Runaway evolution from male-male competition

Allen J. Moore[1] | Joel W. McGlothlin[2] | Jason B. Wolf[3]

[1]Department of Entomology, University of Georgia, Athens, Georgia, United States

[2]Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia, United States

[3]Milner Centre for Evolution and Department of Biology and Biochemistry, University of Bath, Bath, United Kingdom

Email: ajmoore@uga.edu, joelmcg@vt.edu, j.b.wolf@bath.ac.uk

Correspondence may be addressed to any author.

1 **Abstract**

2 Strikingly elaborate weapons and displays are widespread features of male contests for mates

3 across the animal kingdom. Male combat is familiar to students of behavior, and yet while we

4 understand how female mate choice results in a runaway process, how such evolutionary

5 extremes arise from male-male competition is unclear. In a quantitative genetic model of

6 sexual selection for a male signaling trait that mediates aggression in male-male contests, we

7 show that an honest indicator of aggression can generate selection on itself by altering the

8 social environment. This can cause selection to accelerate as the trait is elaborated, which can

9 ultimately lead to runaway evolution. Thus, the key unifying feature of runaway sexual

10 selection driven by either male-male competition or female mate choice is an evolving source

11 of selection provided by the social environment. Our model identifies simple conditions

12 generating runaway evolution and provides clear, testable predictions for empirical studies.

INTRODUCTION

Darwin's (1859, 1871) theory of sexual selection suggested that exaggerated, spectacular, and bizarre structures and behaviors found in males of many species evolve either because they enhance success in contests between males for access to females or because they are preferred by females when choosing mates. The suggestion that male-male competition is common was relatively uncontroversial; as Darwin (1871) wrote, "It is certain that amongst almost all animals there is a struggle between the males for the possession of the female. This fact is so notorious that it would be superfluous to give examples." In contrast, the ability of females to influence evolution through choice of partners was almost immediately questioned and continued to be controversial for decades after Darwin (Wallace 1889; Huxley 1938) . However, theoretical models of evolution via female choice (Lande 1981; Kirkpatrick 1982; Mead & Arnold 2004) and empirical research documenting female preference in nature (Andersson 1982, 1994; Rosenthal 2017) eventually led to mate choice becoming the dominant paradigm in studies of sexual selection. The development of formal mathematical models showing that male traits and female preferences can coevolve in self-reinforcing fashion, an idea first proposed by Fisher (1915, 1930), was particularly crucial to the acceptance of mate choice as an important evolutionary mechanism. The key component of the Fisher process is that female preference and a preferred male trait become genetically correlated. This can cause sexually selected male traits to evolve at ever-increasing speed, a pattern that has been referred to as an evolutionary "runaway" (Fisher 1930; Lande 1981; Bailey & Moore 2012) because the social environment evolves with the male trait influencing the social outcome.

Despite the current bias towards studies focused on mate choice, Darwin was not wrong about male-male competition. Members of entire taxa are characterized by highly modified sexually dimorphic structures that function only in male contests (e.g., Dermaptera,

38   Briceño & Eberhard 1995). Weapons can evolve to be massive and create real functional

39   constraints for the males that bear them, and such bizarrely elaborate and diverse structures

40   associated with duels are indeed found across the animal kingdom (Emlen 2008, 2014;

41   McCullough *et al.* 2016; O'Brien *et al.* 2018). In fact, male-male competition remains a more

42   common source of selection shaping male traits that influence mating success, and traits

43   expressed in male-male interactions can be as elaborate as those that are the target of female

44   preferences (Darwin 1871; Huxley 1938; Andersson 1994; Moore & Moore 2006; Emlen

45   2008, 2014; McCullough *et al.* 2016; O'Brien *et al.* 2018). However, we still lack robust

46   genetic models that may be used to generate testable predictions for the evolution of sexually

47   selected traits via male-male competition. Notably, the potential for male-male competition to

48   result in a runaway process that drives extreme trait elaboration remains unresolved.

49   Many elaborate male traits used in male-male contests, such as showy plumage

50   (Hagelin 2002), color (Seehausen & Schluter 2004), pheromones (Moore *et al.* 1997b), and

51   structures such as antlers (Wilkinson & Dodson 1997), horns (Emlen *et al.* 2005), forceps

52   (Briceño & Eberhard 1995), and claws (Sneddon *et al.* 1997) function as signals that may

53   provide information about some underlying qualities of the individuals, such as the

54   willingness or ability to fight (Parker 1974; Maynard Smith & Harper 1988; Maynard Smith

55   & Harper 2003; Emlen 2008, 2014). For example, there is often a positive association

56   between signals or weapons and other traits such as body size (McCullough *et al.* 2016;

57   O'Brien *et al.* 2018), making the signal or weapon an honest indicator of potential threat to an

58   opponent. As such, males are expected to adaptively modulate their behavior in response to

59   these signaling traits, escalating contests they are more likely to win and withdrawing from

60   ones they are more likely to lose. Because the effect of signaling traits inherently depends on

61   social context, such traits serve as both targets and sources of selection, potentially leading to

62   self-reinforcing and accelerating selection as occurs in the runaway process driven by female

63   preference (Lande 1981; Bailey & Kölliker 2019). However, despite insights from optimality

64   models (Parker 1974; Maynard Smith & Brown 1986; Maynard Smith & Harper 1988;

65   Maynard Smith & Harper 2003; Rutte *et al.* 2006), how this fundamental feature of extreme

66   elaboration—an evolving source of selection—may arise within male-male contests is

67   unclear.

68   Here, we utilize a framework that explicitly incorporates socially contingent trait

69   expression and fitness (Moore *et al.* 1997a; Wolf *et al.* 1999; McGlothlin *et al.* 2010) to

70   model trait evolution arising from male-male competition. We show that when honest signals

71   are used to modulate the behavior of competitors, male-male competition leads to

72   evolutionary elaboration of male traits. We identify the necessary and sufficient conditions for

73   trait elaboration to become a runaway process and outline predictions that can be empirically

74   tested to evaluate this scenario in natural systems. We show that sexual selection by male-

75   male competition can have features that are analogous to those of runaway sexual selection by

76   female choice; just as in female mate choice, the social environment in male-male contests

77   may generate a self-reinforcing source of selection on the traits that mediate the interaction,

78   potentially leading to self-sustaining and escalating selection.

MODEL

80   To capture the influence of the social environment in a model of male-male competition, we

81   assume that individuals adjust their behavior in response to the signaling trait values of their

82   social partners, an assumption that is supported empirically and theoretically (Parker 1974;

83   West-Eberhard 1979; Maynard Smith 1982; West-Eberhard 1983, 1984; Moore *et al.* 1997a;

84   West-Eberhard 2003; O'Brien *et al.* 2018; Tinghitella *et al.* 2018; Rico-Guevara & Hurme

85   2019; Wiens & Tuschhoff 2020). Because the social context (i.e., the social environment) is

4

86   constructed from traits of conspecifics, this flexible response to social context provides the

87   opportunity for indirect genetic effects (Moore *et al.* 1997a), which allow the social

88   environment itself to evolve (Moore *et al.* 2002; Wolf 2003; Bijma & Wade 2008;

89   McGlothlin *et al.* 2010). Evolutionary changes in the social environment can lead to

90   concerted evolution because the social environment can be a source of selection on the traits

91   that themselves compose the social environment (West-Eberhard 1979; Wolf *et al.* 1999;

92   Bailey & Kölliker 2019; Araya-Ajoy *et al.* 2020; McGlothlin *et al.* 2021). Such "social

93   selection" (West-Eberhard 1979, 1983, 1984; Wolf *et al.* 1999; Bijma & Wade 2008;

94   McGlothlin *et al.* 2010) is expected to arise whenever traits act as both the agents and the

95   targets of selection.

96   We assume that males use a trait (designated by the subscript S) to assess some

97   underlying potential threat of their opponents in social contests. Such a trait can be a weapon

98   or display that is used as a signal. Possible examples include traits such as a plumage badges,

99   exaggerated weapons, or vocal or chemical signals. Elaboration of the signal may consist of

100   an increase in size or complexity, although for heuristic simplicity, we discuss the evolution

101   of increased signal size. Males also vary in the underlying quality trait that represents an

102   index of their fighting ability or some other aspect of their phenotype that determines the

103   threat they represent to their opponent in a contest. We describe this trait as body size

104   (designated by the subscript B) for simplicity. As such, the signal may be genetically

105   correlated to body size, providing a degree of signal honesty. Males respond to the assessment

106   of the signal by modulating their behavior toward their opponent ("aggression," designated by

107   the subscript A) within the contest because the signal provides information on the quality of

108   their opponent, and hence provides information on the likelihood that they would win an

109   escalated contest (see below).

110 We assume that both signal size (z_S) and body size (z_B) are normally distributed

111 metric traits influenced by many loci of small effect. Expression of these traits can be

112 partitioned into heritable additive genetic effects (denoted a_S and a_B) and general non-

113 heritable (environmental and nonadditive genetic) effects (denoted e_S and e_B). We assume

114 that neither signal nor body size changes as a result of the social interaction. An individual's

115 total phenotypic value for each trait is then described by a simple sum of the heritable and

116 non-heritable components, or

117 $$z_i = a_i + e_i, \tag{1}$$

118 where a_i is normally distributed with mean $\bar{a}_i$ and variance G_{ii} and e_i is normally distributed

119 with mean 0 and variance E_{ii}. We make the standard quantitative genetic assumption that

120 heritable and non-heritable components are uncorrelated. We assume that signal may be

121 genetically correlated to body size, providing a degree of signal honesty, which is quantified

122 by the covariance between signal size and body size (G_{SB}).

123 For simplicity, we model the outcome of pairwise duels between males drawn at

124 random from the population. Our model is easily generalized to include multiple interactions

125 between males (Appendix). We assume that aggressive behavior (z_A) in these male-male

126 contests is context dependent and influenced by the relative signal size of the competing

127 males, as suggested by West-Eberhard (1979, 1983, 1984). This assumption is well supported

128 by optimality models and empirical studies (Huxley 1938; Parker 1974; Riechert 1984;

129 Sneddon *et al.* 1997; Maynard Smith & Harper 2003; Emlen 2008, 2014). The phenotypic

130 value of aggression can thus be written as

131 $$z_A = a_A + e_A + \delta_{AS}(z_S - z'_S), \tag{2}$$

132 where a_A and e_A represent standard additive genetic and uncorrelated non-heritable

133 components, respectively, z_S is the signal of the focal individual, z'_S is the signal of the focal

6

134   individual's opponent. Here and elsewhere, terms with primes indicate a value assigned to the

135   focal individual's opponent. The coefficient δ_{AS} measures the influence of the difference in

136   signal size on the expression of aggressive behavior. Thus, δ_{AS} is analogous to the ψ term in

137   standard interacting phenotype models (Moore *et al.* 1997a), but differs because it depends

138   upon the value of an interactant's phenotype relative to the focal individual. Because signal

139   size is heritable, the third term in Eq. **2** includes both a modification of the direct genetic

140   effect ($\delta_{AS} a_S$) and an indirect genetic effect ($-\delta_{AS} a_S'$), which is defined as the effect of a

141   social interactant's genes on the expression of a focal individual's phenotype (Moore *et al.*

142   1997a). We describe the relationship between this model and the standard model of indirect

143   genetic effects in the Appendix.

144   Because it is conditional and adjusted depending on the social context, the underlying

145   additive genetic value of aggression is assumed to be uncorrelated to both signal size and

146   body size ($G_{SA} = G_{BA} = 0$). However, the conditional expression of aggression leads males

147   with larger signals and/or larger body size to be more aggressive on average (and vice versa).

148   This can be viewed as the individual with the larger signal being more willing to escalate an

149   encounter, while the individual with the smaller signal tends to retreat from the interaction.

Selection imposed by male-male competition

151   In social interactions, associations between traits and fitness may cause selection via two

152   pathways, nonsocial selection (quantified by the gradient β_N), which arises from effects of a

153   focal individual's traits on its own fitness, and social selection (quantified by the gradient β_S),

154   which arises from the effects of an opponent's traits on the fitness of a focal individual (Wolf

155   *et al.* 1999). When both are present, individual relative fitness can be written as

156    $$w = w_0 + \mathbf{z}^T \boldsymbol{\beta}_N + \mathbf{z'}^T \boldsymbol{\beta}_S + \varepsilon, \tag{3}$$

157   where w_0 is an intercept, $\mathbf{z}$ and $\mathbf{z}'$ are column vectors of focal and opponent traits, $\boldsymbol{\beta_N}$ and $\boldsymbol{\beta_S}$

158   are vectors of nonsocial and social selection gradients, ε is an uncorrelated error term, and the

159   superscript T denotes transposition (Wolf *et al.* 1999). Expressing relative fitness using Eq. 3

160   has two distinct advantages. First, selection gradients can be estimated in natural populations

161   using multiple regression (Lande & Arnold 1983; Wolf *et al.* 1999; Formica *et al.* 2011;

162   Fisher & Pruitt 2019), allowing our model to generate testable predictions. Second, selection

163   gradients can be combined with genetic parameters to predict short-term evolutionary

164   response to selection (Lande & Arnold 1983; Bijma & Wade 2008; McGlothlin *et al.* 2010).

165   While Eq. 3 provides a general framework for capturing sources of selection, to

166   understand the origin and properties (i.e., the magnitude and direction) of these selection

167   gradients, we can use evolutionary game theory to write a mechanistic expression for relative

168   fitness based on the costs and benefits arising from male-male contests with signaling,

169      $$w = w_0 + b_A(z_A - z_A') - c_A z_A z_A' - c_B z_A' z_B' - c_S(\bar{z}_S - \theta_S)z_S + \varepsilon, \qquad (4)$$

170   where terms including b represent fitness benefits and terms including c represent fitness

171   costs. In Eq. 4, the benefit term and the first cost term derive from the hawk-dove model of

172   evolutionary game theory (Maynard Smith & Price 1973; Maynard Smith 1982; McGlothlin

173   *et al.* 2021). The coefficient b_A is the fitness benefit of winning a contest, which we assume

174   derives from greater access to females. In a contest, access to females is determined by a focal

175   individual's aggression relative to its opponent. Multiplying b_A by $(z_A - z_A')$ reflects the fact

176   that the probability of winning a contest increases as a male becomes increasingly more

177   aggressive than its opponent. The term $c_A z_A z_A'$ is the fitness cost of aggression associated with

178   escalation of encounters. Logically, an individual pays a cost for acting aggressive that

179   depends on the level of aggression shown by its opponent. A second fitness cost $(c_B z_A' z_B')$

180   reflects the fact that the fitness impact of aggression by an opponent (z_A') depends on the size

181   of the opponent (z_B'). This cost, which we call the threat of the opponent, derives from the fact

182   that larger males impose a greater risk of harm by being aggressive than do smaller males.

183   Finally, we assume that a third cost ($c_S(\bar{z}_S - \theta_S)z_S$) arises from natural selection favoring

184   some optimal trait value (θ_S), which therefore will oppose signal elaboration. Following a

185   Gaussian model of selection (Lande 1976, 1979), natural selection against elaborate signals

186   becomes stronger as the population mean of the signal ($\bar{z}_S$) becomes further away from its

187   naturally selected optimum (θ_S). Although we do not do so here, this term could be replaced

188   with a multivariate Gaussian term (Lande 1979) to add naturally selected optima for

189   aggression and body size.

190   Because selection gradients are equivalent to partial regression slopes, we can use

191   partial derivatives of Eq. 4 with respect to focal and opponent traits (evaluated at the

192   population mean) to calculate nonsocial and social selection gradients (McGlothlin *et al.*

193   2021). Taking these derivatives, we find nonsocial selection gradients for each trait to be

194     $\beta_{N_S} = -c_S(\bar{z}_S - \theta_S)$ (5a)

195     $\beta_{N_B} = 0$ (5b)

196     $\beta_{N_A} = b_A - c_A\bar{z}_A$ (5c)

197   and social selection gradients to be

198     $\beta_{S_S} = 0$ (6a)

199     $\beta_{S_B} = -c_B\bar{z}_A$ (6b)

200     $\beta_{S_A} = -b_A - c_A\bar{z}_A - c_B\bar{z}_B.$ (6c)

201   In other words, males with large signals are selected against via nonsocial selection but

202   interacting with such males does not directly impose social selection. Body size is not under

203   direct nonsocial selection but imposes a fitness cost via social selection that increases with the

9

204   population mean of aggression. Nonsocial selection favors aggression until the benefits of

205   aggression are outweighed by the costs, while social selection imposed by opponent

206   aggression is always negative, representing a net fitness cost. This gradient becomes

207   increasingly negative as the population mean aggression and body size increase. These

208   selection gradients suggest that signal size itself experiences no direct sexual selection. If

209   signal size increases, it must do so as an indirect response to selection on a correlated trait.

Evolutionary response to selection

211   Selection within a generation is translated into an evolutionary response across generations

212   through the association between the phenotype, upon which selection acts, and the genotype,

213   which contributes to the inheritance of the traits across generations. In quantitative genetics,

214   this genotype-phenotype relationship is most often summarized by the additive genetic

215   variance, which is used to predict evolutionary response to selection across generations

216   (Lande & Arnold 1983; Arnold 1994). However, for traits expressed in social interactions, we

217   must also consider social pathways to fitness, which arise from indirect genetic effects and

218   social selection, when calculating response to selection (Moore *et al.* 1997a; Bijma & Wade

219   2008; McGlothlin *et al.* 2010). Because the model of phenotypic modification described in

220   Eq. 2 deviates from the standard model of indirect genetic effects, we develop a general

221   equation for response to selection in the Appendix (Eq. 20). Using this equation, the response

222   to selection for the three traits in our model can in general be written as

223    $$\Delta \bar{z}_S = \frac{1}{2} G_{SS} \left(\beta_{N_S} + \delta_{AS}(\beta_{N_A} - \beta_{S_A}) \right) + \frac{1}{2} G_{SB} \beta_{N_B} \qquad (7a)$$

224    $$\Delta \bar{z}_B = \frac{1}{2} G_{BB} \beta_{N_B} + \frac{1}{2} G_{SB} \left(\beta_{N_S} + \delta_{AS}(\beta_{N_A} - \beta_{S_A}) \right) \qquad (7b)$$

225    $$\Delta \bar{z}_A = \frac{1}{2} G_{AA} \beta_{N_A}. \qquad (7c)$$

226   The multiplier ½ in Eq. 7 arises because selection is acting only on males. Eq. 7a shows that

227   modification of aggressive behavior in response to the signaling trait (δ_{AS}) causes both

228   nonsocial and social selection gradients for aggression to contribute to signal evolution. This

229   behavioral modification thus effectively causes both a direct genetic correlation between

230   signaling and aggression and a nonrandom association between the genetic effect on

231   aggression in the focal individual and the genetic effect on the signal in its opponent. This

232   behavioral modification also contributes to evolution of body size when the signal is honest

233   ($G_{SB} > 0$; Eq. 7b). In contrast, behavioral modification does not contribute to evolution of

234   aggression (Eq. 7c).

235   By substituting Eqs. 5-6 into Eq. 7, we can predict evolutionary change using our

236   mechanistic fitness model (Eq. 4):

237    $\Delta \bar{z}_S = \frac{1}{2} G_{SS} \big(\delta_{AS}(2b_A + c_B \bar{z}_B) - c_S(\bar{z}_S - \theta_S) \big)$ (8a)

238    $\Delta \bar{z}_B = \frac{1}{2} G_{SB} \big(\delta_{AS}(2b_A + c_B \bar{z}_B) - c_S(\bar{z}_S - \theta_S) \big)$ (8b)

239    $\Delta \bar{z}_A = \frac{1}{2} G_{AA} (b_A - c_A \bar{z}_A).$ (8c)

240   Eq. 8a shows that when fitness is defined as in Eq. 4, evolution of the signaling trait beyond

241   its naturally selected optimum depends crucially on behavioral modification. If males do not

242   change their behavior in response to the signal (i.e., if $\delta_{AS} = 0$), the population mean of the

243   signaling trait cannot increase. From Eq. 8b, the evolution of body size depends on both δ_{AS}

244   and the presence of signal honesty (i.e., genetic covariance between signal and body size,

245   G_{SB}). Eqs. 8a-b also show that evolution of the signaling trait and of male body size is

246   potentially open-ended because the evolutionary response to selection for each trait becomes

247   stronger as the population mean body size increases. In contrast, from Eq. 8c, the evolution of

248   aggression is self-limiting because selection depends on the balance of the benefits and costs

249   of aggression, the latter of which become more intense as mean aggression intensifies. This

11

250   observation suggests that both signal size and body size may experience runaway evolution if

251   the benefits of aggression and the threat of the opponent are strong enough to outweigh

252   natural selection against elaborate signals, whereas aggression should always tend to quickly

253   evolve to an equilibrium value.

254   To solve for equilibrium and to explore the conditions for such a runaway, we set Eqs.

255   8a-c equal to zero and solve for the equilibrium mean of each trait ($\hat{z}_i$), yielding

256    $\hat{z}_S = \theta_S + \delta_{AS} 2 b_A + \delta_{AS} \frac{c_B}{c_S} \hat{z}_B$ (9a)

257    $\hat{z}_B = \frac{c_S}{\delta_{AS} c_B} (\hat{z}_S - \theta_S) - \frac{2 b_A}{c_B}$ (9b)

258    $\hat{z}_A = \frac{b_A}{c_A}.$ (9c)

259   As predicted, aggression will always reach a stable equilibrium whenever there is a cost of

260   aggression (Eq. 9c, Fig. 1). Eqs. 9a-b predicts a line of equilibria for signal size and body size,

261   because their evolutionary change is completely intertwined with the relationship $\Delta \bar{z}_B =$

262    $\frac{G_{SB}}{G_{SS}} \Delta \bar{z}_S$ (Fig. 1). The slope of the line of equilibria predicting mean signal size from mean

263   body size, and hence the evolutionary allometry of signal size, is $\delta_{AS} \frac{c_B}{c_S}$. This relationship

264   indicates that when comparing population means through time or across space, positive

265   allometry (i.e., a slope greater than unity) is predicted when the strength of behavioral

266   modification multiplied by the threat of the opponent ($\delta_{AS} c_B$) is greater than the strength of

267   natural selection on signal size (c_S). In general, when male behavior is more strongly

268   dependent on the signal of their opponent (i.e., when δ_{AS} is larger), more elaborate signals are

269   expected at equilibrium (Fig. 2).

270   Whether an evolving population will reach a predicted equilibrium or overshoot it also

271   depends crucially on the rate of evolution of body size versus natural selection on signal size.

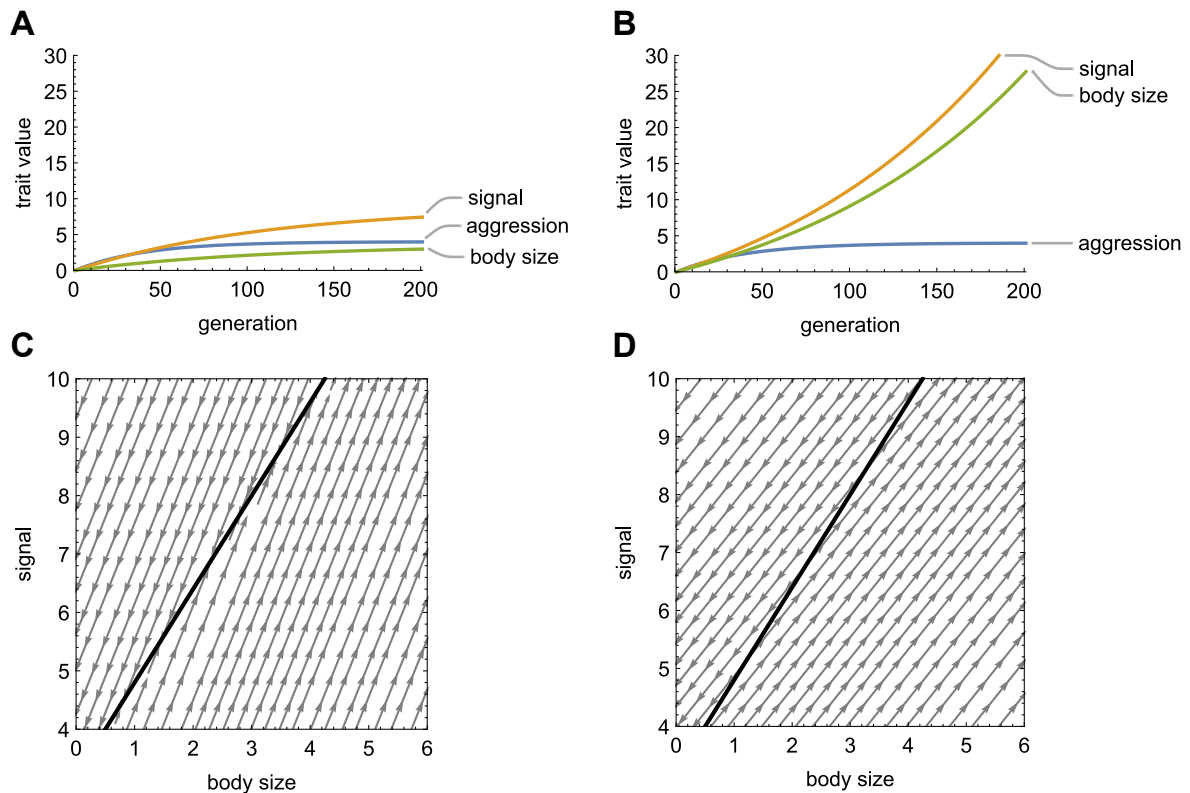272   Specifically, from Eq. 8a, in order for runaway evolution to occur, body size must evolve fast

FIGURE 1   Evolution of a male signal, body size, and aggression in response to male-male competition. Panels A and B show evolutionary trajectories for each trait over 200 generations, and panels C and D show predicted lines of equilibria (heavy line) and their stability (gray arrows). In all panels, all three traits have the same genetic variance ($G = 1$), benefit ($b_A = 0.2$) and cost of aggression ($c_A = 0.05$), fitness cost deriving from the threat of a male's opponent ($c_B = 0.2$), cost of signal size ($c_S = 0.05$; with naturally selected optimum $\theta_S = 0$), and a responsiveness of aggression to body size ($\delta_{AS} = 0.4$). The line of equilibria is calculated from Eq. 9a using these values. In panels A and C, signal size is weakly correlated with body size ($G_{SB} = 0.4$), while in panels B and D, the two traits are more strongly correlated ($G_{SB} = 0.8$). When the genetic correlation between signal size and body size is weak, all three traits reach equilibria (A), with equilibrium aggression predicted solely by costs and benefits. Signal size and body size reach a point on the predicted line of equilibrium (C) that differs depending on their starting values. When the genetic correlation is strong, aggression still reaches an equilibrium, but signal size and body size run away together (B), overshooting the predicted line of equilibria (D). As in Fisherian selection from female mate choice (Lande 1981), male-male competition can drive traits to runaway elaboration or extinction when the line of equilibria is unstable (D).
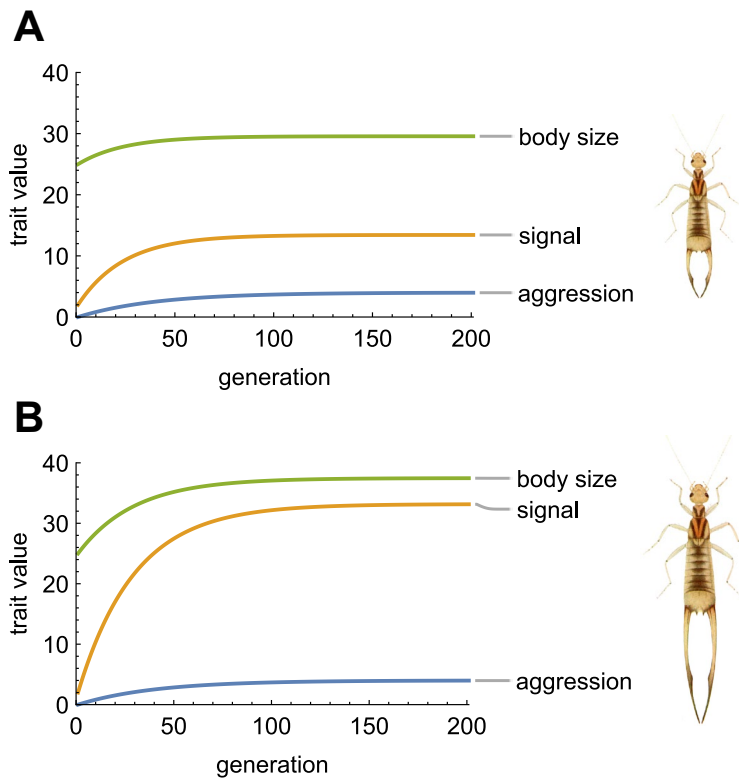
FIGURE 2   Stronger dependence of male aggressive behavior leads to more elaborate traits at equilibrium. Panel A illustrates a relatively weak influence of opponent signal on male aggression ($\delta_{AS} = 0.4$), while panel B illustrates a stronger influence ($\delta_{AS} = 0.8$). In each panel, we use starting values for traits relevant to the highly sexually dimorphic earwig *Labidura riparia*, which uses its forceps as a signaling trait and is shown to the right of each panel (drawing modified from Lucas 1920). Other parameters are the same as Fig. 1A. When the influence of opponent signal is weak (A), both body size and signal show a moderate evolutionary increase. When the influence is stronger (B), both body size and signal increase more, but the final signal size is much larger relative to body size. The highly elaborate elongate forceps in panel B may be found in other earwig species like *Forcipula gariazzi*.

273   enough that $\delta_{AS}(2b_A + c_B\bar{z}_B) > c_S(\bar{z}_S - \theta_S)$ regardless of the population mean signal size.

274   Because b_A and θ_S are constants, this occurs when $\delta_{AS}c_B\Delta\bar{z}_B > c_S\Delta\bar{z}_S$, or equivalently, when

275     $$\frac{G_{SB}}{G_{SS}}\delta_{AS}c_B > c_S. \tag{10}$$

276   This result is also achievable by solving for the condition generating a negative eigenvalue of

277   the Jacobian of $\Delta\bar{z}$, which indicates an unstable equilibrium (Lande 1981; Bailey & Kölliker

278   2019). The condition in Eq.10 indicates that runaway evolution of a signal may occur when it

279   is honest (G_{SB} is strong and positive), when it modifies aggressive behavior of social partners

280   ($\delta_{AS} > 0$), and when aggression imposes a fitness cost that increases when opponents are

281   larger (c_B). Fig. 1 illustrates a scenario in which the predicted outcome (equilibrium or

282   runaway) depends upon the value of the degree of signal honesty (i.e., the genetic covariance

283   G_{SB}).

284   **DISCUSSION**

285   Our model provides explicit conditions for sexual selection arising from male-male

286   competition to result in elaborate signals and runaway evolution. We model the origin of costs

287   and benefits associated with male traits mediating male-male interactions using

288   considerations from evolutionary game theory, which allows us to derive expressions for

289   natural and social selection gradients that reflect the mechanistic properties of male contests.

290   We then incorporate these expressions for selection into a model of trait genetics based on the

291   interacting phenotypes framework, which accounts for the influence of indirect genetic effects

292   arising from interactions with an opponent. Elaboration of a signal occurs whenever males

293   adjust their level of aggression based on the signal of an opponent, and runaway evolution

294   occurs when the genetic correlation between signal size and body size is large (i.e., the signal

295   is honest), when aggression in a social partner is modified based on the focal male signal, and

15

296   when aggression is costly when the opponent is larger (Eq. 10; Fig. 1, 2). In contrast,

297   aggression always reaches an equilibrium, both because the fitness benefit of aggression is

298   relative to that of the opponent and because of the fitness costs of escalated contests. Limits to

299   runaway evolution of the signaling trait depend on the strength of natural selection opposing

300   signal elaboration, which may arise through costs of producing or bearing the signal.

301   Our model provides predictions that are testable in natural populations. Specifically,

302   we expect the evolution of elaborate signaling traits that resolve duels between males to

303   evolve when three conditions are present. First, signals should be reliable predictors of body

304   size or some other proxy of fighting ability. Indeed, such signal honesty, which is often

305   characterized as positive allometry (McCullough *et al.* 2016; O'Brien *et al.* 2018) or a

306   positive genetic correlation (Clark & Moore 1995; McGlothlin *et al.* 2005; Laidre &

307   Johnstone 2013) between size and signal, is a common feature of traits involved in male-male

308   competition. Second, males must modify their behavior in response to their opponent's

309   signal. We assume that males increase their aggression when encountering an opponent with a

310   smaller signal than their own and reduce their aggression when encountering an opponent

311   with a larger signal. Such adjustment is common in species that resolve contests via limited

312   fights or displays (Darwin 1871; West-Eberhard 1979, 1983; Emlen 2008, 2014). In our

313   model, this phenomenon alters the relationship between genotype and phenotype, causing a

314   net force of social selection to contribute to signal evolution (Eqs. 7a, 8a). Finally, we expect

315   social selection to be imposed via the aggression of opponents. This selection becomes

316   stronger as male body size or fighting ability evolves due to the threat of escalation of fights

317   with large opponents. Mean level of aggression need not change if the threat escalates. Our

318   model makes specific predictions for the signs of these gradients when selection on signal

319   size, body size, and aggression can all be measured (Eqs. 5-6). Most crucially, our model

320   predicts negative social selection gradients for both body size and aggression, which reflect

16

321   the costs of escalated contests. In populations that are experiencing an evolutionary runaway,

322   these gradients should become stronger as body size and signal size coevolve. Although few

323   studies have measured social selection gradients, the limited evidence that exists supports the

324   existence of negative social selection gradients imposed by competitors (Formica *et al.* 2011;

325   Fisher & Pruitt 2019).

Parallels to models of female choice

327   The results of our model are conceptually analogous to models of runaway sexual selection

328   via female choice, suggesting some key parallels between the processes. Both our model and

329   Lande's (1981) model of female choice, which was the first formal model of Fisher's

330   runaway process, result in lines of equilibria that may be stable or unstable depending on the

331   genetic parameters. For the scenario of relative mate preference in Lande's model, the line of

332   equilibria for a male trait ($\hat{z}$) and a female preference ($\hat{y}$) can be written as

333     $$\hat{z} = \theta + \frac{b_{SS}}{c_{NS}}\hat{y} \qquad\qquad\qquad (11)$$

334   where θ is the natural selection optimum, b_{SS} is the strength of sexual selection, and c_{NS} is the

335   strength of natural selection. Eq. 11 directly parallels Eq. 9a from our model and emphasizes

336   that in male-male competition, the force of sexual selection is provided not by direct female

337   choice but by male body size (or some other measure of willingness or ability to engage in

338   aggression). In male-male competition, the threat of the opponent (c_B) leads to social

339   selection, which is indirectly translated into evolutionary change in male signals via the

340   parameter δ_{AS}, measuring the dependence of aggression on relative signal size of two

341   competing males.

342   Similarly, the condition for runaway evolution of male traits and female preference

343   driven by mate choice in Lande's model can be written as

17

344 $\quad \frac{B}{G} b_{SS} > c_{NS},$ (12)

345   where B represents the genetic covariance between male trait and female preference and G

346   represents genetic variance of the male trait (Maynard Smith & Harper 2003). The condition

347   in Eq. 12 directly parallels the condition in Eq. 10, emphasizing again that in male-male

348   competition, $\delta_{AS} c_B$ provides the force of social selection that indirectly leads to an

349   evolutionary increase in male signal size. Both types of runaway evolution are driven by

350   genetic covariance. In mate choice, runaway is driven by the covariance between the sexes

351   that arises from choosy females mating with attractive males, but in male-male competition,

352   this effect arises directly from signal honesty, i.e., the genetic covariance between a signaling

353   trait and the threat it signals. Moreover, if the mean level of aggression does not change, in

354   male-male competition increasing costs are associated only with the increasingly elaborated

355   signal. This may occur when aggression is not expressed outside of male-male competition

356   and when limited fights settle contests (Maynard Smith & Harper 1988; Maynard Smith &

357   Harper 2003). These are common conditions (Parker 1974; West-Eberhard 1983, 1984;

358   Maynard Smith & Harper 1988; Andersson 1994), suggesting that runaway from male-male

359   competition may occur frequently (McCullough *et al.* 2016; Rico-Guevara & Hurme 2019).

360   **Conclusion**

361   Ritualized displays and elaborated signals associated with the potential for aggression are

362   readily observed in nature and their importance often obvious and spectacular (Darwin 1871;

363   Parker 1974; Maynard Smith & Harper 1988; Maynard Smith & Harper 2003; Emlen 2008,

364   2014). Yet the details of how these might evolve have been unclear. Previous optimality

365   models have shown that overt aggression can be ameliorated by conventional signals (Parker

366   1974; Maynard Smith 1982; Maynard Smith & Harper 1988; Maynard Smith & Harper 2003;

367   Rutte *et al.* 2006), and verbal models have proposed that signaling traits associated with

368   male-male competition evolve exaggerated expression because social selection is intense

369   (West-Eberhard 1979, 1983, 1984). Male-male competition may well result in intense

370   selection (Maynard Smith & Brown 1986) as mating can be highly skewed toward one or a

371   few males in a population (Darwin 1871; Andersson 1994; Shuster & Wade 2003), but this

372   alone is insufficient to result in exaggerated traits. Our model shows that feedback between

373   the behavioral and morphological traits mediating male-male competition create runaway

374   evolution. Thus, the unifying feature of runaway sexual selection by both male-male

375   competition and female mate choice is an evolving source of selection provided by the social

376   environment.

377   **APPENDIX**

378   **General equation for response to selection**

379   Here, we develop a general model for evolution when trait expression depends upon the

380   difference between a focal individual's own traits and traits of another individual encountered

381   in the context of a social interaction. This model is directly applied to male-male contests in

382   the main text and may be useful for considering many other types of social interactions. First,

383   consider a vector of traits ($\mathbf{z}$) whose expression can be decomposed into three components: a

384   vector of additive genetic effects ($\mathbf{a}$), a vector of environmental effects ($\mathbf{e}$), and a social

385   response term that depends on the difference between the traits of the focal individual and

386   those of a social interactant ($\mathbf{z}'$):

387    $$\mathbf{z} = \mathbf{a} + \mathbf{e} + \boldsymbol{\delta}(\mathbf{z} - \mathbf{z}'). \tag{13}$$

388   The matrix $\boldsymbol{\delta}$ consists of components δ_{ij} that translate the effect of differences in trait j into

389   expression of trait i. Similarly, the phenotype of the social partner can be written as

390    $$\mathbf{z} = \mathbf{a}' + \mathbf{e}' + \boldsymbol{\delta}(\mathbf{z}' - \mathbf{z}). \tag{14}$$

391   As we show below, because the term $\boldsymbol{\delta}(\mathbf{z} - \mathbf{z}')$ in Eqs. 13-14 contains phenotypes of both

392   individuals, it consists of a combination of direct and indirect genetic effects.

393   To calculate a response to selection for traits expressed as in Eq. 13, we first solve for

394   the multivariate phenotypic mean. Assuming that environmental effects have a mean of zero,

395   the trait mean is

396    $$\bar{\mathbf{z}} = \bar{\mathbf{a}} + \boldsymbol{\delta}(\bar{\mathbf{z}} - \bar{\mathbf{z}}) = \bar{\mathbf{a}}, \tag{15}$$

397   which means that the population trait mean will depend only on the mean additive genetic

398   value. The vector of total breeding values ($\mathbf{A}$), which represents the genetic contribution to the

399   population mean and is used to calculate evolutionary responses to selection, is equivalent to

400   the vector of additive genetic effects ($\mathbf{a}$). Next, to derive an explicit definition of the

401   phenotype, we first use substitution to write

$$\boldsymbol{\delta}(\mathbf{z} - \mathbf{z}') = (\mathbf{I} - 2\boldsymbol{\delta})^{-1}\boldsymbol{\delta}(\mathbf{a} + \mathbf{e} - \mathbf{a}' - \mathbf{e}') \tag{16}$$

403   where $\mathbf{I}$ is the identity matrix. After some algebra, Eq. 16 allows us to write explicit

404   definitions of the two phenotypes as

$$\mathbf{z} = (\mathbf{I} - 2\boldsymbol{\delta})^{-1}((\mathbf{I} - \boldsymbol{\delta})(\mathbf{a} + \mathbf{e}) - \boldsymbol{\delta}(\mathbf{a}' + \mathbf{e}')) \tag{17}$$

406   and

$$\mathbf{z}' = (\mathbf{I} - 2\boldsymbol{\delta})^{-1}((\mathbf{I} - \boldsymbol{\delta})(\mathbf{a}' + \mathbf{e}') - \boldsymbol{\delta}(\mathbf{a} + \mathbf{e})). \tag{18}$$

408   Response to selection can then be calculated following McGlothlin *et al.* (McGlothlin *et al.*

409   2010) as

$$\Delta\bar{\mathbf{z}} = \text{Cov}(\mathbf{A}, \mathbf{z}^{\text{T}})\boldsymbol{\beta}_{\mathbf{N}} + \text{Cov}(\mathbf{A}, \mathbf{z}'^{\text{T}})\boldsymbol{\beta}_{\mathbf{S}}. \tag{19}$$

411   Substituting Eqs. **17-18** into Eq. **19** and simplifying yields

$$\Delta\bar{\mathbf{z}} = \mathbf{G}(\mathbf{I} - (1+r)\boldsymbol{\delta}^{\text{T}})(\mathbf{I} - 2\boldsymbol{\delta}^{\text{T}})^{-1}\boldsymbol{\beta}_{\mathbf{N}} + \mathbf{G}(r\mathbf{I} - (1+r)\boldsymbol{\delta}^{\text{T}})(\mathbf{I} - 2\boldsymbol{\delta}^{\text{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}, \tag{20}$$

413   where $\mathbf{G}$ is the additive genetic (co)variance matrix and r is relatedness. Eq. 20 can be used to

414   generate the specific model in the text by setting parameters as

$$\mathbf{G} = \begin{bmatrix} G_{SS} & G_{SB} & 0 \\ G_{SB} & G_{BB} & 0 \\ 0 & 0 & G_{AA} \end{bmatrix}, \boldsymbol{\delta} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ \delta_{AS} & 0 & 0 \end{bmatrix}, \boldsymbol{\beta}_{\mathbf{N}} = \begin{bmatrix} \beta_{N_S} \\ \beta_{N_B} \\ \beta_{N_A} \end{bmatrix}, \boldsymbol{\beta}_{\mathbf{S}} = \begin{bmatrix} \beta_{S_S} \\ \beta_{S_B} \\ \beta_{S_A} \end{bmatrix}, r = 0 \tag{21}$$

416   and multiplying the result by $\frac{1}{2}$ to indicate selection acting only on males.

Relationship to indirect genetic effects models

The model described above differs from previous models of indirect genetic effects in that phenotypes may be adjusted in relation to both the phenotypes of a social partner and other phenotypes of the focal individual. The standard model of phenotypic expression used in trait-based genetic effects models (Moore *et al.* 1997a) is

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + \boldsymbol{\Psi}\mathbf{z}'. \tag{22}$$

The relationship between the two models can be seen by adding an additional term to the standard model:

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + \boldsymbol{\xi}\mathbf{z} + \boldsymbol{\Psi}\mathbf{z}'. \tag{23}$$

The term $\boldsymbol{\xi}\mathbf{z}$, which is similar to the developmental interaction effects considered by Wolf *et al.* (Wolf *et al.* 2001), contains a conditional modification of the direct genetic effect in response to other phenotypic traits, while the term $\boldsymbol{\Psi}\mathbf{z}'$ contains indirect genetic effects (Moore *et al.* 1997a). When $\boldsymbol{\xi} = \mathbf{0}$, model 23 is equivalent to model **22**, and when $\boldsymbol{\xi} = -\boldsymbol{\Psi} = \boldsymbol{\delta}$, model 23 is equivalent to model 13.

Incorporating conditional direct genetic effects is a way to mechanistically represent genetic covariances in a quantitative genetic model (Wolf *et al.* 2001). Combining such effects with indirect genetic effects allows exploration of a wide variety of models of phenotypic adjustment, including behavioral modification, in evolutionary quantitative genetic models. For full generality, we give the equation for multivariate response to selection derived from model 23. First, the vector of total breeding values derived from the trait mean is

$$\mathbf{A} = (\mathbf{I} - \boldsymbol{\xi} - \boldsymbol{\Psi})^{-1}\mathbf{a}. \tag{24}$$

By substitution of Eqs. 23-24 into Eq. 19, we find

22

440 $$\Delta\bar{\mathbf{z}} = (\mathbf{I} - \boldsymbol{\xi} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{I} + r(\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}})^{-1}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}} - \boldsymbol{\Psi}^{\mathrm{T}}(\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}})^{-1}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{N}} +$$

441 $$(\mathbf{I} - \boldsymbol{\xi} - \boldsymbol{\Psi})^{-1}\mathbf{G}(r\mathbf{I} + (\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}})^{-1}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}} - \boldsymbol{\Psi}^{\mathrm{T}}(\mathbf{I} - \boldsymbol{\xi}^{\mathrm{T}})^{-1}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}. \qquad (25)$$

442 This equation is unwieldy in its multivariate form, but one can follow the approach we take

443 here for male-male competition and use Eq. 25 to generate much simpler models of the

444 evolution of systems of responsive traits given a set of assumptions about fitness and trait

445 expression.

446 **Extension to multiple opponents**

447 Our results can be extended to incorporate interactions with multiple opponents. Suppose a

448 male encounters opponents sequentially. The phenotype of a focal individual averaged over

449 all encounters is then

450 $$\bar{\mathbf{z}} = (\mathbf{I} - 2\boldsymbol{\delta})^{-1}((\mathbf{I} - \boldsymbol{\delta})(\mathbf{a} + \mathbf{e}) - \boldsymbol{\delta}(\bar{\mathbf{a}}' + \bar{\mathbf{e}}')), \qquad (26)$$

451 and the average of his social partners is

452 $$\bar{\mathbf{z}}' = (\mathbf{I} - 2\boldsymbol{\delta})^{-1}((\mathbf{I} - \boldsymbol{\delta})(\bar{\mathbf{a}}' + \bar{\mathbf{e}}') - \boldsymbol{\delta}(\mathbf{a} + \mathbf{e})), \qquad (27)$$

453 where an overbar is now taken to indicate an average over an individual male's encounters. If

454 we assume that the fitness effects of individual encounters accrue additively, then Eq. 20 may

455 still be used to predict the evolution of the population mean, with $\boldsymbol{\beta}_{\mathbf{N}}$ and $\boldsymbol{\beta}_{\mathbf{S}}$ now representing

456 vectors of partial regression slopes of fitness on focal individual mean and social group mean

457 phenotypes, respectively. Specific fitness models may be substituted into Eq. 20 in the same

458 way as for models of single pairwise interactions.

ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

465   AJM, JWM, and JBW conceived the idea, developed the model, and wrote the paper.

REFERENCES

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature*, 299, 818-820.

Andersson, M. (1994). *Sexual Selection*. Princeton Univ. Press, Princeton.

Araya-Ajoy, Y.G., Westneat, D.F. & Wright, J. (2020). Pathways to social evolution and their evolutionary feedbacks. *Evolution*, 74, 1894-1907.

Arnold, S.J. (1994). Multivariate inheritance and evolution: a review of concepts. In: *Quantitative Genetic Studies of Behavioral Evolution* (ed. Boake, CR). Univ. of Chicago Press Chicago, pp. 17-48.

Bailey, N.W. & Kölliker, M. (2019). Social runaway: Fisherian elaboration (or reduction) of socially selected traits via indirect genetic effects. *Evolution*, 73, 1549-1563.

Bailey, N.W. & Moore, A.J. (2012). Runaway sexual selection without genetic correlations: social environments and flexible mate choice initiate and enhance the Fisher process. *Evolution*, 66, 2674-2684.

Bijma, P. & Wade, M.J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *J. Evol. Biol.*, 21, 1175-1188.

Briceño, R.D. & Eberhard, W.G. (1995). *The functional morphology of male cerci and associated characters in 13 species of tropical earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae)*. Smithsonian Institution Press, Washington, DC.

Clark, D.C. & Moore, A.J. (1995). Genetic aspects of communication during male-male competition in the Madagascar hissing cockroach: honest signaling of size. *Heredity*, 75, 198-205.

Darwin, C. (1859). *The Origin of Species*. John Murray, London.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

Emlen, D.J. (2008). The Evolution of Animal Weapons. *Annu. Rev. Ecol. Evol. Syst.*, 39, 387-413.

Emlen, D.J. (2014). *Animal Weapons: The Evolution of Battle*. Henry Holt & Co., New York.

Emlen, D.J., Marangelo, J., Ball, B. & Cunningham, C.W. (2005). Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera : Scarabaeidae). *Evolution*, 59, 1060-1084.

498   Fisher, D.N. & Pruitt, J.N. (2019). Opposite responses to selection and where to find them. *J. Evol. Biol.*, 32, 505-518.

500   Fisher, R.A. (1915). The evolution of sexual preference. *Eugen Rev*, 7, 184-192.

501   Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

502   Formica, V.A., McGlothlin, J.W., Wood, C.W., Augat, M.E., Butterfield, R.E., Barnard, M.E. *et al.* (2011). Phenotypic assortment mediates the effect of social selection in a wild beetle population. *Evolution*, 65, 2771-2781.

505   Hagelin, J.C. (2002). The kinds of traits involved in male-male competition: a comparison of plumage, behavior, and body size in quail. *Behav. Ecol.*, 13, 32-41.

507   Huxley, J.S. (1938). Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *Am. Nat.*, 72, 416-433.

509   Kirkpatrick, M. (1982). Sexual selection and the evolution of female mate choice. *Evolution*, 36, 1-12.

511   Laidre, M.E. & Johnstone, R.A. (2013). Animal signals. *Curr. Biol.*, 23, R829-R833.

512   Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30, 314-334.

514   Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution*, 33, 402-416.

516   Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA*, 78, 3721-3725.

518   Lande, R. & Arnold, S.J. (1983). The measurement of selection on correlated characters. *Evolution*, 37, 1210-1226.

520   Lucas, W.J. (1920). *A Monograph of the British Orthoptera*. The Ray Society, London.

521   Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge Univ. Press, Cambridge.

523   Maynard Smith, J. & Brown, R.L.W. (1986). Competition and body size. *Theor. Popul. Biol.*, 30, 166-179.

525   Maynard Smith, J. & Harper, D. (2003). *Animal Signals*. Oxford Univ. Press, Oxford.

526   Maynard Smith, J. & Harper, D.G.C. (1988). The evolution of aggression: can selection generate variability? *Philos. Trans. R. Soc. Lond. B*, 319, 557-570.

528   Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. *Nature*, 246, 15-18.

529   McCullough, E.L., Miller, C.W. & Emlen, D.J. (2016). Why sexually selected weapons are not ornaments. *Trends Ecol. Evol.*, 31, 742-751.

531 McGlothlin, J.W., Akçay, E., Brodie, E.D., III, Moore, A.J. & Van Cleve, J. (2021). A
532   synthesis of evolutionary game theory and quantitative genetic models of social
533   evolution. *bioRxiv*, 10.1101/2021.03.27.437341.

534 McGlothlin, J.W., Moore, A.J., Wolf, J.B. & Brodie, E.D., III (2010). Interacting phenotypes
535   and the evolutionary process. III. Social evolution. *Evolution*, 64, 2558-2574.

536 McGlothlin, J.W., Parker, P.G., Nolan, V., Jr. & Ketterson, E.D. (2005). Correlational
537   selection leads to genetic integration of body size and an attractive plumage trait in
538   dark-eyed juncos. *Evolution*, 59, 658-671.

539 Mead, L.S. & Arnold, S.J. (2004). Quantitative genetic models of sexual selection. *Trends*
540   *Ecol. Evol.*, 19, 264-271.

541 Moore, A.J., Brodie, E.D., III & Wolf, J.B. (1997a). Interacting phenotypes and the
542   evolutionary process: I. Direct and indirect genetic effects of social interactions
543   *Evolution*, 51, 1352-1362.

544 Moore, A.J., Haynes, K.F., Preziosi, R.F. & Moore, P.J. (2002). The evolution of interacting
545   phenotypes: genetics and evolution of social dominance. *Am. Nat.*, 160, S186-S197.

546 Moore, A.J. & Moore, P.J. (2006). The genetics of sexual selection. In: *Evolutionary Genetics*
547   (eds. Fox, CW & Wolf, JB). Oxford Univ. Press Oxford, pp. 339-349.

548 Moore, P.J., Reagan-Wallin, N.L., Haynes, K.F. & Moore, A.J. (1997b). Odour conveys
549   status on cockroaches. *Nature*, 389, 25-25.

550 O'Brien, D.M., Allen, C.E., Van Kleeck, M.J., Hone, D., Knell, R., Knapp, A. *et al.* (2018).
551   On the evolution of extreme structures: static scaling and the function of sexually
552   selected signals. *Anim. Behav.*, 144, 95-108.

553 Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor.*
554   *Biol.*, 47, 223-243.

555 Rico-Guevara, A. & Hurme, K.J. (2019). Intrasexually selected weapons. *Biol. Rev.*, 94, 60-
556   101.

557 Riechert, S.E. (1984). Games spiders play. III. Cues underlying context-associated changes in
558   agonistic behavior. *Anim. Behav.*, 32, 1-15.

559 Rosenthal, G.G. (2017). *Mate Choice: The Evolution of Sexual Decision Making from*
560   *Microbes to Humans*. Princeton Univ. Press, Princeton.

561 Rutte, C., Taborsky, M. & Brinkhof, M.W.G. (2006). What sets the odds of winning and
562   losing? *Trends Ecol. Evol.*, 21, 16-21.

563 Seehausen, O. & Schluter, D. (2004). Male-male competition and nuptial-colour displacement
564   as a diversifying force in Lake Victoria cichlid fishes. *Proc. R. Soc. Lond. B*, 271,
565   1345-1353.

566 Shuster, S.M. & Wade, M.J. (2003). *Mating Systems and Strategies*. Princeton Univ. Press,
567   Princeton.

568 Sneddon, L.U., Huntingford, F.A. & Taylor, A.C. (1997). Weapon size versus body size as a
569   predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav.*
570   *Ecol. Sociobiol.*, 41, 237-242.

571 Tinghitella, R.M., Lackey, A.C.R., Martin, M., Dijkstra, P.D., Drury, J.P., Heathcote, R. *et al.*
572   (2018). On the role of male competition in speciation: a review and research agenda.
573   *Behav. Ecol.*, 29, 783-797.

574 Wallace, A.R. (1889). *Darwinism: An Exposition of the Theory of Natural Selection, with*
575   *Some of its Applications*. Macmillan, London.

576 West-Eberhard, M.J. (1979). Sexual selection, social competition, and evolution. *Proc. Am.*
577   *Phil. Soc.*, 123, 222-234.

578 West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. *Q. Rev.*
579   *Biol.*, 58, 155-183.

580 West-Eberhard, M.J. (1984). Sexual selection, competitive communication and species-
581   specific signals. In: *Insect Communication* (ed. Lewis, T). Academic Press New York,
582   pp. 283-324.

583 West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution*. Oxford Univ. Press,
584   Oxford.

585 Wiens, J.J. & Tuschhoff, E. (2020). Songs versus colours versus horns: what explains the
586   diversity of sexually selected traits? *Biol. Rev.*, 95, 847-864.

587 Wilkinson, G.S. & Dodson, G.N. (1997). Function and evolution of antlers and eye stalks in
588   flies. In: *The Evolution of Mating Systems in Insects and Arachnids* (eds. Choe, JC &
589   Crespi, BJ). Cambridge Univ. Press Cambridge.

590 Wolf, J.B. (2003). Genetic architecture and evolutionary constraint when the environment
591   contains genes. *Proc. Natl. Acad. Sci. USA*, 100, 4655-4660.

592 Wolf, J.B., Brodie, E.D., III & Moore, A.J. (1999). Interacting phenotypes and the
593   evolutionary process. II. Selection resulting from social interactions. *Am. Nat.*, 153,
594   254-266.

595   Wolf, J.B., Frankino, W.A., Agrawal, A.F., Brodie, E.D., III & Moore, A.J. (2001).

596   Developmental interactions and the constituents of quantitative variation. *Evolution*,

597   55, 232-245.