27    partner's signals will define a pair's ability to reproduce. Individual variation in

28    responsiveness, by shaping the formation and maintenance of strong pair bonds, will

29    ultimately influence an individual's reproductive output. Throughout the breeding period,

30    female cowbirds (*Molothrus ater*) respond to male song displays using a vocalization

31    known as the chatter. In this study, we investigated whether variation in chatters

32    remained repeatable across years and predicted reproductive performance. A flock of

33    cowbirds housed in a large aviary complex was observed during the spring of 2011 to

34    2012. We recorded courtship interactions, including singing behavior for males, and

35    chatters and eggs laid by females. The rate with which females responded to song using

36    chatters remained consistent across years, with some females predictably responding to

37    more songs using chatters than others. During 2012, chattering predicted the number of

38    eggs females laid and her paired status. Paired females were more likely to respond to

39    songs with chatters, and there was a strong positive relationship between the number of

40    eggs laid and the proportion of songs she responded to using chatters. Overall, these

41    findings suggest that individual variation in female vocal responsiveness is an important

42    contributing factor to cowbird reproductive success.

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44    Keywords: female vocalizations, reproductive success, courtship, brown-headed cowbird,

45    social responsiveness, temperament, animal personality, individual differences

46

47    **INTRODUCTION**:

48

49        The ability to form and maintain pair bonds is a key factor in reproductive success

50    (1-5). Successful pair bond maintenance requires pairs to coordinate activities and

51    behavior to create strong, enduring, relationships. Within most vertebrate species,

52    individuals possess social displays and vocalizations that attract the attention of, and

53    coordinate activities with, potential or established mates (6). Individual differences in the

54    use of such displays may create stronger social bonds with preferred mates, and

55    ultimately increase reproductive output over time (7).

56

57        Increasingly, female displays and vocalizations are seen as critical factors shaping

58    courtship and pair bonds in a wide array of species (8-11). During the breeding season,

59    male cowbirds perform directed song displays at males and females. During song

60    displays, males orient towards a neighboring individual and perform a song while

61    spreading their wings and bowing (12). Cowbird courtship revolves around the female's

62    response to these song displays, and males modulate the intensity of their visual display

63    in order to minimize female withdrawal (13). Females communicate their mate

64    preferences using both visual (10) and acoustic (14) responses to male song displays.

65    During the fall, males depend on these response displays for the development of their

66    song, with females preferentially responding to, and reinforcing, high-quality song

67    variants (10). Nevertheless, less is known about the factors shaping variation in such

68    female responses, and how such variation predicts later reproductive outcomes for

69    females.

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71      Across many species females utilize vocalizations in response to male courtship

72    displays (e.g., red winged blackbirds, *Agelaius phoeniceus* (15), grasshopper sparrows,

73    *Ammodramus savannarum* (16), dunnocks, *Prunella modularis* (17), and duetting species

74    (18, 19) ). While female cowbirds do not sing, they possess an individually distinct

75    chatter vocalization that is commonly used in response to a male's song display (20).

76    These response chatters often overlap or directly follow the end of a directed song display.

77    In the wild, playbacks of chatters attract attention from both males and female cowbirds

78    (21, 22); in the lab, females who are unselective in their chatters – by responding to

79    playbacks of many different males' song with chatters –are also less likely to maintain a

80    pair bond (23). Females exposed to playbacks of songs followed by a playback of a

81    response chatters also preferred those songs in contrast to females who were only

82    exposed to playbacks of the song alone (14). These studies suggest that in cowbirds, as in

83    many other species (24), the selective and reciprocal exchange of vocalizations across

84    males and females plays a role in communicating mate preferences and maintaining pair

85    bonds.

86

87      The aim of this study was to investigate whether consistent individual differences

88    in the use of female vocalizations predict reproductive output in a semi-naturalistic flock

89    setting. My first aim was to uncover if individual variation in female responsiveness

90    remains repeatable, with some females consistently responding to more song display with

91    chatters than others across two different breeding seasons. Across fall flock changes,

92    female cowbirds exhibit consistent individual differences in the selectivity and frequency

93    of their autumn social interactions (25) and use of affiliative head-down displays (26).

94    Juvenile females who more frequently used affiliative "head-down" displays as juveniles

95    during the fall were also more willing to respond to song using chatters during their first

96    breeding season. This study will expand these findings to uncover if consistent individual

97    differences in chatters are sustained across breeding seasons during adulthood.

98

99    My second aim was to uncover whether variation in the use of female

100   vocalization reflects their reproductive output. Both strong pair bonds (7), and increased

101   vocal responsiveness (27) can influence egg production in birds by stimulating and

102   maintaining female reproductive physiology. As brood parasites, cowbirds do not raise

103   their own young, and lay eggs in host species nests. Thus, the ability to place more eggs

104   in more nests is crucial to gaining higher reproductive success. Cowbirds are also

105   monogamous and maintain a single pair bond throughout the breeding season. I

106   hypothesize that female cowbirds who consistently respond more to a higher proportion

107   of song displays with chatters will be more likely to sustain a pair bond, and also exhibit

108   higher rates of egg production than less responsive females.

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## Methods:

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## Subjects

113   All birds were originally captured in Philadelphia County, Pennsylvania and

114   Monroe County, Indiana and housed in aviaries in Monroe County, Indiana. All subjects

115   were *Molothrus ater ater*. Previous studies have shown no differences in song or social

116   behavior between the Philadelphia and Indiana populations (28). For this study we used

117   28 females including 21 adult (after second year by 2012) and 7 subadult (second year by

118   2012) females. We also used 28 males including 24 adult males and 4 subadult males.

119   Birds ranged in age from 2 to 13 years old with an average age of 4.9 years. All birds had

120   been used in previous studies, and were housed in large flocks prior to the beginning of

121   this study. Each bird was marked with uniquely colored leg bands to allow for individual

122   recognition. All birds were provided daily with a diet of vitamin-treated water (Aquavite

123   Nutritional Research), red and white millet, canary seed and a modified Bronx Zoo diet

124   for blackbirds.

125

## Aviaries:

127   I used a single aviary complex that consisted of 4 subsections each with identical

128   dimensions (9.1 x 21.4 x 3.4 meters), one small subsection (11 x 3 x 3.4 meters), and

129   three indoor enclosures described in detail within Smith et al. (29). The large size of the

130   aviary provides each cowbird with significant degrees of freedom to either engage or

131   avoid interaction with conspecifics. Each large subsection of the aviary contained a

132   covered feeding station and water bowls. Environmental conditions were similar

133   throughout the entire aviary with shrubs, trees and grass that allowed individuals to both

134   forage and hide. All birds were exposed to ambient climatic conditions, wild cowbirds,

135   and the occasional sight of predators.

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## Data collection:

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## Behavioral observations:

Throughout the study, a scan-sampling procedure was used to record behavioral observations; the entire flock was scanned and behaviors were recorded as they were observed (30). During scan sampling all behaviors were recorded using voice recognition technology described in detail by White, King & Duncan (31). When used in combination with voice recognition technology, scan-sampling can accurately acquire a more comprehensive dataset than focal sampling (32). All observations were conducted from 07:00-10:30 AM when cowbirds are most active, and were counterbalanced, so different observers took the same number of scan-sampling blocks in each aviary every day.

From June 9th to July 8th 2011 and from May 1st to June 8th 2012, we recorded courtship behavior, focusing on the vocal and approach behavior of both males and females. Throughout the study courtship behavior was recorded during 15-minute scan sampling blocks. For females, we recorded the number of songs each female received from males, and the number of female chatter vocalizations. Female chatter vocalizations were either response or undirected chatters. Response chatters occur when a female responds to a directed male song with chatter vocalization within a one second time window. Undirected chatter vocalizations occur when the females performs a chatter vocalization outside of singing contexts. For male courtship behavior, we recorded the number of female and male directed songs. Copulations were also recorded in order to assess female pair bonds (see below). During the pre-breeding season from March 18th to April 23rd in 2012 we also recorded approach behavior in separate 7-minute observation

161    blocks. Here an approach was scored when one individual approached another individual

162    with any part of its body within a radius of 30cm.

163

164    **Egg Collection**

165         From May 1st to June 8th we recorded the number of eggs each female laid. Six

166    decoy nests were installed in each of the 4 large subsections of the aviary complex. Each

167    nest was mounted on a forked perch attached to a backboard that contained a video

168    camera, and was installed on posts or bushes within the aviary. All nests were supplied

169    with yogurt-covered raisins as decoy eggs. A decoy egg was added every day to each nest

170    until the nest contained three decoy eggs. Each day all nests were checked for the

171    presence of cowbird eggs laid during the morning. After 8 days in one area each nest was

172    moved to a different location within the aviary, nesting material was replaced, and was

173    treated as a new nest starting with no eggs. All nests were video monitored to determine

174    the identity of laying females by using Geovision software (Geovision Inc. 2008, 9235

175    Research Drive, Irvine, CA, USA) on Dell Vostro 230 computers running a 32-bit

176    Windows 7 operating system. All work was conducted under ASAB/ABS guidelines and

177    approved by the Institutional Care and Use Committee of Indiana University (08-018).

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179    **Procedure**

180         *Year 1: Spring 2011*: From June 9th to July 8th three observers collected a total of

181    240 observation blocks recording courtship behavior.

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183    *Year 2: Spring 2012*: In the pre-breeding season from March 18th to April 23rd,

184    three observers collected a total of 40 blocks recording approach behavior and 164 blocks

185    recording courtship behavior. During the breeding season from May 1st to June 8th, three

186    observers collected a total of 360 observational blocks recording courtship behavior. All

187    decoy nest units were installed on May 1st and used to record the number of eggs laid

188    until the end of the breeding season on June 8th.

189

## Analysis

191    To document the repeatability of chatter across years, we used one-way intraclass

192    correlation coefficients on the rate of each female's chatters per block across 2011 and

193    2012. Intraclass correlation coefficients estimate the proportion of behavioral variance

194    that is due to differences between individuals. To assess the rank ordered consistency in

195    the individual tendency to chatter, we used Spearman's correlations on the rate of

196    response chatter across 2011 and 2012. All further analysis was conducted on the data

197    recorded during spring 2012.

198

199    We considered a female to be paired if she received at least 100 songs and 70% of

200    the songs she received came from a single male, with whom she exclusively copulated

201    from 1 May to 8 June 2012. Furthermore, this female also had to be within the top two

202    highest-ranking females sung to by the male. Thus, paired females maintained a selective

203    relationship with a single male throughout the length of the breeding season, whereas

204    unpaired females did not. We used Mann Whitney U-tests to look at the differences in the

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205     proportion of songs that a female responded to with a chatter, and the number of songs a

206     female received between paired and unpaired females.

207

208     We used permutation-based linear models to investigate how variation in spring

209     behavior predicted a female's reproductive output. As social behavior often does not

210     meet the assumption that errors are independent and normally distributed, permutation

211     methods offer ideal alternatives to calculate probabilities of getting observed statistics

212     after random reshuffling the data (33). For this study we used the lmp function in the

213     lmPerm R package (34). I performed two models in this study: one model for all females,

214     and another model restricted to paired females. Each model used an exact method to

215     produce permutation probabilities and ran a minimum of 5000 permutations. As some

216     explanatory factors were inter-correlated, we used variance inflation factors to assess the

217     multicollinearity of main effects. A variance inflation factor greater than 10 is used to

218     indicate potential multicollinearity, which makes model interpretation difficult (35). In

219     none of our presented models did the VIFs for any main effects exceed 1.5. Post hoc

220     analysis was conducted using Spearman's correlations on continuous explanatory factors,

221     and Wilcoxon rank sum test for categorical explanatory factors. Confidence intervals for

222     Spearman's coefficients were calculated using resampling techniques.

223

224     For both models, the dependent factor was the number of eggs that each female

225     laid. For the all-female model, the explanatory factors included main effects of the total

226     rate of songs received, paired status, the number of approaches initiated during the pre-

227     breeding season, proportion chatter (number of response chatters/ total number of songs),

228   and their age class (sub-adult and adult) and the number of undirected chatters.The

229   paired-female model was restricted to only females in a pair bond, and focused on how

230   interactions in pairs predicted female reproductive output. The explanatory factors for the

231   paired model were the rate of songs received from their paired male, the proportion

232   chatter in response to their paired male, the female's age class (sub-adult and adult),

233   whether they were paired with the same or different male across years (same pair,

234   different pair), and the number of undirected chatters.

235

## Results

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## Repeatability of chatters across years

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239          Across years, females were predictable in their propensity to respond to song

240   displays using chatters. In 2011, we observed a total of 4,152 chatters including 1,272

241   response chatters (*Median per individual* = 28.5) and 2,880 undirected chatters (*Median*

242   *per individual* = 28). During the breeding season in 2012, we observed a total of 6,830

243   chatters, including 2,339 response chatters (*Median per individual* = 27), and 4,491

244   undirected chatters (*Median per individual* = 36). For all females, individual variation in

245   the rate of response chatters was repeatable across both years (*ICC* = 0.50, *p* < 0.0001,

246   95 % CI =  0.17- 0.73). Females also showed significant rank-ordered consistency in the

247   rate of response chatter in relation to other females across years (Spearman's rank

248   correlation: *rho* = 0.43, *N* = 28, *p* = 0.03, 95% CI = 0.06 – 0.73). Within both spring 2011

249   and 2012, females who performed the most undirected chatters also performed the most

11

250    response chatters (2011: *rho* = 0.90, *N* = 28, *p* < 0.0001, 95% CI = 0.80 – 0.94, 2012: *rho*

251    = 0.93, *N* = 28, *p* < 0.0001, 95% CI = 0.85 – 0.97).

252

## 253    **Chatters and pair bonds**

254

255        Response chatters were used very selectively, and were primarily directed

256    towards a single male across the breeding season. From 1 May to 8 June in 2012, we

257    recorded 5,091 songs sung to females, with a median of 177.5 songs per female. For each

258    female, we rank ordered the number of response chatters to each male and calculated the

259    proportion of response chatters in response to each male's songs. The top male accounted

260    for the majority of the female's response chatters (*Median proportion of response chatter*

261    *to top male* = 0.90), and in paired females the top male was always the female's partner.

262    While paired females received more songs than unpaired females (*Median Paired*

263    *Females* = 242, *Median Unpaired females* = 62, Mann-Whitney *U* test: *U* = 44.5, $N_1$ = 14,

264    $N_2$ = 14, *p* = 0.0003), they were also more likely to respond to a higher proportion of

265    songs with response chatters (*Median Paired Females* = 0.60, *Median Unpaired females*

266    = 0.05, *U* = 14, $N_1$ = 14, $N_2$ = 14, *p* = 0.0001, Fig 1).

267

## 268    **Egg output All-Female Model**

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270        During the breeding season, females who laid more eggs responded to a higher

271    proportion of songs with a response chatter. We identified the laying female for 93 eggs

272    (*Mean eggs laid* = 3.32). Our model (Table1) explained 74% of the variance in eggs laid

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273  ($R^2$= 0.74, $F_{(7,20)}$ = 8.12 , $p$ = 0.0001).  The proportion of male song displays followed by

274  a chatter was the only significant predictor of the number of eggs an individual laid

275  (Table 1). Post hoc correlations revealed a significant positive relationship between the

276  numbers of eggs an individual laid and proportion chatter (*rho* = 0.77, *N* = 28, *p* <

277  0.0001, 95% CI = 0.54 – 0.92, Fig 2). Additional analysis also showed that the rate of

278  response chatters before the breeding season (before females were actively laying eggs),

279  from 18 March to 23 April, was also positively correlated with the later number of eggs

280  an individual laid (*rho* = 0.68, *N* = 28, *p* < 0.002, 95% CI = 0.43 – 0.84).

281

282      We identified 72 eggs from adult females (*Mean* = 3.42) and 21 eggs from sub-

283  adult females (*Mean* = 3). Age did not significantly influence the number of eggs

284  produced. There was no significant difference in the number of eggs produced by sub-

285  adults in contrast to adults (*Median Adult* = 2.00, *Median Subadult* = 0.05, $N_1$ = 21, $N_2$ =

286  7, *U* = 88, *p* = 0.45). While paired status did not reach significance in our model, post hoc

287  analysis revealed that paired females produced more eggs than unpaired females (*Median*

288  *Paired* = 3.00, *Median Unpaired* = 0.05, *U* = 145, $N_1$ = 14, $N_2$ = 14, *P* = 0.03).

289

290  **Egg output Paired-Female model:**

291

292      Our paired-female model explained 78% of the variance in egg laying ($R^2$= 0.78,

293  $F_{(5,8)}$ = 5.683, *p* = 0.016) and had only one significant predictor, the proportion of songs

294  followed by a response chatter (Table 1). None of the other variables were significant

295  predictors of the number of eggs a female laid (Table 1). Within paired individuals, the

296   proportion of response chatters was significantly correlated with the number of eggs laid

297   ($rho = 0.72$, $p = 0.004$, 95% CI = 0.33 – 0.92, Fig 2), but neither the number of

298   undirected chatters ($rho = 0.42$, $p = 0.13$, 95% CI = -0.10 – 0.83), nor the number of

299   songs they received from their paired male ($rho = -0.03$, $p = 0.92$, 95% CI = -0.55 – 0.48).

300

301          In order to look at the factors predicting variation in response chatters I conducted

302   an additional permuation based linear model. The dependent variable in this model was

303   the proportion of response chatters to her paired males songs. The explanatory factors

304   were age, songs received from paired males, and if the female maintained a stable pair

305   bond across breeding seasons. This model was not significant ($R^2 = 0.22$, $F_{(3,10)} = 0.93$, $p$

306   = 0.46). The number of songs a female received from her paired male was not

307   significantly correlated with proportion of response chatters ($rho = 0.37$, $N = 14$, $p = 0.19$,

308   95% CI = -0.06 – 0.68). There was also no significant differences in both the proportion

309   of response chatters ($W = 28$, $p = 0.662$), the number of eggs laid ($W = 33.5$, $p = 0.24$)

310   between females who were paired with the same male across both breeding seasons, and

311   females who changed males.

312

## Discussion:

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314

315          I investigated the association between individual differences in courtship behavior

316   and reproductive performance in female brown-headed cowbirds. Female cowbirds

317   exhibited consistent individual differences in their responsiveness to male song, with

318   some females being more likely to respond to male song displays using chatters than

319    others. As vocal stimuli are important for attracting potential partners (36), shaping

320    reproductive physiology (37, 38), and maintaining pair bonds (15, 39), consistency in

321    vocal responsiveness may reliably construct the social relationships needed for increased

322    reproductive output. In accordance with this, I discovered that the proportion of song

323    displays a female responded to with chatters was greater in paired females, and predicted

324    the number of eggs she produced. In paired females, I also found that the proportion of

325    response chatters to their paired male's song display was the only significant predictor of

326    the number of eggs she laid.

327

328        Paired females responded to a higher proportion of songs with chatters than

329    unpaired females. This suggests that the maintenance of pair bonds is associated with the

330    reciprocal exchange of vocal displays from both male and female cowbirds. While

331    recognition of female courtship displays is becoming more widespread (40, 41), little is

332    currently known about how these displays shape their relationship with males. Pervious

333    studies have shown have shown that increased attention, coordination, and synchrony

334    within pairs has multiple benefits, such as increasing vigilance, lowering the energetic

335    demands of foraging and parental care, and more effective mate guarding (42-44). In

336    alpine accentors (*Prunella collaris)* females use complex songs to attract mates (36), and

337    the calls of female whitethroats (*Sylvia communis)* both attract males and shape their

338    courtship behavior (45). In many mammals such as brown rats, *Rattus norvegicus,* (46),

339    grey mouse lemurs, *Microcebus murinus,* (47)*,* and Barbary Macaques, *Macaca sylvanus*,

340    (48),  female vocalizations often reflect reproductive status, and are used to attract males.

341    In the field, playbacks of cowbird chatters often attract males to the location of a speaker

15

342     (22), and males will often follow and peruse females who responded to their song with a

343     chatter  (Kohn, personal observation). By possessing a signal that reflects their

344     reproductive status, female cowbirds who are more vocally responsive will be better able

345     to attract preferred male attention and drive pair coordination across the breeding season.

346

347          Variation in signals used to attract and coordinate activities within pairs can have

348     cascading influences on later survival and fitness. I found that a female's vocal response

349     to male song displays was the strongest predictor of her reproductive output, with more

350     vocally responsive females laying more eggs than less responsive females. Similar

351     findings have been observed in red-winged blackbirds, where females who had a

352     successful nest were more likely to answer male songs with a chit vocalization (39). In

353     many species, the reciprocal displays between members of a pair can also shape

354     reproductive physiology (27, 49). For instance, in ring doves (*Streptopelia risoria*), the

355     presence of a preferred male song stimulates the females to use 'coo' vocalizations (50).

356     In turn, the coo vocalizations themselves stimulate ovarian development (27, 49), which

357     may result in increased egg production. Thus, the contingent displays females use in

358     response to their partners may be an important, albeit under-recognized, component in

359     shaping a pair's reproductive success.

360

361          Currently, the direction of effects between increased reproductive output and

362     coordinated displays between cowbird pairs is unknown. However, females begin

363     responding to male song with chatters prior to the egg laying period, and response chatter

364     rates during this pre-laying period are correlated with egg output the same year. Thus, a

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365    female's own courtship behavior might play a role in providing the necessary stimulation

366    for increased reproductive output. While the mechanisms underlying the relationship

367    between vocal responsiveness, pair bonds, and egg production need further investigation,

368    my results demonstrate that repeated use of response chatters is predictive of increased

369    reproductive output in female cowbirds.

370

371         In cowbirds, female responses to male vocalizations are commonly used to assess

372    the quality and attractiveness of male signals (10). Females use their response chatter

373    selectively, almost exclusively in response to their paired males. As females exclusively

374    copulated with their paired males, response chatters may be a reliable signal of female

375    preferences, and used to reinforce pair bonds. Chatters are also individually distinct (20),

376    and their selective use may facilitate the individual identification needed to sustain a

377    monogamous pair bond (15, 51). Female cowbirds with lesions to their HVC area are not

378    selective in their response chatters, and chatter in response to nearly all song playbacks,

379    regardless of their quality (23). These lesioned females are also unable to sustain a pair

380    bond, and are courted by a larger number of males than other females. I found that

381    females who retained the same pair-bonded males across two different breeding seasons

382    showed no significant differences in vocal responsiveness or egg production when

383    compared to females who changed paired males. The number of songs a female received

384    from males did not reflect the proportion of response chatters to his songs, and further

385    analysis also showed that the number of response chatters a male received across

386    breeding seasons was not correlated or repeatable (Sup 1). While the correlational nature

387    of this study does not allow us to directly test how differences in male quality or song can

17

388    influence female vocal responses, our result suggest that variation in the use of chatters

389    represents different behavioral strategies that females use when engaging and forming

390    pair bonds with preferred males.

391

392          This paper adds to the increasing number of studies showing the importance of

393    female vocalizations in constructing and reinforcing avian pair bonds (52, 53), and

394    further suggests that female vocalizations contributes to their reproductive success.

395    Consistent individual differences in cowbird social behavior can predict an individual's

396    reproductive performance across long timescales (54). Juvenile female cowbirds who

397    initiate more affiliative head-down displays during autumn are more likely to engage

398    males with chatters and form a pair bond during their first breeding season (26). Here we

399    show that such variation in female vocal responses is maintained into adulthood, remains

400    associated with pair-bond status, and predicts reproductive output. In cowbirds, social

401    experiences are critical in the development female mate preferences (55, 56), and may

402    also shape behavioral differences in how females interact with preferred males (26).

403    Further research will explore how the early social environment shapes the development

404    of individual differences in chatter vocalizations among females, and the causal

405    mechanisms linking chatter vocalizations, pair bonds, and increased reproductive output.

406

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411

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566    Figure 1:

567                                                    [[[ Figure 1 ]]]

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569    **Figure 1** The proportion of response chatter vocalizations based on based on an

570    individual's paired status. Boxes represent interquartile ranges with the median in the

571    middle represented by a bold line; whiskers represent the range of the highest and lowest

572    values that are within a range of 1.5 times the interquartile range; dots indicate data

573    points that are outside this range.

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579    Figure 2.

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582                                                    [[[ Figure 2 ]]]

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584    **Fig 2:** Scatterplots for the proportion of response chatters and the number of eggs laid

585    for all females. Females who formed a pair bond during 2012 season are shown as a

586    triangle, and females who did not maintain a pair bond are shown as a circle. Line

587    represents the permuted linear regression with surrounding 95% confidence intervals.

588

589     Table 1.

| A. All- Female Model | Coefficients | P value | A. Paired- Female Model | Coefficients | P value |
|---|---|---|---|---|---|
| **Songs Received** | -0.01 | p = 0.08 | Paired male song | -0.02 | p = 0.16 |
| **Approach** | 0.005 | p = 0.41 | Approach | 0.002 | p = 0.86 |
| **Proportion chatter** | 14.65 | p < 0.00001*** | Proportion paired chatter | 12.47 | p = 0.03* |
| **Age class** | 0.95 | p = 0.50 | Age Class | 4.97 | p = 0.11 |
| **Undirected chatter** | 0.58 | p = 0.69 | Undirected Chatter | 2.27 | p = 0.24 |
| **Pair bond** | 1.28 | p = 0.38 | Stable/ Switched pair bonds | 2.69 | p = 0.20 |

590

591     Table 1: Results of the permutation-based linear models for eggs laid during the breeding

592     season of 2017. Table represents the model for (A) all-females and (B) paired-females.

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