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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.

70

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.

109

110 **Methods:**

111

112 **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

126 **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.

136

137 **Data collection:**

138 **Behavioral observations:**

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

148

149 From June 9th to July 8th 2011 and from May 1st to June 8th 2012, we recorded
150 courtship behavior, focusing on the vocal and approach behavior of both males and
151 females. Throughout the study courtship behavior was recorded during 15-minute scan
152 sampling blocks. For females, we recorded the number of songs each female received
153 from males, and the number of female chatter vocalizations. Female chatter vocalizations
154 were either response or undirected chatters. Response chatters occur when a female
155 responds to a directed male song with chatter vocalization within a one second time
156 window. Undirected chatter vocalizations occur when the females performs a chatter
157 vocalization outside of singing contexts. For male courtship behavior, we recorded the
158 number of female and male directed songs. Copulations were also recorded in order to
159 assess female pair bonds (see below). During the pre-breeding season from March 18th to
160 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).

178

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.

182

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

190 **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

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

236 **Results**

237

238 **Repeatability of chatters across years**

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 $95\% \text{ CI} = 0.17- 0.73$). 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: $\rho = 0.43, N = 28, p = 0.03, 95\% \text{ CI} = 0.06 - 0.73$). Within both spring 2011
249 and 2012, females who performed the most undirected chatters also performed the most

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

269

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

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 permutation 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

313 **Discussion:**

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. Previous
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

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

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

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:

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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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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

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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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