Integration of intra- and inter-sexual selection signaling

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1 Abstract

2 Sexual selection can drive the evolution of dramatic morphological and behavioral

3 signals. This selection acts on both specific components of signals and overall signals that

4 combine multiple sources of information. By studying the structure and variability of

5 signals and their components we can improve our understanding of how sexual selection

6 operates. Signal integration can be understood through the lens of classical signaling

7 hypotheses or more recently defined systems approaches. Using crickets (*Acheta*

8 *domesticus*), we evaluated competing hypotheses about signal integration and how

9 observed patterns of signal integration fit into both systems approaches and classic

10 signaling hypotheses. We measured three call types of 127 male crickets multiple times for

11 a total of 930 observations. We found evidence for an underlying integrated signaling

12 syndrome from which both intra- and intersexual signals stemmed. This syndrome was

13 also affected by mass, suggesting honest signaling in the species. The presence of an

14 integrated syndrome demonstrates that intra- and intersexual signals are incorporated in a

15 redundant signal strategy in *Acheta domesticus*. This support for honest and redundant

16 signaling is also consistent with a systems framework description of signals as degenerate

17 and functionally modular—demonstrating one way in which classic hypotheses can be

18 integrated with modern systems approaches.

19   **Introduction**

20   Sexual selection results from differing reproductive success due to among-

21   individual variation in traits affecting reproductive success. Traits most typically shaped by

22   sexual selection include male and female genital morphology and sexual signals such as

23   color patterns, vocalizations, and courtship displays that relay information to the opposite

24   sex (Andersson and Simmons 2006). Sexual signaling is important across taxa (e.g.

25   Harrison et al. 2013, Moreno-Gomez et al. 2015) and sexual selection frequently leads to

26   the evolution of increasing signal complexity over time (Buchanan et al. 2003, Spencer et al.

27   2003, Woodgate et al. 2012). Signals can also be produced for functionally distinct

28   interactions, with many species producing signals specific to intra- or intersexual

29   communication. Because sexual selection can act on specific components of signals and

30   across functionally distinct signals (Hedrick 1986, Hedrick and Weber 1998, Buchanan et

31   al. 2003, Spencer et al. 2003, Woodgate et al. 2012), studying signal structure and signal

32   production can provide valuable insights regarding the action of sexual selection.

33   The relationship among signal components, i.e. the pattern of phenotypic

34   integration (Pigliucci 2003), has important implications for how signals might be

35   interpreted by receivers. This interpretation by receivers provides the framework for a

36   number of classic hypotheses that have facilitated our general understanding of animal

37   communication (Table 1). For example, the "redundant signal" hypothesis, states that

38   signals convey redundant, shared information to the receiver (Johnstone 1996). As a

39   modification of the redundant signal hypothesis, individuals might have a general signaling

40   phenotype which causally influences the repertoire of signals produced. Such a general

41   signaling phenotype can represent an honest signal, providing accurate information about

42   condition to a receiver (Zahavi 1975, Schluter and Price 1993, Berglund et al. 1996). These

43   non-mutually exclusive hypotheses necessarily require strong patterns of integration (i.e.

44   strong correlations) among signal components. Alternatively, if signals and their

45   components show weak patterns of integration, each signal may provide receivers with

46   distinct information about the signaler, a form of the "multiple-message" hypothesis

47   (Johnstone 1996). If signal components are uncorrelated, this can be interpreted as support

48   for the multiple message hypothesis since the uncorrelated signals are providing

49   independent information about the signaler.

50   Both the redundant signaling and multiple message hypotheses have been

51   supported in a variety of taxa. For example, male eland antelopes (*Tragealphus oryx*)

52   exhibit redundant signaling via facemask darkness, frontal brush size and body greyness—

53   traits correlated with androgen levels and aggression (Bro-Jørgensen et al. 2008).

54   Meanwhile, support for the multiple message hypothesis has also been frequently

55   observed. As one example, bowerbird males (*Ptilonorhynchus violaceus*) signal health and

56   condition with both bower characteristics and plumage coloration (Doucet and

57   Montgomerie 2003). Importantly, the redundant signaling and multiple message

58   hypotheses are not entirely mutually exclusive: while facemask darkness, brush size and

59   greyness indicates aggression in the aforementioned male eland antelopes, independent

60   signals—such as a characteristic knee-click—provides independent information related to

61   fighting ability (Bro-Jørgensen et al. 2008).

62   Recently, Hebets et al. (2016) proposed a systems approach to understanding

63   communication. This framework stresses that an entire signaling system should be

64   evaluated simultaneously (Hebets et al. 2016). The power of this proposal vis-à-vis sexual

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65   selection is that it properly recognizes the entire signal repertoire of an organism, and all

66   the components of that repertoire, as simultaneously affecting reproductive success and

67   therefore fitness. This systems approach formalizes the description of how signals interact

68   both for a single mode of communication where multiple signals are employed or within a

69   multimodal communication framework (sensu Hebets and Papaj 2005). According to this

70   systems approach, signaling can be categorized to one of four different system designs

71   (Table 1; Hebets et al. 2016, Rosenthal et al. 2018): 1) Redundancy, where structure and

72   function are shared among signal components, this is shown by repetition of a song or

73   display. 2) Degeneracy, where different signals or signal components serve similar

74   functions. 3) Pluripotentiality, one signal or component of a signal serves multiple

75   functions in one display (e.g. both intra and intersexual functions) and 4) Modularity, when

76   subsets of signals form linked structural or functional clusters (Hebets et al. 2016,

77   Rosenthal et al. 2018). With this framework Hebets et al. (2016) have provided animal

78   signaling research an overarching approach to describing the relationship among signals

79   and among the components of these signals.

80   Unfortunately, the classic hypotheses and the systems approach possess

81   overlapping terminology—a signaling issue in its own right. For example, the classic

82   redundant signals hypothesis which states that signals convey redundant, shared

83   information to receivers (Johnstone 1996) is not the same as Hebets et al's (2016)

84   redundancy systems approach (i.e. the same signal repeated). While this overlap

85   necessitates clarity in operational definitions, a more general issue is that while the

86   systems approach clearly describes the structure of signals, the connection of the systems

87   approach categorizations to sexual selection theory is less clear. One approach to resolve

88   this issue is to recognize the connections between classical signaling hypotheses and the

89   Hebets et al. (2016) framework to interpret the system structures (Table 1).

90   Here, we sought to determine how intra- and intersexual signals are integrated and

91   used a hypothesis comparison approach to evaluate classic signaling hypotheses in the

92   domestic cricket (*Acheta domesticus*). We simultaneously evaluated how the relationship

93   among signal components fit within the systems approach of Hebets et al. (2016), allowing

94   an integration of classic hypotheses with relevant sexual selection theory. Crickets are ideal

95   for testing questions about signaling, signal complexity, and signal integration because they

96   use the same physical structures in both intra- and intersexual signaling, exposing them to

97   varying selection pressures based on receiver sex. Specifically, male crickets produce three

98   distinct signals: an advertisement call used to attract females from long distances, a

99   courtship call used to induce copulation by females after they have closely approached a

100   male, and an aggression call used between males during agonistic encounters (Gray and

101   Eckhardt 2001, Zuk et al. 2008). This combination of signals and their differing functions

102   and targeted receivers allowed us to use the systems approach structure to describe if and

103   how advertising, courtship, and aggression call types were integrated and which classic

104   signaling hypothesis was supported by observed patterns of integration.

105   **Materials and Methods**

106   *Diet and Rearing*

107   Male nymph *A. domesticus* (obtained from Fluker's Cricket Farm) were reared in

108   plastic containers (34.6 x 21 x 12.4 cm). Each container housed around 10 nymphal

109   crickets and was maintained at 32⬚ C on a 12:12 hr light cycle. Crickets were provided with

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110   egg carton pieces for housing and food and water *ad libitum* (Royauté and Dochtermann

111   2017, Royaut é et al. 2019). Crickets were reared on one of four experimental diet regimes

112   as part of a larger experiment (Royaut é et al. 2019), but these diets had no detectable

113   effect on call components (Garrison 2017) or call covariances (Mantel tests' r > 0.50, Table

114   S1). Once crickets reached maturity, they were moved into individual containers (0.71-L)

115   and fed an assigned diet and water *ad libitum*. Mature crickets were kept at a 12:12 hr light

116   cycle at 25⬛ C

117   *Call Recording*

118   We measured advertisement, courtship, and aggression calls repeatedly for a total

119   of 127 male crickets, with a total of 930 calling trials (Table S2). We attempted to obtain

120   three repeated measures per individual per call type but, due to natural mortality, some

121   call types were recorded more frequently than others (Table S2). We used a repeated

122   measures framework as the call components in crickets are influenced by both genetic and

123   environmental effects (Hedrick 1988). By repeatedly measuring each call, we were able to

124   estimate the among-individual variability of calls and their underlying components

125   (Dingemanse and Dochtermann 2013) and among-individual correlations between call

126   components (Dingemanse et al. 2012). These among-individual correlations estimate the

127   combined contribution of genetic and long-term environmental effects on correlations,

128   separate from temporary environmentally induced effects (Dingemanse and Dochtermann

129   2014).

130   To record advertisement calls, housing containers were surrounded by acoustic

131   foam and USB audio recorders were placed on top of each individual container for 2 hours.

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132   Because females are not necessary to elicit advertisement calls in this species (Garrison

133   2017), males called over this period without a female cricket in the container.

134   To record courtship calls, a female cricket must be present with the male (Garrison,

135   personal observation). Following Zuk et al. (2008), male crickets were introduced into a

136   container the same size as those used for housing but containing only a USB audio recorder

137   and a live female assigned at random. The females used in courtship trials were obtained

138   from our laboratory stock collection so mating status of females was unknown but all males

139   were virgins. Courtship call was then recorded for a period of 5-10 minutes. If a male failed

140   to call within the first 5 minutes of the trial, the trial was stopped, and the male was

141   removed and recorded as not calling. If a female attempted to copulate with (i.e. mounted)

142   the focal male during the trial, recording was also stopped and mating was not allowed to

143   be completed. All courtship calls were conducted at least 48 hours after the final

144   advertisement calls had been recorded since potential contact with a female could alter the

145   male's long-range calling effort.

146   To record aggressive calls, focal males were placed in a novel container with a

147   random male that had been muted by having its forewings removed. A pilot study showed

148   that *A. domesticus* will produce aggressive calls towards other males without a female

149   present as a stimulus (Garrison 2017), so females were not used to elicit aggressive calls.

150   Aggressive calls were recorded for 5-10 minutes. Trials were ended when there was a clear

151   winner (one cricket retreated). If a male failed to call within the first 5 minutes of the trial,

152   the trial was stopped and the male was removed and recorded as not calling and tested

153   again at a later date.

154   *Call Analysis*

155   Each call was analyzed using the sound analysis programs Audacity and Avisoft. We

156   measured 7 calling components: chirp rate, chirp duration, mean number of pulses per

157   chirp, peak frequency, call amplitude, pulse rate and total time calling for all three call

158   types (i.e. 21 total call components).

159   For advertisement calls, we analyzed the middle forty-five minutes of each

160   recording. Courtship calls were more difficult to analyze as males intermittently produced

161   advertisement calls during courtship. To properly analyze courtship calls, only sections of

162   the courtship trial recordings that were exclusively courtship were analyzed. There is a

163   visible difference in call structure between courtship and advertisement calls (Figure 1). A

164   similar issue was encountered with aggression call, but aggression call is easily

165   distinguished based on call waveforms (Figure 1).

166   **Statistical Analysis**

167   *Repeatability by Call Type*

168   As an initial exploratory analysis we estimated adjusted and unadjusted

169   repeatabilities and the variation due to all random and fixed effects for each of the 21 call

170   component using the rptR package (Nakagawa and Schielzeth 2010, Stoffel et al. 2017) in

171   the R statistical language. In addition, which conspecific was present (male opponent for

172   aggression call, female for courtship call), the chamber in which recording occurred

173   (advertisement call), and the developmental box in which an individual was reared (all call

174   types) were included as random effects and corresponding variances components

175   estimated (Table S3).

176 *Comparing Hypotheses of Signal Integration*

177   To test competing hypotheses of phenotypic integration we employed a two-step

178   approach.

179   First, we estimated among- and within-individual covariance and correlation

180   matrices (Dingemanse et al. 2012) for mass and the 9 call components that had previously

181   been found to exhibit the highest repeatabilities in the previous exploratory univariate

182   analyses (Table 2, Table S3). We chose the components with the highest repeatabilities as

183   these will be least affected by temporary environmental effects (Falconer 1996). The

184   among- and within-individual covariance and correlation matrices were estimated using

185   multi-response mixed effects models with temperature (centered), repetition number,

186   batch, and time of recording as well as age since maturation and diet type included as

187   explanatory variables. Male identity was included as a random factor. The 10 response

188   variables were mean and variance standardized to facilitate model fitting. The multi-

189   response mixed effect model was then fit using the MCMCglmm package (Hadfield 2010) in

190   the R statistical language. The model was fit with an MCMC chain with 1.3×10^6 iterations,

191   a 300000 burn-in period, and a thinning interval of 1000 and a prior that was flat for

192   correlations. This chain length led to low autocorrelations and high MCMC effective sample

193   sizes.

194   Second, we specified structural equation models (SEMs) corresponding to nine

195   hypothesized patterns of trait integration (Figure 2) prior to fitting the multi-response

196   mixed effect model. We then fitted each of these SEMs to the posterior distribution of

197   estimated among-individual correlation matrices (the MCMC analyses produced 1000

198   estimates of the correlation matrix) and evaluated SEMs in competition with each other

199   based on Akaike Information Criteria values (AIC) following Araya-Ajoy & Dingemanse

200   (2014). This combination of SEMs and AIC based model comparison approaches allows the

201   testing of specific hypothesis of trait integration (Dochtermann and Jenkins 2007,

202   Dingemanse et al. 2010, Araya-Ajoy and Dingemanse 2014).

203   The among-individual correlation matrices were fit to the following nine *a priori*

204   models (Figure 2):

205   • Model 1: a null hypothesis where all call components are uncorrelated.

206   Because model comparison approaches are based strictly on those models

207   included, the relative ranking of this model gives an indication of the

208   appropriateness of the suite of models (Figure 2A).

209   • Models 2-3: two models falling under the classic "Redundant Signal

210   Hypothesis" wherein signals are providing similar information to the listener.

211   In model 2, advertisement and courtship signals are providing females with

212   redundant information about size and quality and advertisement and

213   aggression calls are providing males with redundant information about size

214   and quality (Figure 2B, paths a and b are active—i.e. allowed to be non-zero).

215   In model 3, courtship and aggression calls are also providing redundant

216   information to the receiver (Bertram and Rook 2012) (Figure 2B, paths a, b

217   and c are active). Both of these models correspond to the Functional

218   Modularity model of the systems approach wherein individual signal

219   components serve a similar function but there are overarching functions for

220   each call type.

221   • Model 4: a model corresponding to a Multiple-Messages Hypothesis wherein

222   all three call types are providing different but complementary information to

223   listening conspecifics (Moller and Pomiankowski 1993, Harrison et al. 2013).

224   This hypothesis corresponds to the Functional Modularity model of the

225   systems approach. The call components of all three call types are

226   uncorrelated in this model (Figure 2B, no lettered paths active).

227   • Model 5: both courtship and aggression call components will be correlated

228   due to the short range that each call travels (Figure 2B, path c is active). This

229   hypothesis also corresponds to the Functional Modularity model of the

230   systems approach. Courtship and aggression calls are functionally used for

231   short range calling.

232   • Model 6: Honest Signaling, all of the calling components stem from a single

233   underlying calling phenotype, with no modularity within the three call types.

234   This underlying calling structure is causally affected by mass (Figure 2D,

235   path e is active). This hypothesis corresponds to the Degeneracy model of the

236   systems approach wherein all signal components serve a similar function.

237   • Model 7: All of the call components stem from a single underlying calling

238   phenotype, with no modularity within the three call types (Figure 2D, no

239   lettered path active). This hypothesis also corresponds to the Degeneracy

240   model under the systems approach terminology.

241 • Model 8: Honest Signaling with Redundant Signals and Modularity, wherein

242 all three call types causally stem from an underlying calling syndrome or

243 phenotype, implying some signal redundancy. However, each call type still

244 exhibits modularity (i.e. components of aggression calls are more closely

245 related to other components of aggression calls than to components of

246 advertisement calls (Wagner and Hoback 1999, Holzer et al. 2003). This

247 underlying calling structure is causally affected by mass (Figure 2C, path d is

248 active) and so downstream call components are honest signals of mass. This

249 hypothesis corresponds to both the Degeneracy and Functional Modularity

250 models of the systems framework. All signal components serve a similar

251 function, while overarching call types/modules serve different functions, and

252 all of this is causally affected by mass.

253 • Model 9: Redundant Signals with Modularity, another version of the

254 redundant signals hypothesis wherein all three call types causally stem from

255 an underlying calling syndrome or phenotype, implying some signal

256 redundancy. However, each call type still exhibits modularity. In this model,

257 mass does not affect calling structure (Figure 2C, no lettered path active), i.e.

258 calls do not honestly signal mass. Like model 8, this structure corresponds to

259 both the Degeneracy and Functional Modularity systems definitions.

260 These models were fit using the lavaan package in R and the ability of each model to

261 explain the pattern of correlations compared based on differences of AIC values among

262 models (ΔAIC) (Dingemanse et al., 2010; Dochtermann & Jenkins, 2007). In addition to the

263 nine models listed above, we also tested a "component model" wherein the same

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264   components from different call types stem from an underlying component phenotype with

265   no modularity (i.e. courtship pulses per chirp and advertisement pulses per chirp are

266   providing shared information, independent of any specific call types). This model was

267   unfittable, indicating that the model departed too far from the data, suggesting lack of

268   biological relevance.

269   Because we estimated among-individual correlations using a Markov Chain Monte

270   Carlo approach, we had 1000 estimates of the correlation matrix. Following Araya-Ajoy &

271   Dingemanse (2014) and Dingemanse et al. (2020) the SEM models were fit to each of the

272   1000 estimated correlation matrices and so we also had 1000 estimates of the AIC and

273   ΔAIC values of each model. Therefore, the model with a ΔAIC whose posterior mode was

274   closest to zero was ranked as the overall best model. This approach allows the estimation

275   of uncertainty around these ΔAIC values so we also considered how often a particular

276   model was ranked as best (i.e. ΔAIC = 0) or could not be distinguished from the best model

277   (i.e. ΔAIC ≤ 2; Dingemanse et al. 2019). We also assessed the "significance" of any particular

278   correlation based on whether its 95% credibility interval overlapped zero (Table S3).

279   **Results**

280   _Repeatability by Call Type_

281   Advertisement call components were moderately to highly repeatable with peak

282   frequency having the highest adjusted repeatability ($\tau = 0.58$) (Table 2). Components of

283   aggression calls were similarly repeatable, with peak frequency once again having the

284   highest repeatability ($\tau = 0.48$) (Table 2). In contrast to advertisement and aggression call

285   components, courtship call components were generally low to moderately repeatable, with

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286   only pulses per chirp (τ = 0.30), chirp duration (τ = 0.30) and chirp rate (τ = 0.38),

287   exhibiting repeatabilites above 0.1 (Table 2). Based on the repeatabilities of all call

288   components estimated from univariate mixed models (Table S3), we used the following

289   components in subsequent analyses: Advertisement – frequency, pulses per chirp and chirp

290   rate, Aggression – frequency, pulse rate, amplitude, Courtship – pulses per chirp, chirp

291   duration and chirp rate (Table 3). Neither the recording chamber in which an individual

292   was recorded nor the box in which an individual was reared contributed substantial

293   variation to any of the call components measured (Table S3). Female ID from courtship

294   trials also did not explain a substantive proportion of the variation present in courtship call

295   components, never explaining more than seven percent of the variation present (Table S3).

296   In contrast, the rival male present explained 5 to 18 % of the variation present in

297   aggression call components (Table S3).

298   *Signal Integration*

299   The best fitting structural equation model corresponded to a model where call

300   components were part of call specific modules (i.e. advertisement vs. aggression vs.

301   courtship calls) and these modules were themselves integrated under a common latent

302   calling syndrome (Model 8; Table 3). This model supports the classic redundant signaling

303   hypothesis as well as both signal degeneracy and functional modularity under the systems

304   approach. Model 9 was also partially supported, with a fit within 2 AIC values over a third

305   of the time (Table 3, Figure 3). These models differed based on whether body mass had a

306   causal effect on call structure, as expected according to the honest signaling hypothesis—

307   with the best fit model supporting this causal link with mass (Table 3, Figures 2 & 3).

308   Overall, the strength of the relationships between the overarching syndrome

309   structure to the call specific latent variables underpinning call components were similar in

310   each model (Figure 3A versus 3B). In both model 8 and 9, all components of advertisement

311   and courtship call were strongly tied to their respective latent variables. In contrast, the

312   aggression latent variable was primarily indicative of call frequency, with limited

313   connections to pulse rate and call amplitude (Figure 3). In addition, the path coefficients

314   connecting the overall calling syndrome latent variable to courtship call approached zero

315   and were substantially weaker than for advertisement and aggression calls (Figures 3A and

316   3B). This suggests that courtship calls provide independent information not captured by

317   either advertisement or aggression calls.

318   With the general structure of Model 8 most well supported (Table 3), it is also

319   noteworthy that the relationship between mass and the underlying "Calling Syndrome" was

320   negative (-0.24, Figure 3A). As a result, mass had a negative effect on the expression of the

321   following call components: advert frequency, advert chirp rate, courtship chirp rate,

322   aggression frequency and aggression pulse rate (direction and magnitudes of relationships

323   can be determined by multiplication of path coefficients) (Figure 3A).

324   **Discussion**

325   Following a systems approach, the two best fit models for *Acheta domesticus*

326   signaling fall under systems definitions of degeneracy and functional modularity. The

327   overall signal syndrome allows different signals to provide similar information

328   (degeneracy) while signal components tie together in lower level modules according to

329   function (functional modularity, Hebets et al. 2016). This result can be further interpreted

330   if the degeneracy hypothesis is integrated with classic signaling hypotheses. Specifically,

331   the Hebets et al. (2016) model of degeneracy closely fits the classic signaling hypotheses of

332   redundant signals, i.e. different signal types provide similar information to receivers

333   (Bertram & Rook, 2012; Harrison et al., 2013). The two best fit models are therefore

334   indicative of an overarching calling syndrome from which the three individual call types

335   stem (see also (Wagner and Hoback 1999, Holzer et al. 2003, Bertram and Rook 2012). The

336   strong link between advertisement and aggression within the overall calling syndrome in

337   the two best fit models (Figure 3) further demonstrates that advertisement and aggression

338   provide similar information about male size and quality (see also Bertram & Rook, 2012).

339   Despite this, the three call types did differ in the strength of association with the calling

340   syndrome and thus level of integration (courtship being the least integrated).

341   While cricket mass was negatively associated with the calling syndrome, the

342   relationship between mass and specific call components is consistent with previous

343   research on female choice and known morphological relationships with call components.

344   For example, mass was positively related with advertisement pulses per chirp (Figure 3),

345   and higher pulses per chirp preferred by female crickets in other species (Gray 1997). Mass

346   was also negatively related to advertisement and aggression frequency (Figure 3). A

347   negative relationship between the two was previously described result for other cricket

348   species (Simmons and Zuk 1992, Simmons 1995) in which females prefer lower

349   frequencies (Simmons and Ritchie 1996). Consequently, call components likely serve as an

350   honest signal of male body-size in *Acheta domesticus*.

351   Many of the call components exhibited repeatabilities greater than the average

352 reported for other behaviors ($\square$ =0.37, (Bell et al. 2009)). In particular, variation in

353 advertisement call components was strongly explained by individual identity (Tables 1 and

354 S3). These high repeatabilities suggest an upper limit for the heritability of call components

355 in *Acheta domesticus* that would be consistent with heritability of calling in other cricket

356 species (Mousseau and Howard 1998). We used mean and variance standardized values for

357 all call components given those were measured on scales varying on numerous orders of

358 magnitude of difference. While this procedure allowed for proper convergence of our

359 statistical models, one drawback is that additional metrics based on calculating coefficients

360 of variation (Wilson 2008, Dochtermann and Royauté 2019) and evolutionary metrics like

361 trait autonomy are not estimable (Houle 1992, Hansen et al. 2011). How much these

362 integrated patterns of call components are likely to constrain evolutionary responses

363 therefore remains an open question.

364   In further examining other contributors to variation in call components, one

365 particularly interesting finding is that variation in courtship call components was not

366 substantially influenced by female receiver identity (Table S3). In other words, the identity

367 of the female being courted did not affect male behavior. This indirectly suggests that males

368 do not modify their own courtship based on differences amongst females, an interesting

369 topic for future research. In contrast to female identity, rival male identity substantially

370 influenced the variation in both amplitude and frequency of aggression calls (Table S3).

371 This makes intuitive sense: a higher quality opponent may deter a lower quality male from

372 producing a strong call. These findings also align with previous research of indirect genetic

373 effects on aggression in other Gryllid species (Santostefano et al. 2016, Santostefano et al.

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374 2017). Finally, despite having accounted for multiple variables involved in courtship

375 expression, more than 55 % of the phenotypic variation stems from unexplained sources of

376 within-individual variation (Table S3). This within-individual variation corresponds to

377 variation arising from temporary environmental effects and are in line with the findings of

378 Harrison et al. (2013) showing a curvilinear relationship between residual mass and

379 courtship pulse and chirp rates wherein both small and large crickets used similar pulse

380 and chirp rates to court females (Harrison et al. 2013). These results suggests that we still

381 know little about what courtship is communicating to females. Further exploration of

382 environmental contributions to courtship plasticity is therefore needed regarding signaling

383 hypotheses for the courtship calls of crickets.

384   Studies evaluating integration and modularity among sexual signaling traits are

385 increasingly common with continued and increasing interest in multimodal

386 communication. For example, in the black field cricket (*Teleogryllus commodus*), call

387 components were found to be highly integrated and vary little among populations or diet

388 quality (Pitchers et al. 2013). Song components in barn swallows have also been found to

389 be tightly integrated but relatively independent from morphology and coloration modules

390 (Wilkins et al. 2015). In contrast, the degree of integration between advertising and

391 aggressive calls varies substantially among species of treefrogs (Reichert and Hobel 2018).

392 The pattern of integration found here (Figure 3) suggests support for both honest signaling

393 as well as degeneracy, depending on which approach is implemented, where particular

394 components of a call type are more strongly related to each other than across call types.

395 Phenotypic integration can occur in a strictly modular fashion or integration can exist with

396 modularity, due to shared developmental pathways or functions (Araya-Ajoy and

397   Dingemanse 2014, Royaute et al. 2015). Such integration with underlying modularity, like

398   that described here, has been termed "quasi-independent modularity" (Larouche et al.

399   2018). Quasi-independent modularity results in an inability of constituent components to

400   evolve independently but, counter-intuitively, can also facilitate rapid evolutionary change

401   (West-Eberhard 2003).

402   Unfortunately, much of the literature on signaling has focused on phenotypic

403   variation which conflates multiple sources of variation (Adolph and Hardin 2007,

404   Dingemanse et al. 2012). Our attempt here to evaluate correlations of call components at

405   the level of among-individual (co)variance should more closely capture the underlying

406   genetic structure of call integration (Dingemanse and Dochtermann 2014, Dochtermann et

407   al. 2015). To the degree that among-individual covariation captures genetic covariation,

408   our results are consistent with advertisement and aggression calls being genetically

409   integrated while courtship calls are their own quasi-independent genetic module. This

410   suggests that advertisement and aggression calls will likely evolve in a correlated manner

411   while courtship calls have the capacity to follow a more independent evolutionary

412   trajectory.

413   The quasi-independent structure that we identified for *Acheta domesticus* combines

414   two categories of the systems framework proposed by Hebets et al. (2016): degeneracy and

415   functional modularity (Figure 2, Table 3). This observed structure is also consistent with

416   hypotheses of redundant signaling and honest signaling. While the systems approach

417   provides more precise mechanistic descriptions of signaling, the classical hypotheses of

418   signaling are more explicitly linked to evolutionary mechanisms and sexual selection.

419   Having two competing conceptual frameworks, particularly when they have

420   overlapping terminology, has the potential to hinder our understanding of communication.

421   Fortunately, these two frameworks can be combined to offer greater insight (Table 1). For

422   example here, cricket calling's degenerate and functional modularity is best described by

423   the systems approach and the connection to mass is best described by classic hypotheses of

424   honest signaling. Combining these two frameworks suggests that cricket calls are

425   structured according to a pattern of honest integration (Table 1). By highlighting this

426   important disconnect between both the classic and modern signaling frameworks as well

427   as similarities between the two frameworks, we have shown that the two frameworks can

428   be integrated together. This combination contributed here to a better understanding of

429   pre-mating signaling phenotypes and of patterns of signal integration.

References

435

436   Adolph, S. C., and J. S. Hardin. 2007. Estimating phenotypic correlations: correcting for bias due to
437   intraindividual variability. Functional Ecology **21**:178-184.

438   Andersson, M., and L. W. Simmons. 2006. Sexual selection and mate choice. Trends in Ecology &
439   Evolution.

440   Araya-Ajoy, Y. G., and N. J. Dingemanse. 2014. Characterizing behavioural 'characters': an
441   evolutionary framework. Proceedings of the Royal Society B-Biological Sciences **281**.

442   Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis.
443   Animal Behaviour **77**:771-783.

444   Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: An evolutionary
445   explanation of traits of dual utility. Pages 385-399, Biological Journal of the Linnean Society.

446   Bertram, S. M., and V. Rook. 2012. Relationship between condition, aggression, signaling, courtship,
447   and egg laying in the field cricket, Gryllus assimilis. Ethology **118**:360-372.

448   Bro-Jørgensen, J., T. Dabelsteen, and J. a. Email authorBro-Jørgensen. 2008. Knee-clicks and visual
449   traits indicate fighting ability in eland antelopes: multiple messages and back-up signals.
450   BMC Biology **6**.

451   Buchanan, K. L., K. A. Spencer, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of
452   past developmental stress in the European starling (Sturnus vulgaris). Proceedings of the
453   Royal Society B-Biological Sciences **270**:1149-1156.

454   Dingemanse, N. J., I. Barber, and N. A. Dochtermann. 2019. Non-consumptive effects of predation:
455   does perceived risk strengthen the genetic integration of behaviour and morphology in
456   stickleback? Ecology Letters.

457   Dingemanse, N. J., and N. A. Dochtermann. 2014. Individual behaviour: behavioural ecology meets
458   quantitative genetics. Quantitative Genetics in the Wild:54-67.

459   Dingemanse, N. J., N. A. Dochtermann, and S. Nakagawa. 2012. Defining behavioural syndromes and
460   the role of 'syndrome deviation' in understanding their evolution. Behavioral Ecology and
461   Sociobiology **66**:1543-1548.

462   Dingemanse, N. J., N. A. Dochtermann, and J. Wright. 2010. A method for exploring the structure of
463   behavioural syndromes to allow formal comparison within and between data sets. Animal
464   Behaviour **79**:439-450.

465   Dochtermann, N. A., and S. H. Jenkins. 2007. Behavioural syndromes in Merriam's kangaroo rats
466   (*Dipodomys merriami*): a test of competing hypotheses. Proceedings Of The Royal Society B-
467   Biological Sciences **274**:2343-2349.

468   Dochtermann, N. A., and R. Royauté. 2019. The mean matters: going beyond repeatability to
469   interpret behavioural variation. Animal Behaviour **153**:147-150.

470   Dochtermann, N. A., T. Schwab, and A. Sih. 2015. The contribution of additive genetic variation to
471   personality variation: heritability of personality. Proceedings of the Royal Society B-
472   Biological Sciences **282**.

473   Doucet, S. M., and R. Montgomerie. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet
474   plumage and bowers signal different aspects of male quality Behavioral Ecology **14**:503–
475   509.

476   Falconer, D. S. 1996. Introduction to Quantitative Genetics. Pages 122-145 *in* T. F. C. Mackay, editor.
477   Pearson Education Limited.

478   Garrison, C. 2017. Environmental Components of Phenotypic Variation: Dietary and Trans-
479   generational Effects on Behavior. North Dakota State University, ProQuest Dissertations and
480   Theses.

481   Gray, D. A. 1997. Female house crickets, Acheta domesticus, prefer the chirps of large males. Animal
482   Behaviour **54**:1553-1562.

483   Gray, D. A., and G. Eckhardt. 2001. Is cricket courtship song condition dependent? Animal Behaviour
484   **62**:871-877.

485   Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
486   MCMCglmm R Package. Journal of Statistical Software **33**:1-22.

487   Hansen, T. F., C. Pelabon, and D. Houle. 2011. Heritability is not evolvability. Evolutionary Biology
488   **38**:258.

489   Harrison, S. J., I. R. Thomson, C. M. Grant, and S. M. Bertram. 2013. Calling, Courtship, and Condition
490   in the Fall Field Cricket, Gryllus pennsylvanicus. Plos One **8**:9.

491   Hebets, E., and D. Papaj. 2005. Complex

492   signal function: developing a framework of testable hypotheses. Behavioral Ecology and
493   Sociobiology **57**:197-214.

494   Hebets, E. A., A. B. Barron, C. N. Balakrishnan, M. E. Hauber, P. H. Mason, and K. L. Hoke. 2016. A
495   systems approach to animal communication. Proceedings of the Royal Society B-Biological
496   Sciences.

497   Hedrick, A., and T. Weber. 1998. Variance in female responses to the fine structure of male song in
498   the field cricket, Gryllus integer. Behavioral Ecology **9**:582-591.

499   Hedrick, A. V. 1986. Female preferences for male calling bout duration in a field cricket. Behavioral
500   Ecology and Sociobiology **19**:73-77.

501   Hedrick, A. V. 1988. Female choice and the heritability of attractive male traits: an empirical study.
502   The American Naturalist **132**:267-276.

503   Holzer, B., A. Jacot, and M. W. G. Brinkhof. 2003. Condition-dependent signaling affects male sexual
504   attractiveness in field crickets, Gryllus campestris. Behavioral Ecology **14**:353-359.

505   Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics **130**:195-204.

506   Johnstone, R. A. 1996. Multiple displays in animal communication: 'Backup signals' and 'multiple
507   messages'. Philosophical Transactions of the Royal Society of London Series B-Biological
508   Sciences **351**:329-338.

509   Larouche, O., M. L. Zelditch, and R. Cloutier. 2018. Modularity promotes morphological divergence
510   in ray-finned fishes. Scientific Reports **8**.

511   Moller, A. P., and A. Pomiankowski. 1993. WHY HAVE BIRDS GOT MULTIPLE SEXUAL ORNAMENTS.
512   Behavioral Ecology and Sociobiology **32**:167-176.

513   Moreno-Gomez, F. N., L. D. Bacigalupe, A. A. Silva-Escobar, and M. Soto-Gamboa. 2015. Female

514   and male phonotactic responses and the potential effect of sexual selection on

515   the advertisement calls of a frog. Pages 79-86, Animal Behavior.

516   Mousseau, T., and D. Howard. 1998. Genetic variation in cricket calling song across a hybrid zone
517   between two sibling species. Evolution **52**:1104-1110.

518   Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical
519   guide for biologists. Biological reviews of the Cambridge Philosophical Society **85**:935-956.

520   Pigliucci, M. 2003. Phenotypic integration: studying the ecology and evolution of complex
521   phenotypes. Ecology Letters **6**:265-272.

522   Pitchers, W. R., R. Brooks, M. D. Jennions, T. Tregenza, I. Dworkin, and J. Hunt. 2013. Limited
523   plasticity in the phenotypic variance-covariance matrix for male advertisement calls in the
524   black field cricket, Teleogryllus commodus. Journal of Evolutionary Biology **26**:1060-1078.

525   Reichert, M. S., and G. Hobel. 2018. Phenotypic integration and the evolution of signal repertoires: A
526   case study of treefrog acoustic communication. Ecology and Evolution **8**:3410-3429.

527   Rosenthal, M. F., M. R. Wilkins, D. Shizuka, and E. A. Hebets. 2018. Dynamic changes in display
528   architecture and function across environments revealed by a systems approach to animal
529   communication. Pages 1134-1145, Evolution.

530   Royauté, R., C. Garrison, J. Dalos, M. A. Berdal, and N. A. Dochtermann. 2019. Current energy state
531   interacts with the developmental environment to influence behavioural plasticity. Animal
532   Behaviour **148**:39-51.

533   Royauté, R., and N. A. Dochtermann. 2017. When the mean no longer matters: developmental diet
534   affects behavioral variation but not population averages in the house cricket (*Acheta*
535   *domesticus*). Behavioral Ecology **28**:337-345.

536   Royaute, R., K. Greenlee, M. Baldwin, and N. A. Dochtermann. 2015. Behaviour, metabolism and size:
537   phenotypic modularity or integration in Acheta domesticus? Animal Behaviour **110**:163-
538   169.

539   Santostefano, F., A. J. Wilson, Y. G. Araya-Ajoy, and N. J. Dingemanse. 2016. Interacting with the
540   enemy: indirect effects of personality on conspecific aggression in crickets. Behavioral
541   Ecology **27**:1235-1246.

542   Santostefano, F., A. J. Wilson, P. T. Niemela, and N. J. Dingemanse. 2017. Indirect genetic effects: a
543   key component of the genetic architecture of behaviour. Scientific Reports **7**.

544   Schluter, D., and T. Price. 1993. HONESTY, PERCEPTION AND POPULATION DIVERGENCE IN
545   SEXUALLY SELECTED TRAITS. Proceedings of the Royal Society B-Biological Sciences
546   **253**:117-122.

547   Simmons, L. W. 1995. Correlates of male quality in the field cricket, *Gryllus campestris* L.: age, size,
548   and symmetry determine pairing success in field populations. Behavioral Ecology **6**:376-
549   381.

550   Simmons, L. W., and M. G. Ritchie. 1996. Symmetry in the songs of crickets. Proceedings of the Royal
551   Society of London, Series B **263**:1305-1311.

552   Simmons, L. W., and M. Zuk. 1992. Variability in call structure and pairing success of male field
553   crickets, *Gryllus bimaculatus*: the effects of age, size and parasite load. Amnimal Behaviour
554   **44**:1145-1152.

555   Spencer, K. A., K. L. Buchanan, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of
556   developmental stress in the zebra finch (Taeniopygia guttata). Hormones and Behavior
557   **44**:132-139.

558   Stoffel, M., S. Nakagawa, and H. Schielzeth. 2017. rptR: Repeatability estimation and variance
559   decomposition by generalized linear mixed-effects models. Methods in Ecology and
560   Evolution.

561   Wagner, W. E., and W. W. Hoback. 1999. Nutritional effects on male calling behaviour in the variable
562   field cricket. Animal Behaviour **57**:89-95.

563   West-Eberhard, M. J. 2003. Developmental Plasticity and Evolution. Oxford University Press.

564   Wilkins, M. R., D. Shizuka, M. B. Joseph, J. K. Hubbard, and R. J. Safran. 2015. Multimodal signalling in
565   the North American barn swallow: a phenotype network approach. Proceedings of the Royal
566   Society B-Biological Sciences **282**.

567   Wilson, A. 2008. Why h2 does not always equal VA/VP? Journal of Evolutionary Biology **21**:647-
568   650.

569   Woodgate, J. L., M. M. Mariette, A. T. D. Bennett, S. C. Griffith, and K. L. Buchanan. 2012. Male song
570   structure predicts reproductive success in a wild zebra finch population. Animal Behaviour
571   **83**:773-781.

572   Zahavi, A. 1975. MATE SELECTION - SELECTION FOR A HANDICAP. Journal of Theoretical Biology
573   **53**:205-214.

574   Zuk, M., D. Rebar, and S. P. Scott. 2008. Courtship song is more variable than calling song in the field
575   cricket Teleogryllus oceanicus. Animal Behaviour **76**:1065-1071.

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Tables & Figures.

Figure 1. Waveform structures of five seconds of advertisement, courtship and aggression song from the same cricket. The y-axis represents the amplitude of the call.

Figure 2. Graphical representations of Structural Equation Models compared. Models are described in the text. Model comparison results are given in Table 3. Single arrows represent causal relationships between a latent variable and call components. Bidirectional arrows represent an undefined correlation between call components.

Figure 3. Structural Equation Model Parameter Estimates of the Degeneracy 3 and 4 Models

Table 1. Classic signaling hypotheses and corresponding systems approach labels, descriptions, examples, and suggested integrated terminology

Classic Signaling Hypothesis	Systems Approach Hypothesis	Description	Example (in *Acheta domesticus*)
Redundant Signals	Degeneracy	Signal components serve a similar function	Call frequency and pulses per chirp provide the receiver information about male body size
Redundant Signals	Functional Modularity	Signal components serve a similar function, while overarching call types/modules serve similar functions	Call frequency and pulses per chirp provide the receiver information about male body size, advertisement and aggression calls both communicate information about signaler's size
Multiple Messages	Functional Modularity	Signal components serve a similar function within a call type/module, while the overarching call types serve different functions	Call frequency and pulses per chirp provide the receiver information about male body size, but aggression and courtship calls are used for different functions
Honest Signaling	Degeneracy	Signal components serve a similar function and are causally affected by condition or "quality"	Call frequency and pulses per chirp provide the receiver information about male body size, with mass affecting both signal components
Honest Signaling & Redundant Signals	Degeneracy & Functional Modularity	Signal components serve a similar function, while overarching call types/modules serve different functions, all of this is causally affected by condition or "quality"	Call frequency and pulses per chirp provide the receiver information about male body size, with mass affecting both signal components, while aggression is used towards other males and courtship is used towards females

Table 2. Repeatabilities from univariate models for the traits chosen for the multi-response mixed-effects model with 95% confidence intervals

Signaling Trait	τ [a]
Advert Frequency	0.58 (0.45, 0.7)
Advert Pulses per Chirp	0.46 (0.29, 0.60)
Advert Chirp Rate	0.42 (0.27, 0.59)
Aggression Frequency	0.39 (0.23, 0.54)
Aggression Pulse Rate	0.31 (0.16, 0.50)
Aggression Amplitude	0.22 (0.09, 0.42)
Courtship Pulses per Chirp	0.32 (0.13, 0.55)
Courtship Chirp Duration	0.32 (0.13, 0.55)
Courtship Chirp Rate	0.29 (0.1, 0.53)

[a] adjusted repeatability, calculated as $V_i/(V_i + V_w)$

Table 3. Model rank along with posterior modal estimates for AIC and ΔAIC values for each model and the number (out of 1000) of MCMC posterior samples for which a particular model was the best fitting (ΔAIC = 0) and or within ΔAIC ≤ 2 from the best fitting model.

| Model number	Model Rank	Classic Signaling Hypothesis	Systems Approach Model	AIC	ΔAIC	AIC = 0	AIC ≤ 2
1	9	Null Hypothesis	Null Hypothesis	2848	148	0	0
2	5	Redundant Signals	Functional Modularity	2725	25	50	84
3	3	Redundant Signals	Functional Modularity	2718	18	129	224
4	6	Multiple Messages	Functional Modularity	2733	33	8	15
5	4	Short Range Calling	Functional Modularity	2721	21	62	107
6	8	Honest Signaling	Degeneracy	2735	35	9	29
7	7	Full Integration	Degeneracy	2734	34	11	30
8	**1**	**Honest Signaling and Redundant Signals with Modularity**	**Degeneracy and Functional Modularity**	**2704**	**3**	**545**	**775**
9	2	Redundant Signals with Modularity	Degeneracy and Functional Modularity	2709	9	186	363
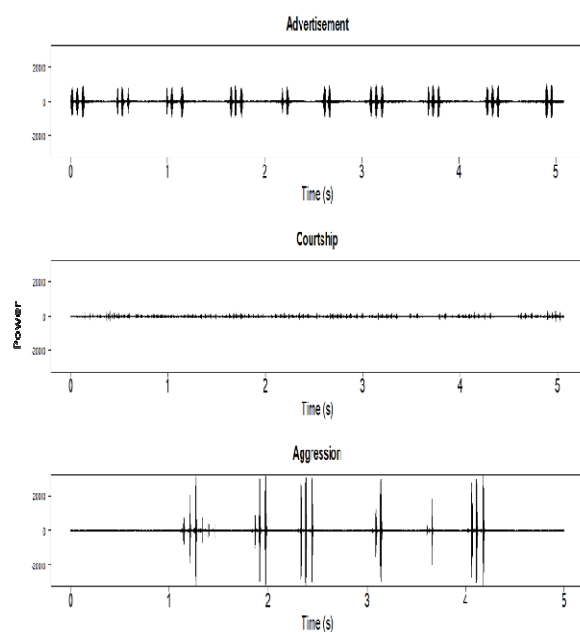
Figure 1.
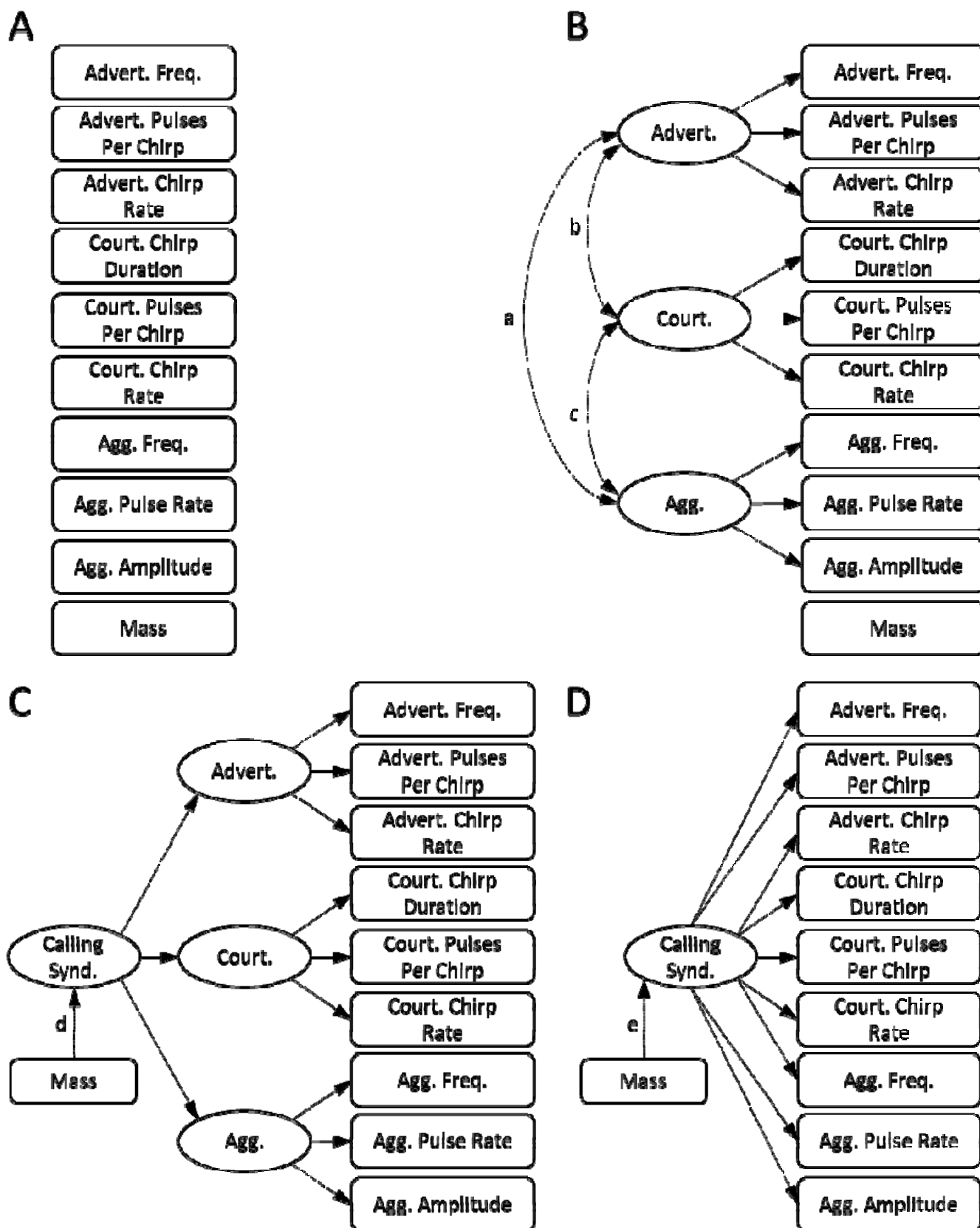
Figure 2.
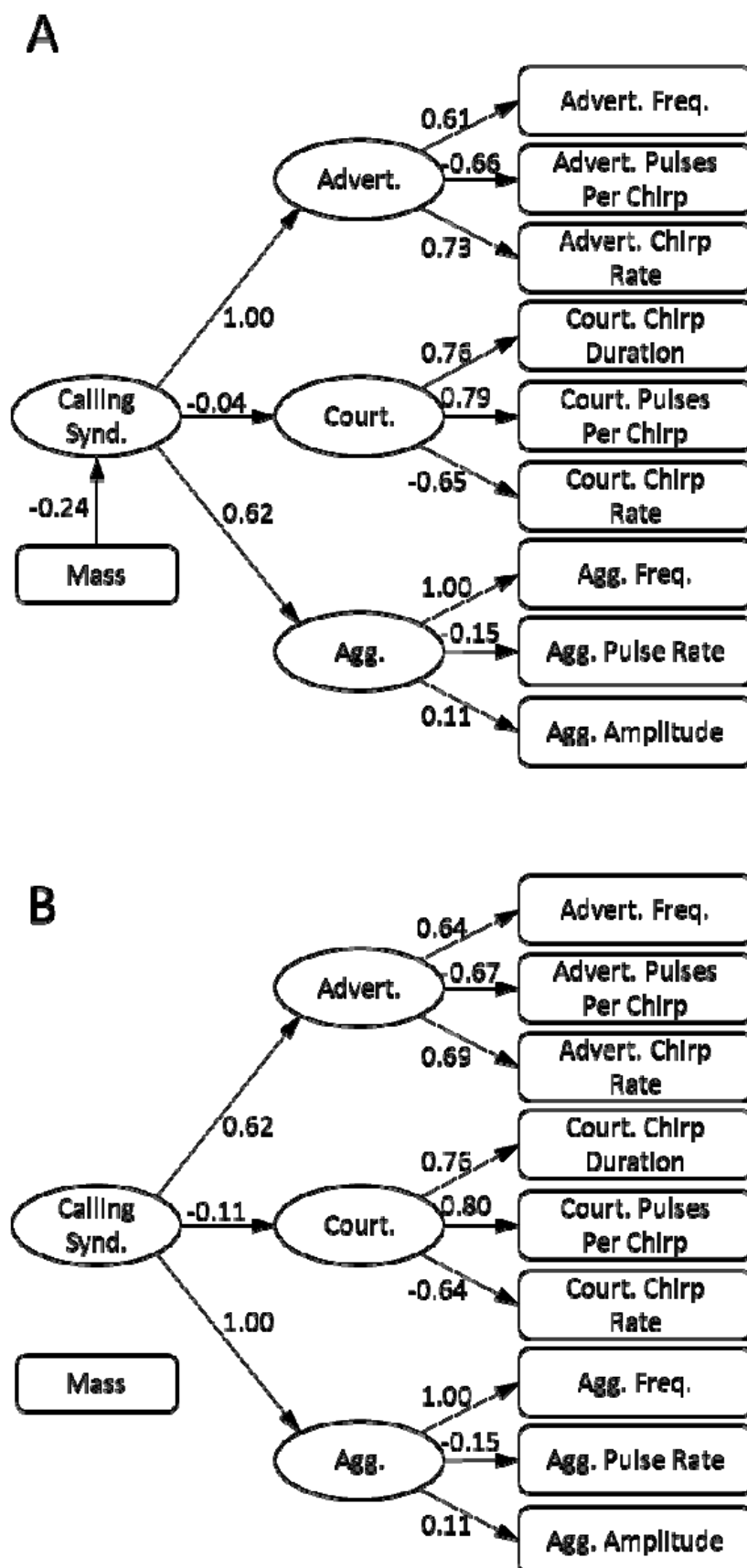
Figure 3.

Supporting Information for:
Integration of intra- and inter-sexual selection signaling

Table S1. Mantel's tests for comparing correlation matrices similarity across diet treatments. The Mantel's *r* represents how closely related the among correlation matrices are between two diets. Bold indicates statistically significant correlations.

Table S2. Number of individuals who went through each repetition of recording for each call type

Table S3. Repeatabilities and variances at the among- and within-individual levels as well as the fixed and random effects for each call parameter calculated using the rptR package with 95% confidence intervals. The bolded call components represent those chosen for the condensed multi-response MCMCglmm model

Table S4. Among and within-individual correlations, along with repeatabilities, as estimated by a multi-response mixed effects model.

Table S1. Mantel's tests for comparing correlation matrices similarity across diet treatments. The Mantel's *r* represents how closely related the among correlation matrices are between two diets. Bold indicates statistically significant correlations.

Diet treatment	Mantel's *r*		
	LQLQ	LQHQ	HQLQ
LQHQ	*r* = 0.80		
	P = 0.001		
HQLQ	*r* = 0.54	*r* = 0.75	
	P = 0.003	P = 0.001	
HQHQ	*r* = 0.68	*r* = 0.83	*r* = 0.81
	P = 0.001	P = 0.001	P = 0.001

Table S2. Number of individuals who went through each repetition of recording for each call type

Repetition	Advertisement	Aggression	Courtship	Total
1	127	91	105	323
2	122	87	101	310
3	107	85	100	292
4	5			5

Table S3. Repeatabilities and variances at the among- and within-individual levels as well as the fixed and random effects for each call parameter calculated using the rptR package with 95% confidence intervals. The bolded call components represent those chosen for the condensed multi-response MCMCglmm model

Call component	$\square^a$	$\square^b$	$V_I{}^c$	$V_W{}^d$
Advert Frequency	0.58 (0.45, 0.7)	0.38 (0.25-0.50)	0.41 (0.28 - 0.62)	0.29 (0.22-0.35)
Advert Pulses per Chirp	0.46 (0.29, 0.60)	0.39 (0.24, 0.52)	0.40 (0.23, 0.64)	0.48 (0.35, 0.57)
Advert Total Time Calling	0.12 (0, 0.30)	0.11 (0, 0.26)	0.11 (0, 0.30)	0.79 (0.57, 0.94)
Advert Chirp Duration	0.45 (0.31, 0.60)	0.36 (0.22, 0.48)	0.37 (0.23, 0.56)	0.43 (0.32, 0.52)
Advert Chirp Rate	0.42 (0.27, 0.59)	0.36 (0.22, 0.49)	0.41 (0.24, 0.65)	0.49 (0.36, 0.59)
Advert Pulse Rate	0.33 (0.17, 0.49)	0.18 (0.10, 0.28)	0.19 (0.09, 0.33)	0.37 (0.28, 0.45)
Advert Amplitude	0.28 (0.13, 0.45)	0.24 (0.10, 0.39)	0.25 (0.12, 0.45)	0.58 (0.42, 0.71)
Aggression Frequency	0.39 (0.23, 0.54)	0.28 (0.15, 0.41)	0.33 (0.17, 0.55)	0.39 (0.27, 0.47)
Aggression Pulses per Chirp	0.21 (0.07, 0.40)	0.19 (0.05, 0.34)	0.20 (0.05, 0.43)	0.61 (0.43, 0.76)
Aggression Total Time Calling	0 (0, 0.21)	0 (0, 0.18)	0 (0, 0.22)	0.91 (0.65, 1.07)
Aggresion Chirp Duration	0.26 (0.09, 0.46)	0.24 (0.09, 0.40)	0.25 (0.11, 0.49)	0.61 (0.43, 0.75)
Aggression Chirp Rate	0.21 (0.06, 0.42)	0.19 (0.04, 0.37)	0.20 (0.06, 0.45)	0.65 (0.45, 0.81)
Aggression Pulse Rate	0.31 (0.16, 0.50)	0.28 (0.14, 0.44)	0.32 (0.14, 0.59)	0.6 (0.42, 0.72)
Aggression Amplitude	0.22 (0.09, 0.42)	0.17 (0.07, 0.31)	0.19 (0.07, 0.38)	0.43 (0.30, 0.53)
Courtship Frequency	0.14 (0, 0.38)	0.08 (0, 0.23)	0.09 (0, 0.30)	0.49 (0.32, 0.63)
Courtship Pulses per Chirp	0.32 (0.12, 0.54)	0.26 (0.09, 0.44)	0.29 (0.10, 0.62)	0.55 (0.34, 0.71)
Courtship Total Time Calling	0 (0, 0.25)	0 (0, 0.23)	0 (0, 0.31)	0.92 (0.58, 1.10)
Courtship Chirp Duration	0.32 (0.13, 0.55)	0.29 (0.10, 0.48)	0.33 (0.12, 0.68)	0.64 (0.38, 0.81)
Courtship Chirp Rate	0.29 (0.1, 0.53)	0.27 (0.07, 0.47)	0.31 (0.09, 0.66)	0.67 (0.43, 0.82)

Courtship Pulse Rate				0.86 (0.56, 1.03)
	0.04 (0, 0.32)	0.04 (0, 0.25)	0.04 (0, 0.32)	
Courtship Amplitude				0.89 (0.57, 1.05)
	0.04 (0, 0.30)	0.04 (0, 0.25)	0.04 (0, 0.29)	

Call component	$V_{Conspecific}$[e]	$V_{Chamber}$[f]	V_{Box}[g]	V_{Fixed}[h]
Advert Frequency	NA	0 (0, 0.04)	0.01 (0, 0.10)	0.38 (0.25, 0.63)
Advert Pulses per Chirp	NA	0.004 (0, 0.06)	0 (0, 0.03)	0.14 (0.09, 0.33)
Advert Total Time Calling	NA	0.04 (0, 0.15)	0 (0, 0.07)	0.10 (0.06, 0.25)
Advert Chirp Duration	NA	0.01 (0, 0.07)	0 (0, 0.08)	0.22 (0.15, 0.42)
Advert Chirp Rate	NA	0.001 (0,0.06)	0.08 (0, 0.26)	0.16 (0.11, 0.39)
Advert Pulse Rate	NA	0.02 (0, 0.07)	0 (0, 0.05)	0.47 (0.36, 0.66)
Advert Amplitude	NA	0 (0. 0.07)	0.07 (0, 0.22)	0.14 (0.09. 0.33)
Aggression Frequency	0.13 (0.02, 0.30)	NA	0 (0, 0.12)	0.33 (0.18, 0.68)
Aggression Pulses per Chirp	0.14 (0.01, 0.35)	NA	0 (0, 0.09)	0.12 (0.08, 0.38)
Aggression Total Time Calling	0.05 (0, 0.20)	NA	0.02 (0, 0.11)	0.08 (0.06, 0.24)
Aggresion Chirp Duration	0.09 (0, 0.27)	NA	0.02 (0, 0.14)	0.09 (0.06, 0.31)
Aggression Chirp Rate	0.06 (0, 0.21)	NA	0.05 (0, 0.19)	0.11 (0.06, 0.35)
Aggression Pulse Rate	0.10 (0, 0.31)	NA	0.02 (0, 0.14)	0.1 (0.06, 0.38)
Aggression Amplitude	0.20 (0.06, 0.44)	NA	0.03 (0, 0.15)	0.26 (0.11, 0.64)
Courtship Frequency	0.06 (0, 0.21)	NA	0 (0, 0.09)	0.44 (0.27, 0.74)
Courtship Pulses per Chirp	0.06 (0, 0.24)	NA	0 (0, 0.14)	0.19 (0.11, 0.50)
Courtship Total Time Calling	0.07 (0, 0.28)	NA	0.06 (0, 0.20)	0.06 (0.05, 0.28)
Courtship Chirp Duration	0.05 (0, 0.23)	NA	0 (0, 0.18)	0.11 (0.08, 0.36)
Courtship Chirp Rate	0 (0, 0.14)	NA	0.07 (0, 0.31)	0.08 (0.06, 0.33)
Courtship Pulse Rate	0 (0, 0.14)	NA	0 (0, 0.11)	0.16 (0.10, 0.38)
Courtship Amplitude	0 (0, 0.15)	NA	0 (0, 0.11)	0.13 (0.09,

0.35)

a – adjusted repeatability, calculated as $V_I/V_I + V_W$; b – unadjusted repeatability, calculated by $V_I/V_I + V_W$ + V_{Fixed}; c – estimated among-individual variance, d – estimated within-individual variance, e – estimated variance due to conspecific id, f –estimated variance due to chamber, g – estimated variance due to developmental box, h - estimated variances due to fixed effects including batch, temperature, rep and diet treatment

Table S4. Among and within-individual correlations, along with repeatabilities, as estimated by a multi-response mixed effects model. Among-individual correlations are above the diagonal, within-individual correlations are below the diagonal, with repeatabilities (calculated from the multi-response model rather than the univariate models of Table 2) shown on the diagonal. Shaded within-individual correlations are inestimable and overlap with zero. 95% credibility intervals for repeatabilities are reported along the diagonal. Bold values are the among- and within-individual correlations whose 95% credibility intervals did not overlap zero.

	Advert_FQ	Advert_PC	Advert_CR	Court_CD	Court_PC	Court_CR	Agg_FQ	Agg_PR	Agg_Amp	Mass
Advert_FQ	0.64 (0.53-0.73)	-0.09	0.09	-0.09	-0.13	0.14	**0.41**	0.00	-0.12	-0.18
Advert_PC	0.12	0.50 (0.39-0.62)	**-0.58**	0.24	0.16	-0.23	-0.08	-0.06	0.21	0.09
Advert_CR	**-0.17**	**-0.71**	0.58 (0.42-0.73)	-0.20	-0.22	**0.30**	0.21	0.25	-0.28	-0.21
Court_CD				0.47 (0.32-0.60)	**0.62**	**-0.48**	-0.03	**-0.33**	0.21	0.15
Court_PC				**0.81**	0.48 (0.34-0.61)	**-0.41**	0.00	-0.27	0.22	0.08
Court_CR				**-0.54**	**-0.49**	0.48 (0.34-0.63)	0.10	0.18	-0.14	-0.19
Agg_FQ							0.53 (0.39-0.63)	-0.09	0.05	-0.13
Agg_PR							**-0.24**	0.45 (0.35-0.62)	-0.29	-0.11
Agg_Amp							**0.42**	**-0.27**	0.45 (0.32-0.55)	0.20
Mass										0.48 (0.35-0.68)

FQ - frequency, PC – pulses per chirp, CR – chirp rate, CD – chirp duration, PR – pulse rate, Amp - amplitude