1   Socially regulated estrogen in an eavesdropping brood parasite

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Abstract

Social regulation of reproductive hormones is a means by which conspecific males and females orchestrate successful reproductive efforts. There is variation, however, in the range of social cues that will initiate a hormone response in the receiver of social signals. We investigate whether social cues modify activity within the hypothalamic-pituitary-gonadal (HPG) axis and the specificity of this response in a social parasite that is known to eavesdrop on the communication signals of other species: the brown-headed cowbird (*Molothrus ater*). Brown-headed cowbirds are obligate brood parasites that do not build nests or care for their own young. Instead, obligate brood parasites always leave their eggs in the nest of a host species thereby receiving the benefits of parental care toward offspring without paying any of the costs. Thus, social parasites must coordinate their breeding attempts with conspecifics as well as potential heterospecific hosts and therefore, social parasites such as cowbirds rely on the communication signals of host species to help locate nests to parasitize during the breeding season. Here, we explore whether the vocal signals of potential host species can also be used as a social cue that modifies the HPG axis of female brown-headed cowbirds. Results reveal that both conspecific and heterospecific song-exposed females exhibit significantly greater circulating estradiol concentrations as compared to silence-exposed females. While conspecific song induces the greatest elevation in circulating estradiol, there is no significant difference in circulating estradiol levels in females exposed to either conspecific or heterospecific songs. This pattern suggests both song types are effective at evoking a reproductive physiological response. On the other hand, circulating progesterone concentrations did not differ among the song- and silence-exposed groups nor did the size of the female's ovarian follicles. These results indicate that heterospecific vocal communication signals can effectively be used as a social cue that simultaneously provides necessary information regarding breeding status of hosts and modifies breeding condition of the eavesdropper.

Highlights
- Brood parasites may coordinate reproductive attempts with potential hosts.
- Therefore, parasites eavesdrop on other species, which helps them find nests.
- Vocal signals from conspecific and heterospecifics elevate estrogen in parasites.
- Hearing potential host songs may enhance reproductive hormones in brood parasites.

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1.0 Introduction

84   Reproductive physiology and behavior can be regulated, in part, by social environment
85 (Lehrman, 1965). Social regulation of reproductive physiology helps coordinate reproductive
86 attempts between males and females that are attending to the social cues of their partners.
87 There is variation, however, in the specificity of social signals that modify the receiver's
88 physiology. Reception of one's own signals and/or reception of conspecific signals modify
89 physiological states of the receiver, help coordinate complex social behaviors, and guide
90 context-appropriate responses (Cheng, 1992; Cheng et al, 1998; Lynch and Wilczynski, 2006;
91 Watts et al, 2016; Roleira et al, 2017). Here, we pair the phenomenon of social-dependent
92 regulation of reproductive physiology with animal behavior studies demonstrating that some
93 species intentionally and routinely eavesdrop on communication signals not intended for them.
94 These species actively seek out signals for which they were not the intended target (i.e.
95 eavesdropping) to obtain vital information that may enhance not just reproduction but also
96 predation and parasitism opportunities, thereby increasing the eavesdropper's fitness (Zuk and
97 Kolluru, 1998; Bernal et al, 2006; 2007; Page and Ryan, 2008).

98   Social parasites that must locate hosts for reproductive purposes eavesdrop on the
99 communication of heterospecifics. One example of a social parasite that eavesdrops is the
100 brown-headed cowbird (*Molothrus ater*), an obligate brood parasite. Avian obligate brood
101 parasites do not build nests, incubate eggs or provision their own young. Instead, the female
102 parasite locates nests of other species that can serve as a host parent to her offspring. One of
103 the ways in which breeding female parasites locate nests is through cryptic observation of hosts
104 and their activities as well as attending to their vocalizations (Hann 1941; Gochfeld 1979;
105 Clotfelter, 1998; Wiley, 1988; Alvarez 1993; Monk and Brush 2007; Janecka and Brush, 2014).
106 This is termed the host-activity hypothesis, which predicts that brood parasites will be attracted
107 to the vocalizations of potential hosts as well as their nest building behavior (Hann 1941;
108 Gochfeld 1979; Wiley and Wiley 1980). Thus, conspicuous host vocalizations and other
109 behaviors may be an important determinant of whether a host nest will be parasitized by
110 eavesdropping brood parasites. Consequently, brood parasites should attend relevant social
111 signals of conspecific and heterospecific species because the brood parasite must coordinate
112 its reproductive behavior with both conspecific mates as well as possible heterospecific hosts.

113   The brown-headed cowbird (hereafter, cowbird) are oscine Passeriformes within the
114 Icteridae family (i.e. blackbirds). Male cowbirds housed with females displayed peak circulating
115 testosterone levels and mature gonads for longer as compared to cowbirds house without
116 females (Dufty and Wingfield, 1990), indicating social regulation of reproductive physiology does
117 occur in this species. Also, brown-headed cowbirds are known to eavesdrop on the activity of
118 heterospecific hosts during the breeding season to aid in host nest location (Clotfelter, 1998).
119 Here, we test the hypothesis that female cowbirds may coordinate their reproductive physiology
120 with that of their hosts using social cues. We predict that heterospecific and conspecific
121 vocalizations are both effective at modifying the reproductive physiology of female cowbirds. If
122 this is the case, reproductive hormones and/or follicles will be significantly greater in conspecific
123 and heterospecific song-exposed females as compared to silence-exposed females. These
124 results will provide insight into whether brood parasites use heterospecific vocal signals as a
125 means of coordinating timing of reproductive events and the specificity in the types of signals
126 that will evoke a physiological response in these birds.

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2.0 Methods
2.1 Housing and stimulus exposure

130   Female cowbirds (N = 18) were collected using bait traps in Travis and Kerr counties in
131 Texas in May, 2016. Birds were transported to outdoor aviaries in Hempstead, NY and housed
132 in semi-natural conditions. Females were fed a modified Bronx zoo diet with mealworm

supplements and were isolated from male brown-head cowbirds to ensure no social interaction with males or male song during this time. In August, females showed no continued signs of breeding behavior. They were then housed in an indoor aviary to habituate for one week on a 16L:8D light schedule. Females were visually isolated from each other while individually housed in 610 mm x 610 mm cages randomly placed in indoor aviaries with varied social conditions: conspecific song exposure (N = 7), heterospecific song exposure (N = 7) or silence (N = 4). This design, including the sample sizes in each group, followed the design described in Bentley et al, (2000). All procedures presented here were permitted by Hofstra IACUC.

Red-winged blackbird (*Agelaius phoeniceus)* songs were chosen as the heterospecific stimulus in this study because they are a common host and geographically sympatric species for the brown-headed cowbird (Lowther, 1993). Red-winged blackbirds are frequently targeted as a host species for the brown-head cowbird and may even be the preferred species in some regions of the cowbirds range. Red-winged blackbirds have a similar breeding initiation timeframe as the cowbird, a lower nest abandonment rate and mite parasitism compared to other blackbirds (Freeman et al, 1990; Ortega and Cruz, 1988; 1990), all of which may result in the red-winged blackbird being a preferred host in some parts of North America. Furthermore, cowbirds are frequently found in mixed flocks that contain red-winged blackbirds. These observations indicate that red-winged blackbirds are likely to be encountered at some point in the cowbirds lifetime; either during developmental or adult stages. Stimuli were designed as described in Lynch et al., 2017. Briefly, five independent examples of song were recorded from different male brown-headed cowbirds (fig. 1a for representative sonogram) or red-winged blackbirds. Each sound was filtered above 2000 HZ and below 500 HZ, and all sounds were normalized to the mean amplitude. To equilibrate the amount of stimulation between experimental and control stimuli, we matched peak amplitude and duration of signals as described in Lynch et al, 2017. Vocalizations were synthesized with 20 s of vocal stimulus / min and arranged so that 1-2 songs from each male recorded was presented in each minute of presentation. The amplitude of song at each cage ranged between 65 and 70 dB as measured by SPL meter 0.5 m from the speaker. Songs were broadcasted for 8 hours / day starting at 6:00 a.m. followed by 16 hours of silence. Stimulus exposure in each condition continued for fourteen days during which time females continued to be fed the modified Bronx zoo diet with constant water supply. After fourteen days of song or silence exposure, females were sacrificed via rapid decapitation to collect blood tissue. As in Lynch et al (2017) and Bentley et al (2000), gonads were measured using calipers. The largest follicle was recorded in females across the three social exposure treatment groups.

2.2 Hormone assays

Immediately after collection, blood was centrifuged for 10min at 10,000rpm. Plasma was stored at -80°C until assayed. Circulating estradiol and progesterone concentrations were measured using modified extraction and assay procedures described in Lynch and Wilczynski, 2005; 2006; 2008. Briefly, steroids were extracted from the plasma using 3 ml of diethyl ether. Samples in all treatment groups were simultaneously extracted. In addition, a pooled sample of plasma was stripped of steroid using charcoal-dextran and spiked with a known concentration of estradiol (250 pg/ml) and measured in the EIA assay to estimate extraction efficiencies. The averaged extraction efficiency was calculated at 72%. Extracted steroids resuspended in assay buffer were used to measure estradiol and progesterone concentrations using ELISA assay kits from Cayman chemical (Ann Arbor, Michigan). To validate these kits for use with cowbird plasma, we extracted estradiol and progesterone from a plasma sample and serially diluted it at three concentrations. We compared the slope of the line for the serially diluted samples and the slope of the line for the area of the curve necessary to estimate the concentration of the diluted samples as described in Lynch and Wilczynski, 2006. The slope of the line for the serially diluted estradiol samples was –25.1, and the slope of the line for the area of the estradiol

184 standard curve in which the samples are estimated was –27.9. The slope of the line for serially
185 diluted progesterone samples was -811 and the slope of the line for the area of the
186 progesterone standard curve in which samples are estimated was -792. Both steroids were
187 measured on a single plate, precluding an inter-assay variation measurement. One subject was
188 removed in the heterospecific group and two were removed from the conspecific group due to
189 high CV estimates for the triplicates (final heterospecific N = 6; final conspecific N = 5). After
190 removal of these two elevated CV samples, the intra-assay variation was 9.08% and 9.87% for
191 estradiol and progesterone respectively. According to the manufacturer, estradiol EIA kits have
192 a 0.1% cross reactivity with testosterone and 5 α-DHT, 0.07% for 17 α-estradiol, and 0.03% for
193 progesterone and the detection limit is 6.6 pg/ml. The progesterone assay has a detection limit
194 of 7.8 pg/ml and the following cross reactivities: pregnenolone 14%, 17β-estradiol 7.2%, 5β-
195 pregnan-3α-ol-20-one 6.7%, and 17α-hydroxyprogesterone 3.6%. All other reported cross
196 reactivities were less than 0.5%.
197
198 **2.3 Statistics**
199 Circulating estradiol and progesterone concentrations as well as follicle sizes were
200 compared separately across three groups of females exposed to different social cues using
201 non-parametric tests due to unequal variances. Separate Kruskall-Wallis tests determined
202 whether there were any significant differences in circulating estradiol or progesterone
203 concentrations across the three social exposure groups: conspecific and heterospecific song
204 exposure as well as silence exposure. Post hoc pairwise comparisons were conducted using
205 independent t-tests. Due to heteroscedasticity, pairwise tests were corrected for unequal
206 variances. Benjamini-Hochberg corrections were used to adjust the false discovery rate for
207 multiple tests as both conspecific and heterospecifc groups were compared to silence. This
208 adjusted the heterospecific and conspecific comparison to silence to an alpha value of 0.025
209 and 0.05 respectively.
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211 **3.0 Results**
212 A significant difference in circulating estradiol concentration across the three treatment
213 groups was detected (H = 6.38; df = 2; P = 0.041). Post-hoc pairwise comparisons reveal that
214 conspecific and heterospecific song exposed females had significantly higher circulating
215 estradiol concentrations as compared to silence (t_4= 2.83, P = 0.047; t_7= 2.37, P = 0.022
216 respectively; fig. 1a). There was no difference in circulating estradiol concentrations between
217 heterospecific and conspecific song exposed females (t_4= -2.27, P = 0.08). On the other hand,
218 no significant difference in circulating progesterone concentration across the three treatment
219 groups was detected (H = 1.1; df = 2; P = 0.57; fig. 1b). Likewise, no significant difference was
220 detected in largest follicle size (H = 2.23; df = 2; P = 0.32; fig. 1c).
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222 **4.0 Discussion**
223 Social signals, including vocalizations, are sufficient to initiate activity within the
224 hypothalamic-pituitary-gonadal (HPG) axis of birds (Bentley et al., 2000; Friedman, 1977;
225 Kroodsma, 1976; Waas et al., 2005, Brockway, 1964; Haase et al., 1976). There is variation
226 across species, however, in the specificity of social signals that will initiate this response
227 (Bentley et al., 2000). In the present study, we apply this well-established phenomenon to the
228 brown-headed cowbird, a species that eavesdrops on a wide array of heterospecific social
229 signals to enhance its own fitness.
230 The results demonstrate that females exposed to either heterospecific or conspecific
231 vocalizations displayed elevated circulating estradiol but not progesterone concentrations in
232 comparison to females exposed to silence. These results indicate that both heterospecific and
233 conspecific vocalizations will initiate a response in estradiol, but not progesterone, production in
234 female cowbirds. Estradiol regulates a range of necessary processes in female songbirds during

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235 reproduction including modifying sensory processing that may enhance detection of male
236 signals (Maney and Pinaud, 2011; Caras et al, 2012), inducing receptive responses to male
237 courtship signals (Searcy and Capp, 1997; Leboucher et al, 1998) and, altering activity of
238 catecholamines that also play a role in reproduction and mating (Matragrano et al, 2001;
239 Rodríguez-Saltos et al, 2018; see Lynch, 2017 for review). Progesterone, on the other hand,
240 has been demonstrated to inhibit reproductive behavior in some female songbirds (Leboucher et
241 al, 2000). Thus, social regulation of circulating estradiol concentration by heterospecific and
242 conspecific social signals may occur because both signals provide meaningful information
243 regarding the commencement or conclusion of breeding season and allows brood parasitic birds
244 to coordinate their reproductive efforts with each other as well as with their heterospecific hosts.
245 　　　While circulating estradiol concentrations were significantly elevated by social exposure
246 in female cowbirds, results indicate that development of ovarian follicles was unaffected by
247 conspecific and heterospecific song exposure. There was no difference in measurements of
248 either the largest follicle or the total size of the follicular cluster across any of the vocal exposure
249 groups and silence. This result is consistent with studies from other songbirds, particularly pine
250 siskins (*Spinus pinus*), European starlings (*Sternus vulgaris*), willow tits (*Parus montanus*) and
251 white crowned sparrows (*Zonotrichia leucophrys pugetensis*). In these studies, females
252 exhibited advanced gonadal development in the presence of a male, which appeared to be a
253 vital cue instigating the progression to yolk deposition and follicular maturation (Perfito et al,
254 2014, Watts et al 2015; Wingfield et al., 1997). Therefore, it is possible that female cowbirds
255 exposed to conspecific and heterospecific songs do not progress to advanced stages of
256 follicular maturation because neither vocal signal is sufficient to initiate this process. As it is also
257 the case that follicular development in song-exposed females is not different from females
258 exposed to 14d of silence, it is possible that physical or visual interaction with males is
259 necessary for advancing to mature follicular stages. This supports the hypothesis that vocal
260 cues may be sufficient to instigate reproductive steroid production but final stages of follicle
261 development require actual interaction with males (Watts et al 2015), suggesting that at least a
262 visual cue from males are needed for the final stages of reproductive readiness to be achieved.
263 　　　The results of this study reflect behavioral studies demonstrating that heterospecific
264 songs provide meaningful information to brood parasites. For instance, in bronzed cowbirds
265 (*Molothrus aeneus*), broadcasted songs of Audubon's orioles are visited at nearly equal rates by
266 orioles and bronzed cowbirds. Because orioles are a preferred host species for bronzed
267 cowbirds this suggests that social cues used by orioles are a potent signal that attracts the
268 attention of the cowbird (Monk and Brush, 2007). In a related study, bronzed cowbirds
269 responded in greater numbers to the songs of orioles species (their preferred hosts) than to the
270 songs of olive sparrows (*Arremonops rufivirgatus*), a lower-quality host species (Janecka and
271 Brush, 2014). Further evidence indicates that female cowbirds use heterospecific songs as a
272 cue during nest searching (Clotfelter, 1998; Janecka and Brush, 2014) and individual female
273 cowbirds exhibit flexible preferences for a few specific host species (Strausberger and Ashley,
274 2005), which suggests memory for heterospecific signals. Thus, songs may help the brood
275 parasite locate host nests and serve as a cue to help them find breeding heterospecifics that
276 may soon build a nest. The results presented in our study suggest that signals from other
277 species not only aid the brood parasite in locating host nests in which to lay eggs but also
278 modulate the cowbirds reproductive hormones. Therefore, by attending to heterospecific signals
279 the cowbird accomplishes two important tasks: it gains information regarding the possible
280 location of nests while simultaneously coordinating its reproductive timing with that of its host
281 species.
282 　　　Social regulation of reproductive physiology via heterospecific signals has occurred in
283 other species albeit not to the extent that conspecific signals evoke the response. For instance,
284 in captive canaries, conspecific song exposure induced marginally significantly greater follicle
285 sizes as compared to heterospecific song exposure but both social exposure groups exhibited

286 significantly greater follicular sizes in relation to silence-exposed females (Bentley et al., 2000).
287 However, when time to lay eggs was measured, conspecific song-exposed females displayed
288 significantly shorter time to lay eggs and laid more of them in relation to heterospecific song-
289 exposed females. Taken together, these experiments reveal conspecific song-exposed female
290 exhibited the greatest responses in ovarian development however, heterospecific song
291 exposure induced a greater response in comparison silence exposure in these measures. This
292 suggests that even in a captive population of canaries, heterospecific songs possess some
293 ecological relevance, albeit less than conspecific songs. This result implies that, to some
294 degree, all birds attend to communication signals not intended for them and that these signals
295 possess ecological relevance as they may inform the receiver of major transitions within the
296 avian community regarding the breeding or non-breeding status of the members of the
297 community.
298   From an evolutionary perspective, physiological responses to song are likely subjected
299 to less selection pressure for discrimination than the female's behavioral response. Thus, a
300 broader range of signals should evoke activity within the HPG axis while only a subset of the
301 most relevant signals should evoke a behavioral response from a female. By broadening the
302 definition of signals that can evoke physiological responses, animals can orchestrate
303 reproductive efforts across multiple biological levels including between individuals, populations
304 and communities.   Consequently, less attractive conspecific signals and even heterospecific
305 signals may evoke physiological responses in reproductive systems in eavesdropping animals
306 and possibly in wide array of free-living animals.
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342   Figure Legends

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344   Figure 1. Results of hormone assays after female brown-headed cowbirds (*Molothrus ater*) were
345   exposed to fourteen consecutive days of silence, conspecific or heterospecific songs. (a)
346   Results comparing circulating estradiol assays, (b) Results comparing circulating progesterone
347   assays and, (c) Results comparing female's largest follicle. All error bars represent S.E.M.

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