1   **Interacting with the enemy: indirect effects of personality on conspecific aggression**

2   **in crickets**

3   Francesca Santostefano[1], Alastair J. Wilson[2], Yimen G. Araya-Ajoy[1], and Niels J.

4   Dingemanse[1],[3]

5   *[1]Research Group Evolutionary Ecology of Variation, Max Planck Institute for*

6   *Ornithology, Seewiesen, Germany*

7   *[2]Centre for Ecology and Conservation, College of Life and Environmental Sciences,*

8   *University of Exeter, Cornwall Campus, Penryn, UK*

9   *[3]Behavioral Ecology, Department of Biology, Ludwig-Maximilians-University of Munich,*

10 *Planegg-Martinsried, Germany*

11 Short title: Indirect effects of personality

22 **TITLE**

23 Interacting with the enemy: indirect effects of personality on conspecific aggression in

24 crickets

25 **RUNNING TITLE**

26 Indirect effects of personality on aggression

27 **ABSTRACT**

28 In animal contests, individuals respond plastically to the phenotypes of the opponents

29 that they confront. These 'opponent' – or 'indirect' – effects are often repeatable, e.g.,

30 certain opponents consistently elicit more or less aggressiveness in others.

31 'Personality' (repeatable among-individual variance in behavior) has been proposed as

32 an important source of indirect effects. Here, we repeatedly assayed aggressiveness of

33 wild-caught adult male field crickets *Gryllus campestris* in staged dyadic fights,

34 measuring aggressiveness of both contestants. Measurements of their personality in

35 non-social contexts (activity and exploration behavior) enabled us to ask whether

36 personality caused indirect effects on aggressiveness. Activity, exploration, and

37 aggressiveness were positively associated into a behavioral syndrome eliciting

38 aggressiveness in conspecifics, providing direct evidence for the role of personality in

39 causing indirect effects. Our findings imply that a multivariate view of phenotypes that

40 includes indirect effects greatly improves our ability to understand the ecology and

41 evolution of behavior.

INTRODUCTION

Over the past decades, research has increasingly focused on the adaptive nature of repeatable among-individual variation in behavior, called 'animal personality' in the behavioral ecology literature (Dall et al. 2004; Sih et al. 2004a,b; Réale et al. 2007, 2010). This field of evolutionary biology thereby increasingly embraces the notion that natural selection can favor behavioral variation at multiple hierarchical levels, such as within *and* among individuals (Dingemanse et al. 2010b; Araya-Ajoy and Dingemanse 2014). While the existence of animal personality is increasingly viewed as representing a ubiquitous feature of natural populations (Bell et al. 2009; Dingemanse et al. 2012b; Garamszegi et al. 2012), recent focus is shifting from questions regarding adaptive causation towards those concerned with the consequences of personality variation for ecological and evolutionary processes (Dall et al. 2012; Wolf and Weissing 2012; Dingemanse and Araya-Ajoy 2015).

Social interactions have recently been implicated as an important factor shaping behavioral variation at both the within- and among-individual level (Bergmüller and Taborsky 2010; Montiglio et al. 2013; Dingemanse and Araya-Ajoy 2015; Niemelä and Santostefano 2015). Variation within individuals may partly occur because individuals modify their behavior as a function of the phenotypes expressed by conspecifics (so-called 'indirect effects'; see below). Individuals may alter a particular behavior either in response to the same trait or a different trait expressed by conspecifics. An example of the former effect is provided by reciprocal aggression in

65   escalating fights, while an example of the latter is provided by aggression in response

66   to opponent body size (Moore et al. 1997).

67   Indirect effects can have major consequences for ecological and evolutionary

68   processes especially when caused by repeatable differences in phenotypes of social

69   partners that are underpinned by genetic variation. In such cases, the genes of an

70   individual influence the (behavioral) expression of a trait expressed by an interacting

71   individual; such effects are termed 'indirect genetic effects' (IGEs) (Wolf et al. 1998,

72   1999; McGlothlin et al. 2010). IGEs can greatly influence evolutionary processes

73   particularly when they are correlated with direct genetic effects (DGEs) of an

74   individual's genes on its own phenotype. In mice, for example, aggressiveness is

75   heritable (a DGE), aggressiveness elicited in conspecifics is heritable too (an IGE), and

76   aggressive genotypes elicit greater levels of aggressiveness in conspecifics. Such

77   positive genetic correlations between DGEs and IGEs are predicted to speed up the

78   response to directional selection compared to predictions derived from classic

79   quantitative genetics theory (e.g., McGlothlin et al. 2010). By contrast, negative

80   genetic correlations between DGEs and IGEs might instead impose evolutionary

81   constraints. In gulls, for example, genes expressed in females that contribute to early

82   egg laying (a DGE) actually delay the egg laying date of other females when expressed

83   in their male partners (an IGE) (Brommer and Rattiste 2008). Obviously, phenotypes

84   that are relatively repeatable (e.g., body size) and affect fitness in interaction partners

85   are most likely to induce indirect effects in nature.

86   The consequences of indirect (genetic) effects for evolutionary processes are

87   even more profound when we fully acknowledge the multivariate nature of most

88   phenotypes (Moore et al. 1997; McGlothlin and Brodie 2009; Araya-Ajoy and

89   Dingemanse 2014; Bijma 2014). Behavioral traits are often structured into syndromes

90   (Garamszegi et al. 2012), i.e., whole suites of behaviors are correlated at the among-

91   individual level; such syndromes may impose constrains on micro-evolution of

92   behavior (Dochtermann and Dingemanse 2013). This would, for example, occur when

93   selection favors multivariate behavioral phenotypes that are not present in the

94   population due to strong syndrome structure. To date, studies of syndromes have

95   considered only correlations among 'direct' sources of behavioral variation. However,

96   it is likely that indirect effects are also integrated as parts of syndromes. This would

97   occur if, for instance, opponent personality is itself an important source of indirect

98   effects on focal behavior. Indirect effects are expected for behaviors such as

99   aggressiveness and dominance (Moore et al. 1997, 2002), which are themselves often

100   correlated with other behaviors such as boldness, exploration and activity (Garamszegi

101   et al. 2012). Social partner effects should therefore be incorporated as part of

102   behavioral syndromes to better understand the evolution of correlated traits.

103   Aggressiveness represents a good example of an 'interacting phenotype'

104   studied both in quantitative genetics and behavioral ecology (Wilson et al. 2009; Briffa

105   et al. 2015). Aggressiveness is interesting because of its reciprocal nature and

106   documented occurrence of opponent (also called 'social partner') effects (Wilson et al.

107   2009, 2011, 2013; Camerlink et al. 2012, 2013; Alemu et al. 2014). Interestingly,

108   contest theory has traditionally focused on the role of morphological traits such as

109   weapons and body size in shaping the intensity of aggressive interactions (Arnott and

110   Elwood 2008). In empirical studies, however, morphological traits often explain only a

111   moderate portion of the variation in contest behavior (Briffa et al. 2015). The

112   behavioral stress physiology literature implies that behavioral traits may also play an

113   important role because 'proactive' (active, aggressive, explorative, bold) individuals are

114   less responsive to intentions signaled by interaction partners compared to 'reactive'

115   (less active, aggressive, explorative, bold) individuals (Koolhaas et al. 1999; Coppens et

116   al. 2010). While effects of personality on social responsiveness are predicted by game

117   theory (Maynard-Smith 1982; Dall et al. 2004), the idea has received little empirical

118   testing to date (Briffa et al. 2015; Dingemanse and Araya-Ajoy 2015).

119   Crickets are an ideal system to address the occurrence of indirect effects of

120   personality on the expression of aggressiveness. Males of the European field cricket

121   (*Gryllus campestris*) are territorial and frequently engage in agonistic contests to

122   monopolize resources such as burrows or mates (Ritz and Köhler 2007). Wild European

123   field cricket populations show repeatable among-individual differences in suites of

124   traits such as activity, aggressiveness, boldness, and exploratory tendency (Rodríguez-

125   Muñoz et al. 2010; Fisher et al. 2015a,b; Niemelä et al. 2015).

126   Specific study designs are required to quantify variation in individual-level traits

127   where both direct and indirect effects are targeted (Moore et al. 1997; McGlothlin and

128   Brodie 2009; Bijma 2014). We focus here on a design where the same individual has

129   social interactions both as a 'focal' and as an 'opponent', and where each individual

130   plays each role repeatedly across behavioral trials (Wilson et al. 2009, 2013;

131   Dingemanse and Araya-Ajoy 2015). Such a setup enables the partitioning of the total

132   phenotypic variance in behavior expressed in focal individuals to variance attributable

133   to (i) the focal individual's identity (a direct effect), (ii) the opponent's identity (an

134   indirect effect), and (iii) residual within-individual variance (see Wilson et al. 2009,

135   2011, 2013 for worked examples). Moreover, because each individual is both used as a

136   focal individual and as an opponent, we can additionally ask whether individuals that

137   (on average) have a high value for a particular behavior also elicit this behavior in

138   conspecifics. Statistically this is measured as the correlation between direct and

139   indirect effects (i.e., the phenotypic components of the genetic correlation between

140   DGEs and IGEs detailed above). Application of this design has, for example,

141   demonstrated that mice with aggressive personalities also elicit aggressiveness in their

142   interaction partners (Wilson et al. 2009). When other traits are additionally measured,

143   their effects may readily be incorporated to ask which (combination of) traits exactly

144   induce social responsiveness in interaction partners (McGlothlin and Brodie 2009;

145   Bijma 2014).

146   Here, we applied this paradigm to the study of aggressiveness expressed in

147   pairwise interactions. We asked whether the personality of an individual (measured by

148   its average level of activity, exploratory behavior, and aggressiveness across repeated

149   observations) affects the aggressiveness expressed in conspecifics, thus integrating the

150   indirect effects in a multivariate view of the phenotype. We repeatedly assayed

151   activity, exploratory tendency, and aggression to determine the presence of

152   repeatable among-individual variation in these traits ('personality'). To address their

153   indirect effects, we applied a design where each male cricket fought repeatedly in

154   dyadic interactions, equally often as a focal and as an opponent. We then quantified (i)

155   whether activity, exploratory behavior, and aggressiveness harbored repeatable

156   among-individual variation, (ii) whether individuals were also repeatable in the level of

157   aggressiveness elicited in opponents, (iii) whether an individual's average level of

158   aggressiveness predicted aggressiveness elicited in opponents or (iv) whether other

159   key individual-level characteristics (activity, exploratory tendency, body weight) did so

160   instead. Our second objective was to integrate indirect effects into our description of

161   behavioral syndrome structure. We therefore tested the relative fit of nine alternative

162   hypotheses (models) concerning syndrome structure based on literature, with a

163   structural equation modelling approach (Dochtermann and Jenkins 2007; Dingemanse

164   et al. 2010a); this allowed us to test explicit predictions on the correlation structure

165   among behaviors (detailed in Figure 1). Doing so enabled us to determine the nature of

166   associations between behavioral traits and indirect effects in contest behavior, and

167   thereby forcefully address the consequences of variation in 'personality' during social

168   interactions.

169   **METHODS**

170   **Cricket collection**

171   Crickets were collected from a meadow adjacent to the Max Planck Institute for

172   Ornithology (Seewiesen), Germany (47°58'35.5'N 11°14'04.5'E), between the 2nd week

173   of May and the 1st week of June 2013. The main collection site was a south-west facing

174   slope within the meadow. From the 4th week of April onwards, we searched the field

175 daily for burrows of newly emerged individuals and marked each with a numbered

176 flag. Our aim was to trap individuals close to adulthood because our interest was in

177 quantifying adult behavior (detailed below). We attempted to catch crickets in this

178 stage with funnel traps (detailed in Niemelä et al. 2015) set at the burrow entrance

179 between 10h00-17h00, for up to 30 minutes and up to 4 times per day per burrow,

180 until the individual was caught. We succeeded in catching most crickets within the first

181 two days of attempted catching. Because we monitored burrows on a daily basis, we

182 could track each individual's developmental stage; all captured adults were no more

183 than 1 day post-molting, implying that they lacked experience with mating and

184 fighting. Following capture, crickets were placed in individual containers and

185 transported to a climate room at the Ludwig Maximilians University of Munich. We

186 collected a total of 57 males of which we randomly selected 32 at the onset of the

187 experiments.

188 **Housing**

189 All individuals were housed in a climate room (dimensions: 4.5 l x 3.6 w x 2.7 h m) at

190 26°C (±0.5) and 65% (±0.5) humidity, under a light:dark photoperiod that wild crickets

191 experienced at the time of capture (14:10 h). Each individual was housed alone in a

192 plastic container (10 x 10 x 9 cm) with a sand-covered floor and a flow-through plastic

193 netted lid that prevented escape but allowed air circulation. Each container included

194 an artificial, half-cylindrical shelter (6 x 3.5 x 2 cm), a petri dish (3.5 cm diameter) with

195 food, and another petri dish with water held within a cotton-plugged vial. Individuals

196   were fed with a mix of dry bird food (Aleckwa Delikat, Germany) and fresh food (carrot

197   and apple) *ad libitum*. Food and water were replaced every 3-4 days. Containers were

198   checked daily for newly molted adults, enabling us to assign age since final molting for

199   each individual not yet molted.

200   **Experimental protocol**

201   Behavioral trials were conducted between the 26th of May and 24th of June 2013. Each

202   individual was repeatedly assayed for each of 3 behaviors (activity, exploration,

203   aggression; described in detail below), on each of 12 consecutive days. Because

204   individual identification is required for the aggression test, subjects were marked with

205   colored tape on the pronotum (red or blue, randomly assigned each time) the day

206   before a trial. The three tests were always done sequentially and in the same order

207   (table 1, figure 2); carry-over effects (from one test on the next) could therefore not be

208   modelled. We chose this set-up because it ensured that all individuals were given the

209   exact same treatment since this greatly facilitates comparison between individuals

210   (Dingemanse et al. 2007; Dochtermann 2010).

211   We initially selected 32 individuals randomly from the 57 collected individuals.

212   These were divided into eight groups of four individuals according to their estimated

213   age (i.e., days post-molting) to ensure that all the individuals of the same group were

214   approximately the same age. It has been shown that adult crickets within one week

215   post-molting do not show fully developed aggressive behavior (Hofmann and

216   Schildberger 2001); the behavioral assays were therefore conducted when individuals

217   were at least 7 days post-molting. Groups were on average 9.8 days (standard

218   deviation (SD): 2.6) post-molting at the onset of their behavioral trials. Six individuals

219   died before the end of the experiment and were replaced, increasing the total number

220   of tested individuals to 38. For data analysis (see below), we used all data, including

221   behavioral trials of individuals that died during the experiment and of their

222   replacements.

223   Within each group of four, each individual was subjected to an aggression test

224   once on each of 12 consecutive days. From previous work, we know that this inter-test

225   interval prevents carry-over effects caused by winner or loser effects (Khazraïe and

226   Campan 1999). To maximize the number of unique pairwise dyads, and sample size per

227   dyad, each individual fought four times with each of the three interaction partners

228   within its group. All individuals within a group of four were tested on the same day,

229   and each of two groups were assayed at the same time (i.e., 8 individuals

230   simultaneously, one group per shelf). To minimize within-group variation in micro-

231   environmental effects, each group was assayed at a fixed time of day over the 12

232   consecutive days (either between 9h00-12h00, 12h00-15h00 or 15h00-18h00). After

233   each group was tested, walls and dividers of the testing arenas were thoroughly

234   washed with warm water; sand was raked and mixed in a stock container in order to

235   minimize the presence of contact pheromones that could otherwise affect future

236   contests (Judge and Bonanno 2008).

237   All trials were performed on a rack fitted with two shelves, each equipped with

238   a camera, in the same climate room where the individuals were housed. Arenas were

239   not acoustically isolated from the rest of the room such that all the individuals were

240   exposed to abundant background noise typical of conditions experienced in the wild.

241   To prevent any visual disturbances, the shelves were isolated from the climate room

242   by white curtains; entrance to the room was not permitted during trials. All trials were

243   recorded using high-resolution digital video cameras (Basler GenICam, Germany) fitted

244   43 cm above each testing arena. The cameras were connected to a computer outside

245   of the climate room and managed using the software MediaRecorder (Noldus,

246   Netherlands). Videos were recorded at 27.81 frames per second and 1600 x 1200

247   pixels resolution.

248   A small number of trials were excluded from the final dataset: 32 of 382 activity

249   and 29 of 382 exploration trials (8.4% and 7.6% respectively) due to technical problems

250   with data recording, and 24 of 191 aggression trials (12.6 %) because males failed to

251   engage in aggressive interactions. Note that the total number of aggression trials is

252   approximately half of that of other trials since two individuals are involved in each

253   aggression test. The final sample size was therefore 350 tests for activity (mean

254   number per individual: 9.2, SD 3.7), 353 for exploration (mean number per individual:

255   9.3, SD 3.4) and 167 for aggression (mean number per individual: 8.8, SD 3.8).

256   **Behavioral trials and scoring**

257   *Activity:* The general level of activity in a familiar environment was recorded in the

258   individual's home container. Those home containers were large enough to allow free

259   movement reflecting its routine activity. Prior to the onset of the behavioral trials,

260   selected individuals were carefully moved to the recording shelves inside their home

261   container and given 30 minutes to acclimatize. To optimize the automated video

262   tracking, the lid, water vial, food and petri dishes were removed from the home

263   containers. Activity was recorded automatically for 60 minutes (Table 1; Figure 2a).

264   *Exploration:* Following the activity test, we gently moved the subject (inside its home

265   container) to the side of the shelf where it had previously been filmed, after which we

266   placed two arenas under each camera. These arenas (29.5 l x 15.5 w x 9 h cm) had

267   floors covered with white sand and an opaque removable divider in the middle. When

268   the divider was lowered, the two halves (14.5 l x 15.5 w x 9 h cm) of a single arena

269   could be used as arenas to simultaneously screen, in isolation, exploratory behavior of

270   each of the two individuals that would later meet in an aggression test. At the onset of

271   the exploration test, each individual was moved (inside its own shelter) from its home

272   container to a (randomly allocated) half of the arena. We ensured that all individuals

273   were inside their shelter at the onset of the exploration trial, after which exploratory

274   activity was recorded automatically for 60 minutes (Table 1; Figure 2b).

275   Activity and exploration videos were analyzed using Ethovision X 10.0 (Noldus, the

276   Netherlands). This software package enables tracking of isolated individuals and

277   extracts the spatial coordinates for each video frame. For both the activity and

278   exploration tests, we used the Pythagorean equation to calculate the distance moved

279   from one frame to the next, using the X and Y coordinates of the individual's center

280   point at each sampling point (User manual of Ethovision X 10.0, Noldus Information

281   Technology 2013). The frame rate at which the videos were analyzed was adequately

282   set to 6.95 per sec, and we therefore acquired 25020 positions per individual for these

283   60-min trials. We then summed up all distances to calculate the total distance moved,

284   in the familiar environment (activity test) viewed as a measure of 'activity'. The total

285   distance moved in the novel environment (exploration test) is viewed as a measure of

286   'exploratory behavior' (following Réale et al. 2007).

287   *Aggression:* Following the exploration test, the shelters were removed and the

288   individuals given a further 10 minutes to acclimatize to their half of the arena. The

289   divider was then lifted, after which we filmed each dyad engaging in social interactions

290   for a period of 10 minutes (Table 1, Figure 2c). At the end of each aggression test, each

291   individual was weighed on an electronic balance (precision: 0,001 g). We then changed

292   each individual's color tag according to the next day's schedule, and returned it to the

293   home container in the allotted housing slots within the climate room.

294   We assayed three behaviors that represented an individual's willingness to

295   engage in aggressive interactions: 'approaching', 'singing', and 'chasing' (defined

296   below). An interaction was defined as starting when any part of one individual touched

297   any part of the other (Bertram et al. 2011), and ended if the contact was interrupted

298   for more than two seconds. Within the 10-minute trial, for each interaction, we scored

299   for each member of the dyad whether it did or did not perform each of these three

300   behaviors. We subsequently counted how often a behavior occurred per individual

301   over the entire trial, resulting in three count variables for each combination of

302   individual and trial. The total number of interactions observed over all 167 trials was

303   2589 (mean number of interactions per trial = 15.05, min = 1, max = 52). To acquire the

304 behavioral data, each video was played in slow motion and scored blindly by one of

305 three observers.

306 Approaching: We scored an individual as 'approaching' during an interaction when it

307 moved towards the other individual from any angle until they came into contact.

308 When only one individual was actively approaching the other (i.e. the other cricket sat

309 still), we assigned the behavior to that individual alone. In cases where both

310 contestants approached each other at the same time, we assigned the behavior to

311 both. The mean number of approaches per individual per trial was 9.64 (min = 0, max =

312 48). Approach behavior has been used by several studies quantifying aggressiveness in

313 male crickets, sometimes called 'initiating first contact' or 'initiating first aggression'

314 (Brown et al. 2006, 2007).

315 Singing: Male crickets produce songs by rubbing their wings together when they

316 encounter rivals and this has been reported as an indication of male aggressive intent

317 (Alexander 1961). Singing involves wing movements and is visually easily distinguished

318 from courtship songs and victory songs, the latter produced only by the winner *after*

319 an interaction. The mean number of times singing recorded per individual per trial was

320 1.73 (min = 0, max = 19).

321 Chasing: A chase was recorded when one of the contestants (namely, the winner)

322 actively pursued its opponent immediately after the interaction had ended. We

323 defined chases as pursuits in the direction of the loser initiated within 2 seconds after

324 termination of the physical contact. Chasing represents a behavior indicating

325 aggressiveness (i.e. the motivation to continue the fight after contact has ended), and

326   has also been used as a measure of aggressiveness in several other studies (e.g. Jang et

327   al. 2008; Bertram et al. 2011; Fitzsimmons and Bertram 2013). Unlike the other two

328   behaviors, chasing after an interaction is mutually exclusive for the two individuals, i.e.

329   only the winner ever chases the opponent away. The mean number of chases recorded

330   per individual per trial was 1.46 (min = 0, max = 22).

331   **Statistical analyses**

332   We conducted two sets of statistical analyses. First we partitioned the variation for

333   each measured trait into within- and among-individual variance using a univariate

334   mixed-effect modelling framework. Univariate models allow a straightforward

335   interpretation of fixed effects, and allow for testing repeatabilities of single behaviors.

336   As a second step, we estimated patterns of among-trait covariance at each estimable

337   hierarchical level using a multivariate extension of this framework. All models were

338   fitted using restricted maximum likelihood; dependent variables were mean-centered

339   and variance standardized to facilitate comparison of variance components across

340   traits. Throughout, we assumed a Gaussian error distribution, which was confirmed for

341   all response variables after visual inspection of model residuals.

342   *Univariate mixed-effects models*

343   Sources of variation in traits repeatedly measured in a non-social context (i.e., activity,

344   exploration, and body weight) were estimated by fitting the focal trait as the response

345   variable into a univariate mixed-effect model. To statistically control for potential

346   sources of variation not relevant to our biological hypotheses we included the

347   following fixed effects: test sequence (covariate, range 0-11), time of the day (minutes

348   from midnight, covariate), shelf (categorical variable with two levels), and location of

349   the arena within a shelf (categorical variable with four levels). Test sequence was

350   coded as the progressive order of repeats for the same assay (0 to 11), such that the

351   fixed effect intercept of the model was estimated for the first test (e.g. Dingemanse et

352   al. 2012a). Time of day was mean-centered, such that the fixed-effect intercept of the

353   model was estimated for the phenotype expressed on the average testing time

354   (following Dingemanse and Dochtermann 2013). We fitted random intercepts for

355   group (8 levels), date (28 levels), and the focal individual's identity (38 levels). Effects

356   of variables fitted to control for variation induced by the experimental design (time of

357   day, shelf, location, group, and date) were unimportant (results not shown) and are

358   not discussed further, except for the variable test sequence which explained significant

359   variation.

360   Prior to the analysis of the traits repeatedly measured in a social context (i.e.,

361   approaching, singing, and chasing), one individual in each trial was randomly assigned

362   the focal and the other the opponent role. Since we hypothesize that focal behavior

363   will depend on opponent phenotype, random intercepts for both focal and opponent

364   identity are included in the univariate model of the focal individual's behavior.

365   Furthermore, because the same individual is the focal in some aggression trials but the

366   opponent in others, the model can be expanded to estimate the covariance (or

367   correlation) between focal and opponent identity effects on focal behaviors. If positive

368   (vs. negative), individuals that are on average aggressive as focal animals also tend to

369   induce (vs. reduce) aggressiveness in others when acting as the opponent. If opponent

370   identity effects are present but this correlation is zero, individual-level traits of the

371   opponent other than its aggressiveness affect the focal individual's aggressiveness.

372   While previous studies applying this design have analyzed sources of variation

373   in the focal individual's behavior alone (e.g. Wilson et al. 2009), we were able to record

374   detailed behaviors performed by both individuals in each dyad (i.e. the designation of

375   focal and opponent identities as described above was arbitrary). In order to fully utilize

376   all available behavioral data for parameter estimation we therefore modified the

377   modelling strategy described above as follows. First, we estimated focal and opponent

378   identity effects (as well as their correlation) for the behavior expressed by the focal

379   individual. Second, we structured the dataset in a way that enabled us to

380   simultaneously estimate focal and opponent identity effects (and their correlation) in

381   the behavior of the opponent (as detailed in the Supplementary Text). Third, because

382   focal and opponent roles were randomly assigned, (i) focal identity effects in the focal

383   individual's behavior should equate opponent identity effects in the opponent's

384   behavior, (ii) opponent identity effects in the focal individual's behavior should equate

385   focal identity effects in the opponent's behavior, and (iii) the covariance between focal

386   and opponent identity effects as well as any other fixed-effect (e.g. time of day) and

387   random-effect (e.g. group, date) estimates should be the same for the focal's and

388   opponent's aggressive behavior. We thus implemented a bivariate mixed-effect model

389   with the focal's and opponent's behavior fitted as the two response variables where

390   parameters that were logically identical were constrained to be identical. This bivariate

391   implementation thereby enabled us to utilize all data at hand while simultaneously

392   avoiding pseudo-replication and biasing effects of arbitrary assignment of focal versus

393   opponent roles. Because of the imposed model constraints, the bivariate model

394   effectively represents a univariate model, and is treated as such in the remaining text.

395   Adjusted individual repeatability was estimated for each trait by calculating the

396   proportion of the total phenotypic variance not attributable to fixed effects that was

397   explained by individual identity (Nakagawa and Schielzeth 2010). For behaviors

398   expressed in a social context, we additionally calculated the proportion of the total

399   phenotypic variance that was explained by the identity of the opponent and was not

400   attributable to fixed effects, which we call 'adjusted opponent repeatability' (Wilson et

401   al. 2009).

402   *Multivariate mixed-effects models*

403   We estimated patterns of trait covariance at each estimable hierarchical level using a

404   multivariate mixed-effects model. We fitted activity, exploration, and weight as

405   response variables as well as approach as a proxy for aggressiveness. Though we had

406   measured various proxies of aggressiveness (detailed above), we used here only

407   approach because multivariate models including other proxies of aggression did not

408   converge. However, we were able to confirm with sets of simpler models that all

409   proxies for aggressiveness were highly correlated (Results not shown), implying that

410   our decision to use approach as a measure of aggressiveness was justified (for a

411   further discussion on rationale of this approach, see Araya-Ajoy & Dingemanse 2014).

412   To avoid over-parameterization, we only included fixed (sequence) and random effects

413   (identity of the focal individual) that explained significant variation in the univariate

414   analyses (see Results). Modelling random intercepts for the focal individual's identity

415   enabled decomposition of phenotypic covariances (and hence correlations derived

416   from them) into among-individual and residual within-individual components (Wilson

417   et al. 2009). Among-individual correlations occur when an individual's average

418   phenotype over all repeated measures is correlated across traits, called a 'behavioral

419   syndrome' in the context of behavior (Dingemanse et al. 2012b); within-individual

420   correlations occur when two phenotypic traits show correlated changes in expression

421   within the same individual due to the combined effects of integration of within-

422   individual plasticity and/or correlated measurement error (Dingemanse and

423   Dochtermann 2013). We further included random intercepts for the opponent's

424   identity for the response variable approach during the aggression test, which enabled

425   us to assess whether individuals were repeatable in the aggressiveness elicited in

426   conspecifics (we will sometimes present this indirect effect as a trait, 'eliciting

427   aggressiveness', for clarity). Because the same individual repeatedly played focal in

428   some and opponent in other trials (see above), we also estimated (i) the correlation

429   between the focal and opponent identity effect on aggressiveness (see above for

430   biological interpretation) as well as (ii) the correlation between the opponent identity

431   effect on aggressiveness and the focal identity effect on each of the other traits

432   (activity, exploration, body weight). This latter type of correlation tests whether

433   individuals that elicit more aggressiveness in others are themselves more (or less)

434   active, explorative, or heavier than individuals eliciting less aggressiveness in others.

Significance testing in mixed-effects models

436 We tested statistical significance of fixed effects using numerator and denominator

437 degrees of freedom (df) estimated from the algebraic algorithm in ASReml 3.0

438 (Gilmour et al. 2009). We used likelihood ratio tests (LRTs) to evaluate the statistical

439 significance of random effects. This χ^2-distributed test statistic is calculated as twice

440 the difference in log-likelihood between a model where a target random effect was

441 fitted versus not fitted (Shaw 1991). Variances are bound to be positive, therefore

442 probability (P) of a LRT applied to a variance was calculated assuming an equal mixture

443 of P (χ^2, df=0) and P (χ^2, df=1), i.e. df=0.5 (Self and Liang 1987; Pinheiro and Bates

444 2000; Visscher 2006). Covariances (correlations) are not bound to be positive, and

445 their probability was therefore calculated assuming P (χ^2, df=1). LRTs involving one

446 variance and one covariance were tested assuming an equal mixture of P (χ^2, df=1) and

447 P (χ^2, df=2), i.e. df=1.5. We applied this latter test, for example, to evaluate support for

448 opponent identity effects in aggressiveness, which requires fitting both a variance (i.e.

449 the variance attributable to the opponent's identity) and a covariance (i.e. the

450 covariance between focal and opponent identity effects). All models were

451 implemented in ASReml 3.0 (Gilmour et al. 2009).

452 *Structural equation modelling*

453 To test our *a priori* hypotheses on behavioral syndrome structure, we applied

454 structural equation modelling to nine *a priori* conceived scenarios based on the

455 behavioral syndrome literature (described in Figure 1). We analyzed the among-

456 individual correlation matrix estimated from the multivariate mixed-effects model

457   using the package 'SEM' in the software R v. 3.1.0. (Team R Core 2012). We then

458   statistically compared the models using the Akaike information criterion (AIC) (Akaike

459   1973; Burnham and Anderson 2002), and evaluated the relative support for each

460   based on AIC differences relative to the model with the lowest AIC (ΔAIC), which

461   represents the best fitting model; we also calculated each model's weight and relative

462   likelihood   (Anderson 2008).

463   **RESULTS**

464   **Sources of variation in single traits**

465   Exploration, approach, and weight changed significantly within individuals as a

466   function of test sequence (Supplementary Table S1). On average individuals became

467   leaner, less explorative, and less aggressive over the 12-day course of the experiment.

468   None of the traits were significantly affected by tag color, time of day, testing shelf or

469   within-shelf test location (Results not shown); neither did the traits vary between

470   groups or days (Supplementary Table S1).

471   All traits except singing were significantly repeatable (Table 2); adjusted

472   behavioral repeatabilities were highest for exploration (0.40, SE 0.10) and activity

473   (0.33, SE 0.09), and substantially lower (though significant) for approaching (0.19 SE

474   0.06) and chasing (0.09 SE 0.05) during the aggression test. Approaching and chasing

475   were significantly affected by the identity of the opponent, though singing was not

476   (Table 2). For approaching and singing, the proportion of variance explained by

477   opponent identity (i.e. adjusted opponent repeatability) was of a similar magnitude

478   (0.16, 0.06 SE for approaching; 0.12, 0.05 SE for chasing) when compared to adjusted

479   individual repeatability (0.19 and 0.09, respectively). Opponent identity effects imply

480   that unidentified individual-level characteristics of opponents affect the behavior of

481   focal individuals. These effects did not appear to be due to repeatable differences in

482   approaching, chasing or singing among opponents, since the correlation between focal

483   and opponent identity effects was rather weak and non-significant for all three

484   behaviors expressed in the aggression test (Table 2).

485   Body weight was, as expected also repeatable (Table 1). Interestingly,

486   repeatability was relatively low (0.46, SE 0.11) compared to what might typically be

487   expected. This indicates that body weight strongly depended on day-to-day changes in

488   environmental conditions experienced by our crickets.

489   **Among-trait correlations**

490   *Among-individual correlations*

491   The multivariate mixed-effects model provided strong evidence for the existence of

492   among-individual correlations between most traits (Table 3; Supplementary Table S2,

493   Supplementary Table S4). Individuals that were on average relatively aggressive

494   towards conspecifics were also relatively active in a novel environment ('explorative')

495   and relatively active in a familiar environment, providing strong evidence for the

496   existence of an aggressiveness-activity-exploration syndrome. Furthermore, aggressive

497   individuals were relatively heavy compared to less aggressive individuals.

498   Our univariate analysis implied that aggressiveness elicited in conspecifics also

499   harbored among-individual variation (Table 2). Aggressiveness elicited in conspecifics

500   was not (tightly) related to an individual's average level of aggressiveness, owing to a

501   non-significant correlation between focal and opponent identity effects (Table 2, see

502   also Table 3). Our multivariate analysis revealed that individuals that were on average

503   relatively explorative in novel environments also elicited approach by opponents in the

504   aggression test (Table 3). This among-individual correlation was relatively strong (0.45,

505   SE 0.17), implying that personality variation with respect to exploratory tendency

506   constitutes a major factor explaining why individuals are repeatable in the level of

507   aggressiveness that they elicit in others.

508   *Residual within-individual correlations*

509   Various traits were also correlated within individuals, implying the existence of

510   integration of within-individual plasticity across multiple traits and/or correlated

511   measurement error. Specifically, when individuals increased their body weight across

512   trials, they also became significantly more explorative in the novel environment

513   (though not more active in familiar environments) (Table 3, Supplementary Table S4).

514   In contrast to patterns observed at the among-individual level, most traits were only

515   weakly and non-significantly associated at the within-individual level.

Behavioral syndrome structure

516

517 Based on literature, we constructed and compared nine different *a priori* conceived

518 models of behavioral syndrome structure (Figure 1)*.* The domain-general syndrome,

519 which included correlations between activity, exploration, aggression, and aggression

520 elicited (model 3; Figure 4), best explained the observed data, as inferred from it

521 having the lowest AIC score (Table S3). The second-best model, hypothesizing a

522 domain-general structure with only exploration eliciting aggressiveness (model 9) also

523 had a relatively good fit to the data (model 9: ΔAIC=2.35; Table S3). The domain

524 general model nevertheless fitted the data 3.26 times better compared (Akaike weight

525 of model 3 (0.75) divided by the Akaike weight of model 9 (0.23); Table S3), and is

526 therefore treated as the sole best-fitting model throughout the remaining text.

527 The four observed behaviors were, notably, also partially independent from

528 each other, as the syndrome structure implied in our best-supported model explained

529 relatively little variation in aggressiveness (Figure 4)*.* Exploration behavior represented

530 an extreme case, where all the among-individual variance was captured by the

531 hypothesized syndrome structure. We verified that this was not an artefact caused by

532 the tight among-individual correlation between exploration and activity, as re-analyses

533 of the data after excluding activity yielded the same results (not shown). These

534 findings therefore provide strong support for the presence of a domain-general

535 syndrome that includes indirect effects*.*

536 **DISCUSSION**

537 This study investigated the occurrence of indirect effects on aggressiveness in male

538 European field crickets, and asked whether such effects could be driven by personality.

539 As expected, we found evidence for indirect effects as individuals differed consistently

540 in the level of aggressiveness that they elicited in others. Direct and indirect effects on

541 focal behavior were integrated within an overarching behavioral syndrome, existing

542 largely because more explorative individuals were also more active and aggressive, and

543 tended to elicit more aggressiveness in conspecifics. This finding constitutes

544 unambiguous evidence for the notion that an individual's aggressiveness-activity-

545 exploration type influences aggressiveness of conspecifics. Our study thus implies that

546 repeatable differences in behavior represent an important component of the social

547 environment affecting social behaviors of conspecifics. If representing heritable

548 patterns of variation, these findings imply that personality variation in the

549 environment will have consequences for evolutionary trajectories of socially expressed

550 behaviors that would only be appropriately predicted by quantitative genetics theory

551 developed to model indirect genetic effects (Montiglio et al. 2013; Dingemanse and

552 Araya-Ajoy 2015).

553 **Individual and opponent repeatabilities**

554 All behaviors (except singing during the aggression test) were repeatable and their

555 estimates were within the range reported for behavioral traits (meta-analysis: Bell et

556 al. 2009). Values of repeatabilities of non-social behavioral traits (activity, exploration)

557 were also similar to those documented previously in our and other cricket species

558   (Wilson et al. 2010; Niemelä et al. 2012a,b; Dochtermann and Nelson 2014; Fisher et

559   al. 2015a,b). In contrast, behaviors expressed in a social context (approaching, singing,

560   chasing) had relatively low repeatabilities (0.09-0.19) compared to those expressed in

561   a non-social context (0.33-0.40; Table 2). This was not unexpected since the social

562   environment experienced varied substantially within-individuals across trials, whereas

563   the non-social trials represented a more stable environment. As advocated in recent

564   reviews (Briffa et al. 2015; Dingemanse and Araya-Ajoy 2015), our setup allowed us to

565   assess repeatability of social behavior as it would typically be expressed in the wild

566   (i.e., across an ecologically relevant sample of partners) rather than artificially

567   minimizing social environment effects by using dummies or video playback stimulation.

568   Few other studies of aggression have explicitly modelled such indirect effects by

569   considering identity effects of interaction partners; all such studies have focused on

570   vertebrates. Importantly, the repeatability estimates in these few studies were in the

571   same range of ours (0.11 to 0.27; Wilson et al. 2009, 2011, 2013). These estimates of

572   repeatability are lower compared to the ones reported by meta-analyses (Bell et al.

573   2009), where aggression was one of the most repeatable classes of behaviors (roughly

574   R=0.50). Our findings therefore imply that published estimates might often be

575   substantially biased upwards due to the usage of unnatural standardization

576   standardized experimental conditions (e.g. size matching) that may lack ecological

577   relevance.

578   Of course, the magnitude of indirect effects that we detected might be less

579   substantial under field conditions. In the wild, other environmental effects (kept stable

580   under laboratory conditions), such as temperature, availability of mates, or predators

581 might affect the amount of among-individual variation in aggressiveness and

582 aggressiveness elicited in conspecifics. Importantly, studies based on dyadic

583 interactions might typically overestimate the magnitude of IGEs for species that

584 naturally interact in larger groups (Hadfield and Wilson 2007; Bijma 2014). This critic

585 may not be applicable in our case because male-male interactions over ownership of

586 burrows or mates in our study species are typically dyadic under field conditions too

587 (personal observation NJD and FS, Fisher et al. 2016). Therefore, our staged dyadic

588 interactions accurately reflect the natural social environment in which aggressive

589 interactions take place.

590   The opponent effect provides clear evidence for the notion that individuals

591 plastically adjusted their aggression level in response to the opponent's phenotypic

592 traits that vary at the individual level. Among-individual variation in opponents

593 therefore explains part of the within-individual variation in aggression, which can be

594 interpreted as a social form of phenotypic plasticity, or 'social responsiveness'

595 (Webster and Ward 2011; Taborsky and Oliveira 2012; Wolf and McNamara 2013; Wolf

596 and Krause 2014; Dingemanse and Araya-Ajoy 2015). By modelling the opponent

597 identity as a random effect, we integrated the influence of all the aspects of an

598 opponent's individual-level phenotype. However, by also measuring phenotypic traits

599 of the opponent (including its personality), we were able to tease apart which traits

600 were driving the opponent effect as we describe below.

601   **Individual-level correlations of behavioral traits across contexts**

602   Among-individual correlations between focal aggression, exploration and activity were

603   positive, confirming our predictions and revealing a syndrome structure including

604   behaviors expressed in social and non-social contexts. Positive correlations among

605   activity and exploration behavior are well-documented in the behavioral syndrome

606   literature (Sih et al. 2004b; Réale et al. 2007; Garamszegi et al. 2012), and are generally

607   supported in crickets (e.g. Wilson et al. 2010, but see Dochtermann and Nelson 2014)

608   The coping style literature predicts the presence of bold, exploratory, and aggressive

609   individuals called 'proactive' types (Koolhaas et al. 1999; Coppens et al. 2010), which

610   we indeed found in our study. We note however, that the relationship between

611   aggressive behavior and other personality traits is often population-specific (Bell 2005;

612   Dingemanse et al. 2007). Our findings therefore confirm the notion that behaviors

613   from different functional contexts covary and that domain-general syndromes may be

614   common among organisms (Sih et al. 2004a,b; Bell 2007; Dochtermann and Jenkins

615   2007). Such a structure may be important from an evolutionary perspective because

616   trait correlations are known to affect evolutionary trajectories (Lande and Arnold

617   1983; Sih et al. 2004b; Sprenger et al. 2012; Dochtermann and Dingemanse 2013).

618   The repeatable part of an individual's weight was correlated with an

619   individual's average level of exploration and aggressive behavior, implying that

620   repeatable variation in body condition might have proximately underpinned the

621   observed behavioral syndrome (see e.g. Royauté et al. 2015b). However, post hoc

622   analyses showed this not to be the case: we S3conducted a set of SEMs expanding

623 upon our best-supported (domain-general) model. We then compared the relative fit

624 of models where body weight constituted an additional expression of the latent

625 variable rather than representing the latent variable itself (versus a null model where

626 body weight was not associated with behavior) (Figure S1, Table S5). The domain-

627 general model, where body weight also constituted an expression of the latent

628 variable, was best supported; this finding implies that weight indeed did not 'drive' the

629 syndrome structure. Interestingly, body size has often been hypothesized to

630 represent an important mediator of agonistic behavior in the animal contest literature

631 (Briffa et al. 2015). Our study implies that social partners responded to personality

632 rather than other characteristics of conspecifics, such as their body weight. It is of

633 course possible that crickets instead responded to *relative* differences in body weight.

634 However, this scenario is not supported by our data because it should result in effects

635 of the unique combination of focal and partner identity effects (so-called 'pair identity'

636 effects), which were not present when modelled in our data (Results not shown).

637   Because behaviors are plastic, feedbacks between traits may occur during

638 interactions and can either increase or decrease the amount of among-individual

639 variation (Moore et al. 1997; Wolf et al. 1998, 1999; Dingemanse and Araya-Ajoy 2015;

640 Sih et al. 2015). The level of aggression in one individual is often affected by the

641 aggression displayed by the interacting individual in escalated fights (Huntingford and

642 Turner 1987), and positive correlations between the focal and opponent effects on this

643 trait would indicate this type of reciprocal feedback. By contrast, if aggression in part

644 reflects dominance (e.g., with dominant individuals only displaying aggression towards

645 subordinates), negative correlations can arise (Wilson et al. 2011). Interestingly, the

646   lack of a significant correlation between being aggressive and eliciting aggression in

647   others may suggest the absence of feedback loops (either positive or negative) in this

648   trait. However, our SEM-analysis uncovered a relationship between being aggressive

649   and eliciting aggressiveness underpinned by the behavioral syndrome (see below),

650   indicating that positive feedbacks may have been present instead.

651   In contrast to patterns found at the among-individual level, most traits were

652   only weakly and non-significantly associated at the within-individual level. This

653   suggests that trait correlations were caused by different proximate mechanisms within

654   versus among individuals (van Noordwijk and de Jong 1986; Hadfield et al. 2007). This

655   finding contrasts recent studies reporting within- and among-individual correlations of

656   similar magnitude (Araya-Ajoy and Dingemanse 2014; Brommer et al. 2014; Royauté et

657   al. 2015a). The partial difference in correlation structure at the within vs. among

658   individual level highlights the importance of separating the two in order to make

659   unbiased inferences about behavioral syndrome structure (Dingemanse et al. 2012b;

660   Dingemanse and Dochtermann 2013; Brommer et al. 2014).

661   **Integration of indirect effects as part of a multivariate behavioral phenotype**

662   All behavioral traits were linked with aggressiveness elicited in conspecifics as part of a

663   behavioral syndrome, highlighting the key importance of considering the opponent's

664   personality in the expression of social behaviors. These findings are supported both by

665   the multivariate mixed-effect model and the SEM. Because exploration, aggression and

666   activity were highly correlated, we expected that they would jointly affect the

667   aggression of conspecifics, implying that the syndrome as a whole would explain the

668   indirect effects on aggression (model 3). This was indeed the case: despite the

669   'penalization' for a higher number of parameters, the best-supported model was the

670   one with a domain-general behavioral syndrome (Table S3, Figure 4). A mechanism for

671   the overarching indirect effect could be that individuals who explore a new

672   environment are likely to also be involved in more social interactions and this may

673   result in more attacks received by others within an aggression trial. This interpretation

674   is warranted by the strong bivariate correlation between indirect effects on aggression

675   and exploration in the among-individual correlation matrix. Indeed, exploration was

676   the factor loading most strongly with the latent variable in our structural equation

677   model. The overarching importance of exploration behavior was implied by the

678   second-best fitting model, which attracted some support (Table S3). Indeed,

679   movement variables may represent obvious cues of an individual's aggressiveness.

680   Nevertheless, other components of the behavioral syndrome definitely played an

681   important role in eliciting aggression because a full domain-general model was over

682   three times better supported. Because indirect effects were integrated as part of the

683   behavioral syndrome, our findings imply that studies of the evolution of behavior

684   should explicitly recognize that behavioural phenotypes are multivariate and include

685   responses of the social environment.

686   **Evolutionary implications**

687 Adaptive explanations in the field of behavioral ecology are often based solely on

688 phenotypic observations, with evolutionary inference relying on the 'phenotypic

689 gambit', assuming correspondence of phenotypic and genetic patterns of (co)variation

690 (Grafen 1984). Support for this position has been provided by a behavioral meta-

691 analysis in which phenotypic correlations explained 75% of the variation in genetic

692 correlations (Dochtermann 2011), although this correspondence should not readily be

693 assumed for individual cases. Despite this important caveat in our knowledge, the

694 presence of indirect effects documented here suggests a strong potential for IGEs to

695 contribute to evolutionary trajectories of aggression and/or traits genetically

696 correlated with it, which in our case include exploration and activity. Our study thus

697 implies that behavioral types certainly have the potential to alter the evolutionary

698 trajectories of behavioral traits by inducing indirect effects in a social context. Further

699 partitioning the repeatable among individual behavioral variance into additive genetic

700 and environmental effects would enable us to move from studying causes to revealing

701 the consequences of personalities. This would ultimately enable us to predict the

702 evolutionary consequences of the very existence of personality types in natural

703 populations.

704 **LITERATURE CITED**

705 Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving

706 average models. Biometrika 60:255 –265.

707 Alemu, S. W., P. Bijma, S. H. Møller, L. Janss, and P. Berg. 2014. Indirect genetic effects

708   contribute substantially to heritable variation in aggression-related traits in group-

709   housed mink (Neovison vison). Genetics Selection Evolution 46:30.

710   Alexander, R. D. 1961. Aggressiveness , Territoriality , and Sexual Behavior in Field

711   Crickets (Orthoptera : Gryllidae). Behaviour 17:130–223.

712   Anderson, D. R. 2008. Model based inference in the life sciences: A primer on

713   evidence.

714   Araya-Ajoy, Y. G., and N. J. Dingemanse. 2014. Characterizing behavioural "characters":

715   an evolutionary framework. Proceedings. Biological sciences / The Royal Society

716   281:20132645.

717   Arnott, G., and R. W. Elwood. 2008. Information gathering and decision making about

718   resource value in animal contests. Animal Behaviour 76:529–542.

719   Bell, A. M. 2005. Behavioural differences between individuals and two populations of

720   stickleback (Gasterosteus aculeatus). Journal of evolutionary biology 18:464–73.

721   Bell, A. M. 2007. Future directions in behavioural syndromes research. Proceedings.

722   Biological sciences / The Royal Society 274:755–61.

723   Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour : a

724   meta-analysis. Animal Behaviour 77:771–783.

725   Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche

726   specialisation. Trends in Ecology & Evolution 25:504–11.

727   Bertram, S. M., V. L. M. Rook, J. M. Fitzsimmons, and L. P. Fitzsimmons. 2011. Fine- and

728   Broad-Scale Approaches to Understanding the Evolution of Aggression in Crickets.

729   Ethology 117:1067–1080.

730   Bijma, P. 2014. The quantitative genetics of indirect genetic effects: a selective review

731   of modelling issues. Heredity 112:61–9.

732   Briffa, M., L. U. Sneddon, and A. J. Wilson. 2015. Animal personality as a cause and

733   consequence of contest behaviour. Biology Letters 11:20141007.

734   Brommer, J. E., P. Karell, K. Ahola, and T. Karstinen. 2014. Residual correlations, and

735   not individual properties, determine a nest defense boldness syndrome. Behavioral

736   Ecology 25:802–812.

737   Brommer, J. E., and K. Rattiste. 2008. "Hidden" reproductive conflict between mates in

738   a wild bird population. Evolution 62:2326–2333.

739   Brown, W. D., A. J. Chimenti, and J. R. Siebert. 2007. The Payoff of Fighting in House

740   Crickets: Motivational Asymmetry Increases Male Aggression and Mating Success.

741   Ethology 113:457–465.

742   Brown, W. D., A. T. Smith, B. Moskalik, and J. Gabriel. 2006. Aggressive contests in

743   house crickets: size, motivation and the information content of aggressive songs.

744   Animal Behaviour 72:225–233.

745   Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference:

746   a practical information-theoretic approach. Ecological Modelling (Vol. 172). Springer-

747   Verlag, New York.

748   Camerlink, I., P. Bijma, B. Kemp, and J. E. Bolhuis. 2012. Relationship between growth

749   rate and oral manipulation, social nosing, and aggression in finishing pigs. Applied

750   Animal Behaviour Science 142:11–17.

751   Camerlink, I., S. P. Turner, P. Bijma, and J. E. Bolhuis. 2013. Indirect Genetic Effects and

752   Housing Conditions in Relation to Aggressive Behaviour in Pigs. PLoS ONE 8:1–9.

753   Coleman, K., and D. Wilson. 1998. Shyness and boldness in pumpkinseed sunfish:

754   individual differences are context-specific. Animal Behaviour 56:927–936.

755   Coppens, C. M., S. F. de Boer, and J. M. Koolhaas. 2010. Coping styles and behavioural

756   flexibility: towards underlying mechanisms. Philosophical transactions of the Royal

757   Society of London. Series B, Biological sciences 365:4021–4028.

758   Dall, S. R. X., A. M. Bell, D. I. Bolnick, and F. L. W. Ratnieks. 2012. An evolutionary

759   ecology of individual differences. Ecology Letters 15:1189–98.

760   Dall, S. R. X., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of

761   personality: consistent individual differences from an adaptive perspective. Ecology

762   Letters 7:734–739.

763   Dingemanse, N. J., and Y. G. Araya-Ajoy. 2015. Interacting personalities: behavioural

764   ecology meets quantitative genetics. Trends in Ecology & Evolution 30:88–97.

765   Dingemanse, N. J., I. Barber, J. Wright, and J. E. Brommer. 2012a. Quantitative genetics

766   of behavioural reaction norms : genetic correlations between personality and

767   behavioural plasticity vary across stickleback populations. Journal of Evolutionary

768   Biology 25:485–496.

769   Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in

770   behaviour: Mixed-effect modelling approaches. Journal of Animal Ecology 82:39–54.

771 Dingemanse, N. J., N. A. Dochtermann, and S. Nakagawa. 2012b. Defining behavioural

772 syndromes and the role of "syndrome deviation" in understanding their evolution.

773 Behavioral Ecology and Sociobiology 66:1543–1548.

774 Dingemanse, N. J., N. A. Dochtermann, and J. Wright. 2010a. A method for exploring

775 the structure of behavioural syndromes to allow formal comparison within and

776 between data sets. Animal Behaviour 79:439–450.

777 Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2010b. Behavioural reaction

778 norms: animal personality meets individual plasticity. Trends in Ecology & Evolution

779 25:81–9.

780 Dingemanse, N. J., J. Wright, A. J. N. Kazem, D. K. Thomas, R. Hickling, and N. Dawnay.

781 2007. Behavioural syndromes differ predictably between 12 populations of three-

782 spined stickleback. Journal of Animal Ecology 76:1128–1138.

783 Dochtermann, N. A. 2010. Behavioral syndromes: Carryover effects, false discovery

784 rates, and a priori hypotheses. Behavioral Ecology 21:437–439.

785 Dochtermann, N. A. 2011. Testing Cheverud's conjecture for behavioral correlations

786 and behavioral syndromes. Evolution 65:1814–1820.

787 Dochtermann, N. A., and N. J. Dingemanse. 2013. Behavioral syndromes as

788 evolutionary constraints. Behavioral Ecology art002.

789 Dochtermann, N. A., and S. H. Jenkins. 2007. Behavioural syndromes in Merriam's

790 kangaroo rats (Dipodomys merriami): a test of competing hypotheses. Proceedings.

791 Biological sciences / The Royal Society 274:2343–2349.

792   Dochtermann, N. A., and A. B. Nelson. 2014. Multiple Facets of Exploratory Behavior in

793   House Crickets (Acheta domesticus): Split Personalities or Simply Different Behaviors?

794   Ethology 120:1110–1117.

795   Fisher, D. N., M. David, T. Tregenza, and R. Rodriguez-Munoz. 2015a. Dynamics of

796   among-individual behavioral variation over adult lifespan in a wild insect. Behavioral

797   Ecology arv048.

798   Fisher, D. N., R. Rodríguez-Muñoz, and T. Tregenza. 2016. Comparing pre- and post-

799   copulatory mate competition using social network analysis in wild crickets. Behavioral

800   Ecology arv236.

801   Fisher, D. N., T. Tregenza, and R. Rodriguez-Munoz. 2015b. Behaviour in captivity

802   predicts some aspects of natural behaviour , but not others , in a wild cricket

803   population. Proceedings of the Royal Society B: Biological Sciences 282:20150708.

804   Fitzsimmons, L. P., and S. M. Bertram. 2013. Playing to an audience: the social

805   environment influences aggression and victory displays. Biology Letters 9:20130449.

806   Garamszegi, L. Z., G. Markó, and G. Herczeg. 2012. A meta-analysis of correlated

807   behaviours with implications for behavioural syndromes: mean effect size, publication

808   bias, phylogenetic effects and the role of mediator variables. Evolutionary Ecology

809   26:1213–1235.

810   Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. ASReml user guide

811   release 3.0. VSN International Ltd.

812   Grafen, A. 1984. Natural selection, kin selection and group selection. Behavioural

813   Ecology.

814   Hadfield, J. D., a. Nutall, D. Osorio, and I. P. F. Owens. 2007. Testing the phenotypic

815   gambit: phenotypic, genetic and environmental correlations of colour. Journal of

816   Evolutionary Biology 20:549–557.

817   Hadfield, J. D., and A. J. Wilson. 2007. Multilevel selection 3: Modeling the effects of

818   interacting individuals as a function of group size. Genetics 177:667–668.

819   Hofmann, H. A., and K. Schildberger. 2001. Assessment of strength and willingness to

820   fight during aggressive encounters in crickets. Animal Behaviour 62:337–348.

821   Huntingford, F., and A. Turner. 1987. Animal conflict (Animal Beh.). Chapman & Hall

822   Ltd.

823   Jang, Y., H. C. Gerhardt, and J. C. Choe. 2008. A comparative study of aggressiveness in

824   eastern North American field cricket species (genus Gryllus). Behavioral Ecology and

825   Sociobiology 62:1397–1407.

826   Judge, K. A., and V. L. Bonanno. 2008. Male Weaponry in a Fighting Cricket. PLoS ONE

827   3:e3980.

828   Khazraïe, K., and M. Campan. 1999. The role of prior agonistic experience in

829   dominance relationships in male crickets Gryllus bimaculatus (Orthoptera: Gryllidae).

830   Behavioural Processes 44:341–348.

831   Koolhaas, J. M., S. M. Korte, S. F. De Boer, B. J. Van Der Vegt, C. G. Van Reenen, H.

832   Hopster, I. C. De Jong, et al. 1999. Coping styles in animals: Current status in behavior

833   and stress- physiology. Neuroscience and Biobehavioral Reviews 23:925–935.

834   Lande, R., and S. Arnold. 1983. The measurement of selection on correlated characters.

835   Evolution 37:1210–1226.

836   Maynard-Smith, J. 1982. Evolution and the Theory of Games. Cambridge University

837   Press.

838   McGlothlin, J. W., and E. D. I. Brodie. 2009. How to measure indirect genetic effects:

839   the congruence of trait-based and variance-partitioning approaches. Evolution

840   63:1785–95.

841   McGlothlin, J. W., A. J. Moore, J. B. Wolf, and E. D. Brodie. 2010. Interacting

842   phenotypes and the evolutionary process. III. Social evolution. Evolution 64:2558–

843   2574.

844   Montiglio, P., C. Ferrari, and D. Réale. 2013. Social niche specialization under

845   constraints: personality, social interactions and environmental heterogeneity.

846   Philosophical transactions of the Royal Society of London. Series B, Biological sciences

847   368:20120343.

848   Moore, A. J., E. D. I. Brodie, and J. B. Wolf. 1997. Interacting Phenotypes and the

849   Evolutionary Process : I . Direct and Indirect Genetic Effects of Social Interactions.

850   Evolution 51:1352–1362.

851   Moore, A. J., K. F. Haynes, R. F. Preziosi, and P. J. Moore. 2002. The Evolution of

852   Interacting Phenotypes : Genetics and Evolution of Social Dominance. The American

853   Naturalist 160:S186–S197.

854   Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian

855   data: A practical guide for biologists. Biological Reviews 85:935–956.

856   Niemelä, P. T., N. Dirienzo, and A. V Hedrick. 2012a. Predator-induced changes in the

857   boldness of naïve field crickets , Gryllus integer , depends on behavioural type. Animal

858   Behaviour 84:129–135.

859   Niemelä, P. T., E. Z. Lattenkamp, and N. J. Dingemanse. 2015. Personality-related

860   survival and sampling bias in wild cricket nymphs. Behavioral Ecology arv036.

861   Niemelä, P. T., and F. Santostefano. 2015. Social carry-over effects on non-social

862   behavioral variation : mechanisms and consequences. Frontiers in Ecology and

863   Evolution 3:1–12.

864   Niemelä, P. T., A. Vainikka, S. Lahdenperä, and R. Kortet. 2012b. Nymphal density ,

865   behavioral development , and life history in a field cricket. Behavioral Ecology and

866   Sociobiology 66:645–652.

867   Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Statistics

868   and Computing. Springer.

869   Réale, D., N. J. Dingemanse, A. J. N. Kazem, and J. Wright. 2010. Evolutionary and

870   ecological approaches to the study of personality. Philosophical transactions of the

871   Royal Society of London. Series B, Biological sciences 365:3937–46.

872   Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007.

873   Integrating animal temperament within ecology and evolution. Biological Reviews

874   82:291–318.

875   Ritz, M. S., and G. Köhler. 2007. Male behaviour over the season in a wild population of

876   the field cricket Gryllus campestris L . Ecological Entomology 32:384–392.

877   Rodríguez-Muñoz, R., A. Bretman, J. Slate, C. A. Walling, and T. Tregenza. 2010. Natural

878   and Sexual Selection in a Wild Insect Population. Science 328:1269–1272.

879   Royauté, R., C. M. Buddle, and C. Vincent. 2015a. Under the influence: Sublethal

880   exposure to an insecticide affects personality expression in a jumping spider.

881   Functional Ecology 29:962–970.

882   Royauté, R., K. Greenlee, M. Baldwin, and N. A. Dochtermann. 2015b. Behaviour,

883   metabolism and size: Phenotypic modularity or integration in Acheta domesticus?

884   Animal Behaviour 110:163–169.

885   Self, S. G., and K.-Y. Liang. 1987. Asymptotic Properties of Maximum Likelihood

886   Estimators and Likelihood Ratio Tests Under Nonstandard Conditions. Journal of the

887   American Statistical Association 82:605–610.

888   Shaw, R. G. 1991. The Comparison of Quantitative Genetic Parameters between

889   Populations. Evolution 45:143–151.

890   Sih, A., A. M. Bell, and J. C. Johnson. 2004a. Behavioral syndromes: an ecological and

891   evolutionary overview. Trends in ecology & evolution 19:372–8.

892   Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004b. Behavioral Syndromes: An

893   Integrative Overview. The Quarterly Review of Biology 79:241–177.

894   Sih, A., K. J. Mathot, M. Moirón, M. Wolf, P. Montiglio, and N. J. Dingemanse. 2015.

895   Animal personality and state – behaviour feedbacks : a review and guide for

896   empiricists. Trends in Ecology & Evolution 30:50–60.

897   Sprenger, D., N. J. Dingemanse, N. A. Dochtermann, J. Theobald, and S. P. W. Walker.

898   2012. Aggressive females become aggressive males in a sex-changing reef fish. Ecology

899   Letters 15:986–992.

900   Taborsky, B., and R. F. Oliveira. 2012. Social competence: An evolutionary approach.

901   Trends in Ecology and Evolution 27:679–688.

902   Team R Core. 2012. R: A language and environment for statistical computing. R

903   Foundation for Statistical Computing, Vienna, Austria, 2012.

904   van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and Allocation of Resources:

905   Their Influence on Variation in Life History Tactics. The American Naturalist 128:137.

906   Verbeek, M. E. M., A. Boon, and P. J. Drent. 1996. Exploration, aggressive behaviour

907   and dominance in pair-wise confrontations of juvenile male great tits. Behaviour

908   133:945–963.

909   Visscher, P. 2006. A note on the asymptotic distribution of likelihood ratio tests to test

910   variance components. Twin research and human genetics : the official journal of the

911   International Society for Twin Studies 9:490–495.

912   Webster, M. M., and A. J. W. Ward. 2011. Personality and social context. Biological

913   Reviews 2:759–773.

914   Wilson, A. D. M., E. M. Whattam, R. Bennett, L. Visanuvimol, C. Lauzon, and S. M.

915   Bertram. 2010. Behavioral correlations across activity , mating , exploration ,

916   aggression , and antipredator contexts in the European house cricket , Acheta

917   domesticus. Behavioral Ecology and Sociobiology 64:703–715.

918   Wilson, A. J., M. de Boer, G. Arnott, and A. Grimmer. 2011. Integrating personality

919   research and animal contest theory: Aggressiveness in the green swordtail

920   xiphophorus helleri. PLoS ONE 6:e28024.

921   Wilson, A. J., U. Gelin, M. Perron, and D. Réale. 2009. Indirect genetic effects and the

922   evolution of aggression in a vertebrate system Indirect genetic effects and the

923   evolution of aggression in a vertebrate system. Proceedings of the Royal Society B:

924   Biological Sciences 276:533–541.

925   Wilson, A. J., A. Grimmer, and G. G. Rosenthal. 2013. Causes and consequences of

926   contest outcome: Aggressiveness, dominance and growth in the sheepshead swordtail,

927   Xiphophorus birchmanni. Behavioral Ecology and Sociobiology 67:1151–1161.

928   Wolf, J. B., Brodie, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary

929   consequences of indirect genetic effects. Trends in Ecology and Evolution 13:64–69.

930   Wolf, J. B., E. D. I. Brodie, and A. J. Moore. 1999. Interacting Phenotypes and the

931   Evolutionary Process . II . Selection Resulting from Social Interactions. The American

932   Naturalist 153:254–266.

933   Wolf, M., and J. Krause. 2014. Why personality differences matter for social

934   functioning and social structure. Trends in Ecology and Evolution 29:306–308.

935   Wolf, M., and J. M. McNamara. 2013. Adaptive between-individual differences in social

936   competence. Trends in Ecology and Evolution 28:253–254.

937   Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and

938   evolution. Trends in Ecology & Evolution 27:452–61.

939

FIGURE LEGENDS

941   **Figure 1.** Models (1–9) of hypothesized relationships between behaviors (syndrome

942   structure). Unidirectional arrows represent causal relationships between variables,

943   bidirectional arrows represent correlations. Solid lines represent relationships present

944   across the whole set; dashed, dotted, and mixed lines represent relationships

945   expressed in specific syndrome structures. Model 1: null model of behavioral

946   independency (Coleman and Wilson 1998). Model 2: coping styles with 'proactive' and

947   'reactive' types (correlations among exploration, activity and aggression) (Koolhaas et

948   al. 1999; Coppens et al. 2010). Model 3: The dashed arrow is active; a modification of

949   model 2, where all behaviors including the indirect effects are expression of a general-

950   domain syndrome. Models 4-6: the dashed arrow alone is active in model 4, the mixed

951   arrow alone in model 5, both in model 6. Semi-independency of modules (Sih et al.

952   2004b) for different contests (social and non-social behaviors). Model 7: the dashed

953   arrow is active; combination of model 2 with reciprocal feedbacks on aggressiveness

954   (covariance between aggression and eliciting aggressiveness) (Moore et al. 1997;

955   Wilson et al. 2009). Models 8-9: the mixed arrow is active only in model 8, the dotted

956   arrow is active only in model 9; combination of model 2 with ideas from (Verbeek et al.

957   1996). Exploration, aggression, and activity are part of syndrome and either

958   exploration (8) or activity (9) has a direct of effect on aggressiveness of others.

959   **Figure 2**. Daily experimental timeline, showing a top view of the experimental setups

960   used to measure a) activity b) exploration and c) aggression.

961   **Figure 3.** Graphical illustration of the indirect effect of exploration behavior on

962   aggression. We present here correlations between BLUPs derived from the

963   multivariate mixed-effects model: individual-mean levels of exploration (x axis) and

964   aggression elicited in the opponents (y axis). Each point represents the BLUP of an

965   individual (in standard deviation units) with its associated standard error.

966   **Figure 4.** Parameter estimates of the structural equation model that best fitted our

967   data. For each variable, we report the variance explained by the SEM structure (R^2) and

968   factor loadings with the corresponding SE in parentheses. These represent how

969   behavioral responses are predicted to change based on changes to the underlying

970   syndrome structure.

971 **TABLES**

972 **Table 1.** Timetable of the daily experimental procedure (see the Methods for further

973 details). Each individual was subjected to this procedure for 12 consecutive days.

Order within day	Action/behavioral test	Location	Duration
1	Food and water removal + acclimation	Home container	30 min
2	Activity	Home container	1 hr
3	Transfer to exploration arena		1 min
4	Exploration	Exploration arena	1 hr
5	Shelter removal + acclimation	Exploration arena	10 min
6	Aggression	Exploration arena w/o divider	10 min

974 **Table 2.** The proportion of total phenotypic variation not attributable to fixed effects explained by focal identity (adjusted individual

975 repeatability; direct effects) and opponent identity (adjusted opponent repeatability; indirect effects), and the correlation between focal

976 and opponent identity effects. Positive values for this correlation indicate patterns where individuals that on average express a high value

977 for the given behavior also elicit an increased expression of this behavior in opponents. Estimates (with SE) are derived from univariate

978 mixed-effect models with random intercepts for focal and opponent identity as appropriate, and associated χ^2-values, degrees of

979 freedom (df), and values of P derived from likelihood ratio tests where the full model is compared to one where the random effect of

980 interested was excluded.

Trait	Individual repeatability (SE)	χ^2_{df}	P	Opponent repeatability (SE)	χ^2_{df}	P	Focal - opponent correlation (SE)	χ^2_{df}	P
Activity	**0.33** (0.09)	$65.60_{0.5}$	**<0.01**	-	-	-	-	-	-
Exploration	**0.40** (0.10)	$92.56_{0.5}$	**<0.01**	-	-	-	-	-	-
Weight	**0.46** (0.11)	$253.37_{0.5}$	**<0.01**	-	-	-	-	-	-
Approach	**0.19** (0.06)	$17.65_{1.5}$	**<0.01**	**0.16** (0.06)	$14.74_{1.5}$	**<0.01**	0.22 (0.26)	0.70_{1}	0.40
Chase	**0.09** (0.05)	$6.49_{1.5}$	**<0.05**	**0.12** (0.05)	$9.72_{1.5}$	**<0.05**	-0.34 (0.39)	0.71_{1}	0.40
Sing	0.07 (0.05)	$3.60_{1.5}$	0.11	0.05 (0.05)	$1.86_{1.5}$	0.28	-0.21 (0.56)	0.15_{1}	0.69

982   **Table 3.** Estimated among- and residual within-individual correlations (with associated SE) for two non-social behaviors (activity and

983   exploration), two social behaviors (aggressiveness and aggressiveness elicited in opponents), and weight. We present among-individual

984   correlations on the upper off-diagonals and within-individual correlations on the lower off-diagonals. Correlations printed in bold-face are

985   significant based on likelihood ratio tests derived from the multivariate model detailed in the main text. Note that the experimental setup

986   solely allowed for estimating of among-individual correlations with aggressiveness elicited in other individuals.

	Aggressiveness	Activity	Exploration	Weight	Aggressiveness elicited
Aggressiveness	-	**0.39** (0.18)	**0.39** (0.17)	**0.43** (0.16)	0.09 (0.22)
Activity	-0.02 (0.07)	-	**0.81** (0.08)	**0.17** (0.15)	0.16 (0.20)
Exploration	0.03 (0.07)	**0.17** (0.06)	-	0.22 (0.14)	**0.45** (0.17)
Weight	0.05 (0.06)	0.06 (0.06)	**0.13** (0.06)	-	-0.31 (0.18)

FIGURES
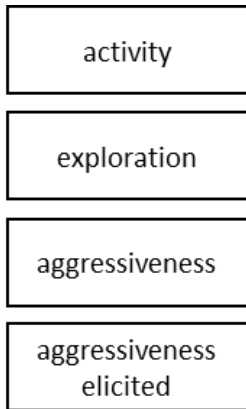
Model 1
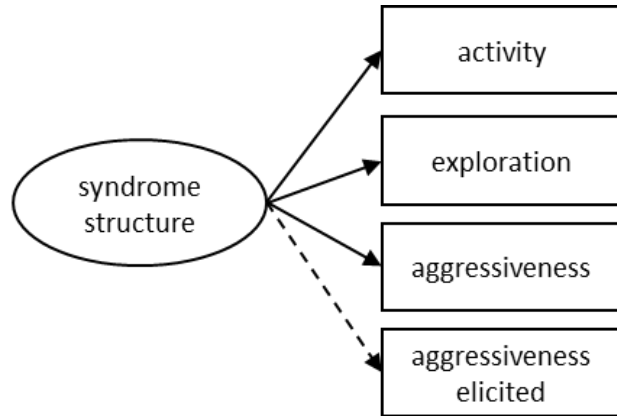
Models 2-3
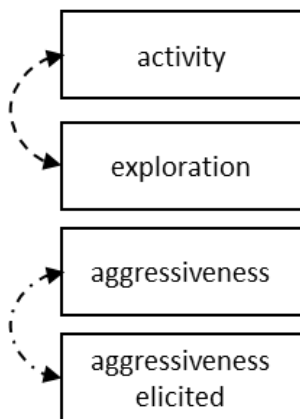
Models 4-6
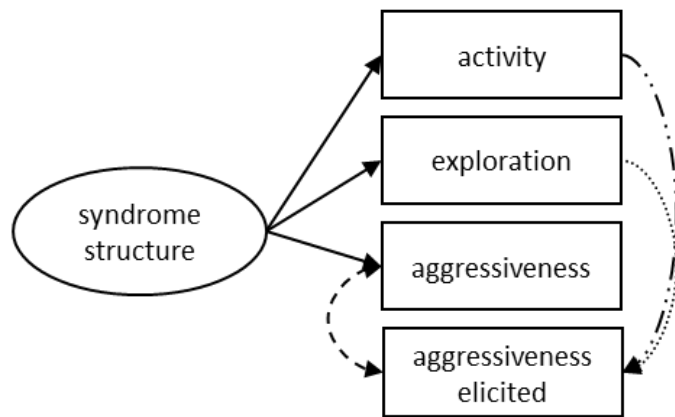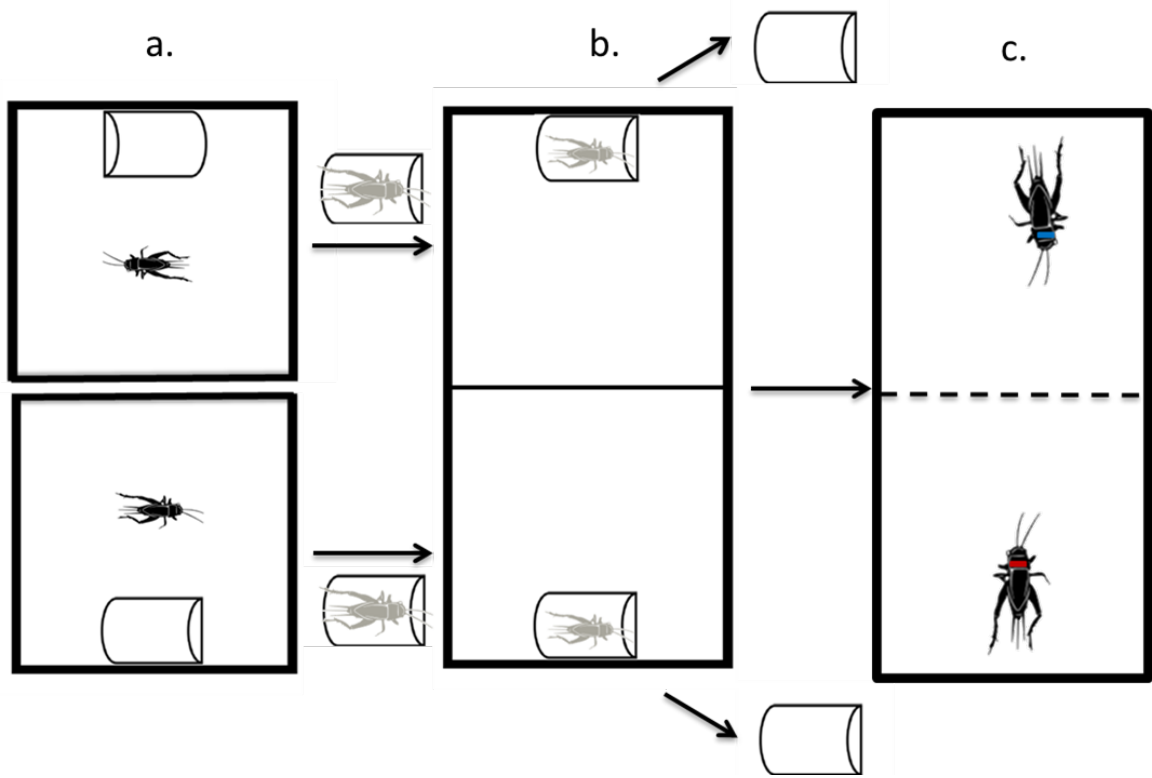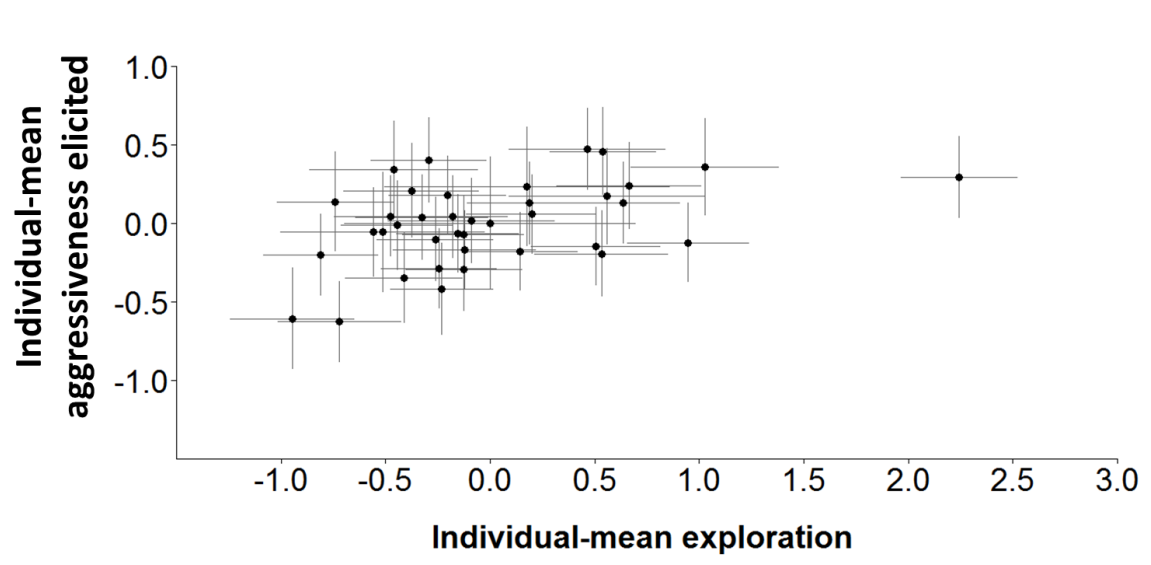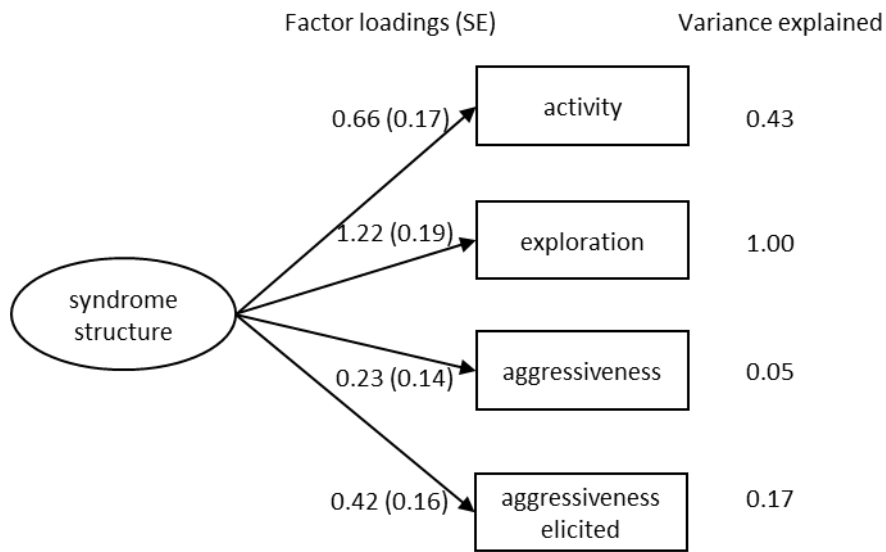
Models 7-9

Figure 1.

Figure 2.

Figure 3.

Figure 4.

987

SUPPLEMENTARY TEXT

989   As detailed in the main text, analyses of aggressiveness that estimate focal and

990   opponent identity effects typically focus on variation in the behavior expressed by the

991   (arbitrarily assigned) focal individual alone. Here we detail how we incorporated

992   information on the same behavior measured on the opponent in the statistical model

993   while avoiding pseudo-replication. We started with the following data structure, where

994   each line consisted of information regarding the identity of both individuals, one

995   arbitrarily called 'Individual A' and the other 'individual B', with associated information

996   regarding their aggressiveness:

trial ID	Individual A	Individual B	Aggressiveness A	Aggressiveness B
1	14	12	3	6

997   We then rearranged the data in the following way:

trial ID	Focal	Opponent	Dataset	Aggressiveness 1	Aggressiveness 2
1	14	12	1	3	NA
1	12	14	2	NA	6

998   In this re-ordered dataset, the data is printed over two lines, once viewing individual A

999   as the 'focal' individual in trial 1 (Dataset 1) and once viewing individual B as the 'focal'

1000   individual in trial 1 (Dataset 2). Importantly, the behavior of the individual dubbed

1001 'focal' in Dataset 1 was printed in another column (Aggressiveness 1) than the

1002 behavior of the individual dubbed 'focal' in Dataset 2 (column Aggressiveness 2). We

1003 then proceeded to estimate model parameters under the imposed assumption that all

1004 model parameters (fixed effect coefficients and (co)variance components) are equal

1005 for the homologous traits as defined in the two non-overlapping data sets (i.e.,

1006 Aggressiveness 1, Aggressiveness 2). Practically this can be achieved for a pair of

1007 homologous traits by fitting a bivariate mixed effect model with the following code in

1008 ASReml, which we have annotated in footnotes below:

1009 agg1 agg2 ~mu !r !{Trait.foc Trait.opp !}

1010 1 2 1

1011 0

1012 Trait 0 US !GPZP !=a0a !S2==1   #A

1013 0.5

1014 0   0.5

1015 Trait.foc 2

1016 4 0 US   !GPZPUZPZUZP !=a0ab0c0b0c   #B

1017 0.5

1018   0   0.5

1019   0.1   0   0.5

1020   0   0.1   0   0.5

1021   foc

1022   The !{Trait.tag Trait.opp !} command enables joining the focal and opponent variance-

1023   covariance matrix into a single matrix such that covariances between focal and

1024   opponent identity effects can be estimated.

1025   A – Residual covariance structure. Residual variances are constrained to be positive

1026   and equal for the two traits. A starting value of 0.5 is supplied. Since no line of data is

1027   informative for both traits the residual covariance is not estimable and is fixed

1028   (arbitrarily) to zero.

1029   B – Among-individual covariance structure. There are four random effects in the model

1030   (focal and opponent effects on two homologous traits) so a 4x4 covariance matrix is

1031   specified. Variances are constrained to be positive (starting value of 0.5 supplied for

1032   each), while covariance terms are identifiable between focal and opponent effects

1033   with each trait (starting value of 0.1 supplied). Covariance parameters for Aggression 1

1034   are constrained to equal those of Aggression 2. All other cross-trait covariance terms

1035   are fixed to zero.

1036 **SUPPLEMENTARY TABLES**

1037 **Table S1.** Parameter estimates (with standard errors) of fixed and random effects

1038 derived from our univariate models fitted to analyze variation in activity, exploration,

1039 weight, and aggressiveness (approach, chasing, singing). Values printed in bold face

1040 represent significant effects based either on Wald F tests (fixed effects) or likelihood

1041 ratio tests (random effects) detailed in the main text. Values of adjusted individual and

1042 opponent repeatability reported in Table 2 (main text) are derived from the univariate

1043 models printed here.

Table S1 continued

	Activity	Exploration	Weight	Approach	Chase	Sing
Fixed effects	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)
Intercept	-0.01 (0.20)	0.16 (0.22)	-0.21 (0.23)	0.33 (0.12)	0.07 (0.10)	0.06 (0.01)
Sequence	-0.03 (0.02)	**-0.04** (0.01)	**-0.04** (0.01)	**-0.07** (0.01)	-0.02 (0.02)	-0.01 (0.02)
Random effects	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)
Focal	**0.32** (0.11)	**0.40** (0.10)	**0.46** (0.11)	**0.19** (0.07)	**0.09** (0.05)	0.08 (0.05)
Opponent	-	-	-	**0.16** (0.07)	**0.12** (0.06)	0.05 (0.05)
Group	0.01 (0.07)	0.06 (0.10)	0.15 (0.15)	0.03 (0.09)	0.00 (0.00)	0.00 (0.00)
Date	0.00 (0.02)	0.00 (0.01)	**0.18** (0.06)	0.00 (0.03)	0.00 (0.00)	0.04 (0.09)
Residual	**0.66** (0.07)	**0.55** (0.08)	**0.22** (0.04)	**0.63** (0.07)	**0.78** (0.08)	**0.85** (0.09)
Covariance				Cov (SE)	Cov (SE)	Cov (SE)
Focal - Opponent	-	-	-	0.04 (0.05)	-0.03 (0.04)	-0.01 (0.03)

1045 **Table S2.** Estimated bivariate among-individual correlations for all traits included in our

1046 multivariate model (Table 3): activity, exploration, aggression, aggression elicited in others, and

1047 body weight. We print here the χ^2-value (associated degrees of freedom = 1 in all cases) and

1048 values of P associated with likelihood ratio tests (LRTs) detailed in the main text (Methods).

Traits	r (SE)	X^2_1	P
activity - exploration	0.81 (0.08)	18.2	**<0.001**
activity - aggression	0.39 (0.18)	3.88	**<0.05**
activity - aggression elicited	0.16 (0.20)	0.63	0.426
exploration - aggression	0.39 (0.17)	230.5	**<0.001**
exploration - aggression elicited	0.45 (0.17)	5.54	**<0.05**
aggression - aggression elicited	0.09 (0.22)	0.14	0.700
weight - activity	0.17 (0.15)	225.4	**<0.001**
weight - exploration	0.22 (0.14)	2.27	0.132
weight - aggression	0.43 (0.16)	5.66	**<0.05**
weight - aggression elicited	-0.31 (0.18)	2.58	0.110

1049 **Table S3.** Relative fit of nine candidate models (detailed in the main text) based on the Akaike's

1050 information criterion (AIC). We present each model's AIC-value relative to the model with the

1051 lowest AIC-value (ΔAIC), its weight, and relative likelihood.

Model	ΔAIC	Akaike Weight	Relative LL
3 - Full domain behavioural syndrome	0	0.75	1
9 – Behavioural syndrome with aggressiveness elicited only affected by exploration	2.35	0.23	0.31
2 - Behavioural syndrome with aggressiveness elicited independent	8.91	0	0.01
8 – Behavioural syndrome with aggressiveness elicited only affected by activity	9.90	0	0
7 – Behavioural syndrome with aggressiveness elicited linked only to aggressiveness	10.78	0	0
4 – General activity syndrome with social behaviours independent	11.62	0	0
6 – Independent social behaviours and general activity syndromes	13.33	0	0
1 – Behavioural independence	48.94	0	0
5 – Social behaviours syndrome with general activity behaviours independent	50.65	0	0

1052 **Table S4.** Estimated among-individual (a) and residual within-individual (b) variances and covariances/correlations (with SE) for two non-

1053 social behaviors (activity and exploration), two social behaviors (aggressiveness and aggressiveness elicited in opponents), and weight.

1054 We present variances on the diagonal, and covariances (correlations) on the lower (upper) off-diagonals, respectively.

1055 Covariances/correlations printed in bold-face are significant based on likelihood ratio tests derived from the multivariate model detailed

1056 in the main text.

a.	Aggressiveness	Activity	Exploration	Weight	Aggressiveness elicited
Aggressiveness	**0.21** (0.07)	**0.39** (0.18)	**0.39** (0.17)	**0.43** (0.16)	0.09 (0.22)
Activity	**0.11** (0.06)	**0.35** (0.06)	**0.81** (0.08)	**0.17** (0.15)	0.16 (0.20)
Exploration	**0.13** (0.06)	**0.33** (0.08)	**0.49** (0.10)	0.22 (0.14)	**0.45** (0.17)
Weight	**0.17** (0.07)	**0.08** (0.08)	0.13 (0.09)	**0.70** (0.13)	-0.31 (0.18)
Aggressiveness elicited	0.02 (0.04)	0.04 (0.05)	**0.13** (0.06)	-0.11 (0.07)	**0.18** (0.06)

Table S4 continued

| b.	Aggressiveness	Activity	Exploration	Weight
Aggressiveness	**0.61** (0.06)	-0.02 (0.07)	0.03 (0.07)	0.05 (0.06)
Activity	-0.01 (0.04)	**0.65** (0.06)	**0.17** (0.06)	0.06 (0.06)
Exploration	0.02 (0.04)	**0.10** (0.04)	**0.52** (0.04)	**0.13** (0.06)
Weight	0.03 (0.03)	0.03 (0.03)	**0.06** (0.03)	**0.35** (0.03)

1058 **Table S5.** Relative fit of three a posteriori considered models (detailed in the main text)

1059 based on the Akaike's information criterion (AIC). We present each model's AIC-value

1060 relative to the model with the lowest AIC-value (ΔAIC), its weight, and relative

1061 likelihood. Here we investigate how body weight is best incorporated into the best-

1062 fitting SEM presented in Table S3. For a visualization of each model's structure, see Fig.

1063 S1.

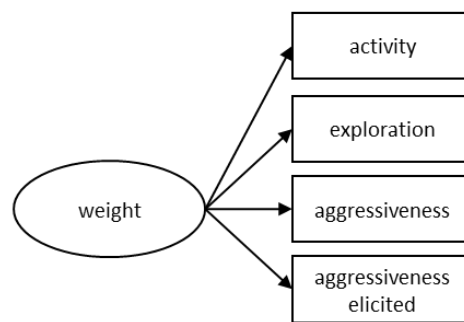| Model	ΔAIC	Akaike Weight	Relative LL
B – Weight as part of the full syndrome	0	0.73	1
A - Weight independent from full domain behavioural syndrome	1.98	0.27	0.37
C – Weight driving the behavioral syndrome	44.93	0	0

1064 **SUPPLEMENTARY FIGURES**
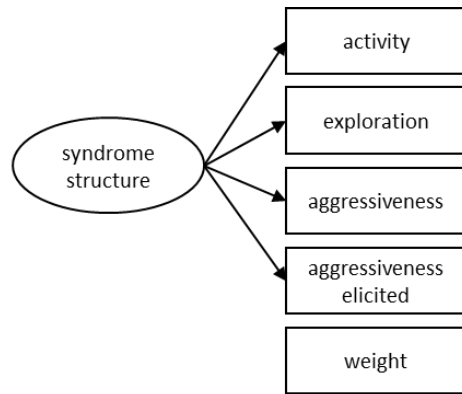
Model A
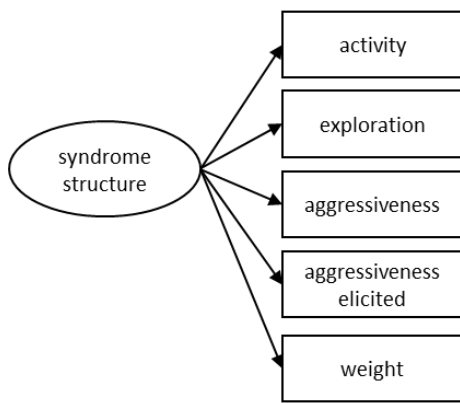
Model B

Model C

1065 **Figure S1.** Three a posteriori considered models. The relative fit of these models (Table

1066 S5) was considered to investigate how body weight is best incorporated into the best-

1067 fitting SEM presented in Table S3. Model A: weight is independent from the behavioral

1068 syndrome; model B: weight is part of the syndrome; model C: weight causes the

1069 behavioral syndrome.