1 An evolutionary resolution of manipulation conflict

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Abstract

Individuals can manipulate the behavior of social partners. However, manipulation may conflict with the fitness interests of the manipulated individuals. Manipulated individuals can then be favored to resist manipulation, possibly reducing or eliminating the manipulated behavior in the long run. I use a mathematical model to show that conflicts where manipulation and resistance coevolve can disappear as a result of the coevolutionary process. I find that while manipulated individuals are selected to resist, they can simultaneously be favored to express the manipulated behavior at higher efficiency (i.e., providing increasing fitness effects to recipients of the manipulated behavior). Efficiency can increase to a point at which selection for resistance disappears. This process yields an efficient social behavior that is induced by social partners, and over which the inducing and induced individuals are no longer in conflict. A necessary factor is costly inefficiency. I develop the model to address the evolution of advanced eusociality via maternal manipulation (AEMM). The model predicts AEMM to be particularly likely in taxa with ancestrally imperfect resistance to maternal manipulation. Costly inefficiency occurs if the cost of delayed dispersal is larger than the benefit of exploiting the maternal patch. I discuss broader implications of the process.

Introduction

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33 In some taxa, individuals can control partially or completely the behavior of other individuals, an action

34 referred to as manipulation (Alexander, 1974, Dawkins, 1978). For example, baculoviruses manipulate

35 their host, a moth caterpillar, to climb trees; the caterpillars then die and liquefy at the tree top causing

36 a "virus rain" in the foliage below, thereby facilitating infection of new hosts (Hoover *et al.*, 2011).

37 Workers in social insects can induce their siblings to develop as workers or queens by adjusting their

38 siblings' nutrition (Wheeler, 1986, O'Donnell, 1998). *Drosophila* males manipulate their sexual partners

39 by transferring seminal proteins during mating (Wolfner, 2002). Manipulation is facilitated when an

40 individual has direct access to another individual's physiology, as is the case for internal parasites

41 (Hughes *et al.*, 2012, Adamo and Webster, 2013), for parents and offspring (Haig, 1993), and for mating

42 partners (Arnqvist and Rowe, 2005). In the absence of direct access to another individual's physiology,

43 an individual may manipulate another one through coercion, sensory exploitation, deception, and

44 self-deception. In particular, dominant individuals may coerce subordinates into helping roles

45 (Clutton-Brock and Parker, 1995), males may stimulate females' pre-existing preferences to induce

46 mating (Holland and Rice, 1998), and humans may deceive themselves to fool social partners into

47 behaving in a given fashion (Trivers, 2011).

48   Manipulation can give rise to unlikely behaviors because the costs of expressing the behaviors are

49 not paid by the manipulators, but by the subjects of manipulation (or "subjects" for short). As a result,

50 costly behaviors can evolve under less stringent conditions (i.e., smaller benefit-cost ratios) than if the

51 behaviors were performed spontaneously; that is, without manipulation (Alexander, 1974, Trivers, 1974,

52 Charlesworth, 1978). However, costly behaviors diminish the reproductive success of the subjects.

53 Resistance to manipulation is then favored if resistance is less expensive than accepting manipulation

54 (Pagel *et al.*, 1998). Manipulators and subjects can thus disagree in their preferred expression level of

55 the manipulated behavior, which constitutes an evolutionary conflict (Trivers, 1974).

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56   Evolutionary conflicts can have diverse results. Mathematical theory indicates that a manipulation

57   conflict can yield at least four possible outcomes. First, the complete victory of resistance where the

58   manipulated behavior is eliminated. Second, the complete victory of manipulation where the

59   manipulated behavior is fully maintained. Third, an intermediate behavior between the favored

60   outcomes of the two parties. And fourth, perpetual cycles between high and low manipulation and

61   resistance (e.g., Parker and Macnair, 1979, Robert *et al.*, 1999, Gavrilets *et al.*, 2001). Which outcome is

62   reached depends on the magnitude and nature of the costs paid by each party (Godfray, 1995,

63   Clutton-Brock, 1998, Uller and Pen, 2011), the initial conditions, and the relative genetic variances of

64   manipulation and resistance (Gavrilets, 2000, Gavrilets and Hayashi, 2006).

65   As the evolution of manipulation and resistance proceeds, the nature of the conflict can change. In

66   particular, the costs and benefits of the manipulated behavior can evolve if they have a genetic basis

67   (Charlesworth, 1978, Worden and Levin, 2007, Akçay and Roughgarden, 2011). A genetic basis for the

68   costs and benefits of a manipulated behavior is possible because they depend on the extent with which

69   the manipulated behavior is expressed, which can be controlled by manipulators and subjects of

70   manipulation. The evolution of costs and benefits could then increase or decrease the level of conflict.

71   As a result, the outcome of a conflict can be substantially different from what it would be if costs and

72   benefits are taken as constants. Here I ask what the evolution of fitness payoffs can do to the outcome of

73   a manipulation conflict.

74   I show that the manipulation conflict can disappear as a result of the evolution of payoffs released by

75   manipulation. This conflict resolution brings the interests of the subjects of manipulation to match

76   those of the manipulator. The reason is that manipulation not only favors the evolution of resistance,

77   but also the evolution of the efficiency with which the manipulated behavior is performed. If the

78   efficiency of the manipulated behavior becomes sufficiently high, resistance to manipulation becomes

79   disfavored. Because the conflict is eliminated, I refer to the resulting behavior as being induced rather

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80   than manipulated. The result is an efficient induced behavior over which inducing and induced

81   partners do not conflict. To show this, I develop a mathematical model of maternal manipulation where

82   offspring are manipulated to stay in the maternal patch. As offspring evolve resistance to manipulation,

83   they also become efficient helpers giving large fitness benefits to siblings. The outcome is offspring that

84   are 1) maternally induced to stay in the maternal patch, 2) that are efficient helpers, and 3) that are not

85   in conflict with their mother over their helping role. These three items match defining features of

86   advanced eusociality, where workers are maternally induced into worker roles, can be highly

87   specialized to perform tasks, and show relatively little conflict over their helping role (Wilson, 1971,

88   Michener, 1974, Sherman *et al.*, 1991, Crespi and Yanega, 1995, Hölldobler and Wilson, 2009, Bignell

89   *et al.*, 2011). The model predicts that advanced eusociality arising from this process requires ancestrally

90   imperfect resistance probability and ancestral inefficiency costs.

Model

92   Consider a finite population of sexual individuals with deterministic reproduction, so genetic drift is

93   ignored. The genetic system can be diploid or haplodiploid. The population is distributed in an area of

94   a fixed size which is subdivided into patches, all of approximately the same size. In each patch, one

95   singly mated female and possibly her mating partner gather resources for reproduction. The amount of

96   resources they gather is proportional to the patch size. The mated female produces offspring, the

97   number of which is proportional to the amount of resources gathered. So offspring number is

98   proportional to the patch size. The average patch size decreases as the population increases, and

99   increases as the population decreases. Hence, the population size remains constant.

100   The mother produces offspring in two subsequent broods. The first brood reaches adulthood while

101   the second brood is not yet mature. The mother and possibly the father provide parental care to both

102   broods. Once the second brood reaches adulthood, the parents die. After each brood reaches

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103 adulthood, the brood disperses from the maternal patch to a common mating pool. All individuals in

104 the mating pool mate once and randomly. Then, each mated female colonizes a random patch, possibly

105 together with her mating partner, and the cycle starts anew. Competition for patch size is thus global.

106 Maternal manipulation and offspring resistance are allowed to occur. A focal mother manipulates

107 offspring by attempting to delay the dispersal of the first brood with probability p_m, so that first-brood

108 offspring stay in the maternal patch for a fraction of their adulthood. I make the simplifying assumption

109 that the mother manipulates both sexes equally. A manipulated first-brood individual resists with

110 probability q_1 and leaves the maternal patch without delay. Alternatively, a manipulated first-brood

111 individual acquiesces (i.e., does not resist) with probability $1 - q_1$ and stays in the maternal patch for

112 some portion of its adulthood. An acquiescing (i.e., delayed) individual expresses parental care with

113 probability y_1 while in the maternal patch. I also make the simplifying assumption that the probability

114 of expressing parental care is equal for acquiescing individuals of either sex. This alloparental care is

115 directed randomly to the available brood (i.e., the second one). I refer to y_1 as helping efficiency. I

116 assume manipulation p_m, resistance q_1, and helping efficiency y_1 to be uncorrelated quantitative

117 genetic traits. The population average values of manipulation, resistance, and helping efficiency are p,

118 q, and y respectively. The three decisions individuals can make are illustrated in Fig. 1.

119 Manipulation is assumed to be executed in a way that does not affect the condition of the subjects of

120 manipulation, and that does not affect the ability of the mother to produce the second brood. Thus, I

121 assume both resistance and manipulation to be costless. These assumptions may hold for instance if

122 manipulation is done via cheap pheromones that first-brood individuals can block with little direct

123 fitness costs. The assumptions of costless manipulation and resistance lead to a simpler model, and

124 highlight that the evolution of acquiescence does not require resistance costs (for an evaluation of the

125 effect of resistance and manipulation costs on the evolution of manipulated behaviors, see

126 González-Forero and Gavrilets (2013)). However, manipulation affects the ability of acquiescing

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127   individuals to become parents themselves. First, regardless of whether an acquiescing individual helps,

128   this individual has a reduced probability of becoming a parent if delayed dispersal translates into

129   missed reproductive opportunities or less time to start a new nest. Second, if an acquiescing individual

130   helps, a reduced probability of becoming a parent arises if by helping, the individual spends energy

131   necessary for its own dispersal and reproduction. In contrast, if an acquiescing individual does not

132   help, it can exploit the resources of the maternal patch for its own benefit, thereby increasing its

133   potential to become a parent itself.

These fitness payoffs are modeled as follows. The reduction in the probability that a delayed

individual becomes a parent, independently of whether the delayed individual helps, is denoted by c_d.

The additional reduction in the probability that a delayed individual becomes a parent due to helping is

c_h. On the other hand, the increase in the probability of becoming a parent due to the exploitation of

the maternal patch while not helping is b_e. For simplicity, I ignore any frequency dependence in the

payoffs c_d, c_h, and b_e, and I treat them as constant. The total cost of acquiescence for a focal delayed

first-brood individual is thus equal to

$$c = c_d + y_1 c_h - (1 - y_1) b_e \qquad (1a)$$

$$= c_{\text{eff}} y_1 + c_{\text{ineff}}(1 - y_1), \qquad (1b)$$

where the cost of efficiency and inefficiency are defined as

$$c_{\text{eff}} = c_d + c_h \qquad (2a)$$

$$c_{\text{ineff}} = c_d - b_e. \qquad (2b)$$

134   In this paper, I report the behavior of the model when there is a cost of inefficiency ($c_{\text{ineff}} > 0$), so I

135   assume throughout that the cost of delayed dispersal is greater than the benefit of exploiting the

136   maternal patch ($c_d > b_e$).

137   It remains to account for the fitness effects of manipulation on the second brood. A delayed

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138 first-brood individual that helps increases the survival of recipient second-brood offspring. The

139 increase in survival received by a random second-brood recipient is

$$b = b_{\max} Y, \tag{3}$$

140 where Y is the average helping probability among delayed individuals in the patch, and $b_{\max}$ is the

141 benefit a recipient of help gets when all delayed individuals in the patch help at their maximum

142 efficiency. Denoting by s_0 the baseline probability of becoming a parent (i.e., the probability that

143 offspring become parents when manipulation does not occur), I let $b_{\max} = 1 - s_0$.

144 I follow the methods of Taylor and Frank (1996) and Frank (1997) to obtain dynamic equations for

145 the coevolution of manipulation p, resistance q, and helping efficiency y (see Appendix). At any given

146 time the population is divided into three classes of individuals: mothers, first-brood individuals, and

147 second-brood individuals. This treatment yields three regression relatednesses that affect the

148 evolutionary dynamics: the relatedness ρ_{21} of first-brood offspring toward second-brood offspring, and

149 those of the mother toward the first and second brood (ρ_{1m} and ρ_{2m} respectively). For class-structured

150 populations, the direction of evolutionary change usually depends on regression relatedness weighted

151 by the individual reproductive value of the recipient over that of actor, which is called life-for-life

152 relatedness (Hamilton, 1972, Bulmer, 1994). However, here the direction of evolutionary change is

153 found to be determined by regression relatednesses weighted by equilibrium class frequencies rather

154 than by individual reproductive values. The weighting by class equilibrium frequencies arises because

155 the evolving traits affect survival rather than fertility. Thus, the dynamics are in terms of the equilibrium

156 relatednesses r_{ji} of actor i toward recipient j, which are defined as $r_{ji} = \rho_{ji} u_j / u_i$. The quantities u_i

157 and u_j are the equilibrium frequency of individuals of class i and j respectively. For simplicity, I drop

158 the subscripts for the relatedness of first-brood offspring toward second-brood offspring and write

159 $\rho = \rho_{21}$, and $r = r_{21}$.

Results

Numerical illustration

162 The coevolution of manipulation, resistance, and helping efficiency can change the direction of

163 selection for resistance. For illustration, suppose that the population is diploid. Thus, with the

164 assumptions stated in the model section, the regression relatednesses of mother-to-offspring and of

165 first- to second-brood offspring are $\rho_{1m} = \rho_{2m} = \rho = 1/2$ (Bulmer, 1994, Roze and Rousset, 2004).

166 Numerical solutions for manipulation p, resistance q, and helping efficiency y from the dynamic

167 equations (19) are shown in Fig. 2. Both maternal manipulation and offspring resistance are favored at

168 the start of the process in Fig. 2. In Fig. 2A there is no genetic variation for helping efficiency, which

169 then cannot evolve. In this case, resistance eliminates the manipulated behavior and all first-brood

170 offspring disperse upon reaching adulthood (i.e., the attained equilibrium is $p^*(1-q^*) = 0$). In Fig. 2B

171 genetic variation for helping efficiency is present. In this case, helping efficiency increases over time

172 although individuals are initially disfavored to stay in the maternal patch. After around thirty thousand

173 generations, helping efficiency becomes high enough that first-brood individuals become favored to

174 stay in the maternal patch. The outcome is that mothers cause all first-brood individuals to stay,

175 first-brood individuals acquiesce, and help at their maximum efficiency.

176   This coevolutionary process eliminates the mother-offspring conflict over offspring dispersal.

177 Throughout the process, the mother's inclusive fitness through maternal manipulation is maximized at

178 zero offspring resistance (Fig. 3A). In contrast, first-brood offspring's inclusive fitness through

179 resistance is initially maximized at full resistance, but the slope of their inclusive fitness gradually

180 changes from positive to negative (Fig. 3B). The change in slope of offspring's inclusive fitness through

181 resistance renders this inclusive fitness maximized at zero resistance, thereby eliminating the

182 mother-offspring conflict (Fig. 3C). Because of the lack of conflict, I refer to the final maternally

183   triggered behavior as being induced rather than being manipulated.

184   **Evolutionary change in each trait**

The population-average manipulation p, resistance q, and helping efficiency y increase respectively

(see eqs. (19) in the Appendix) when

$$br_{2m} > cr_{1m} \tag{4a}$$

$$br > c \tag{4b}$$

$$br > c - c_{\text{ineff}}. \tag{4c}$$

185   Manipulation, acquiescence, and helping efficiency are each favored when their respective inclusive

186   fitness effect is positive (conditions (4)). Manipulation conflict occurs when manipulation is favored

187   but acquiescence is not (i.e., when ineq. (4a) is met but ineq. (4b) is not). In that case, mothers attempt

188   to delay first-brood offspring in the maternal patch against the latter's inclusive fitness interests.

189   Offspring can rebel against manipulation by either resisting (i.e., dispersing from the maternal patch) or

190   by refusing to help. The conditions for the evolution of these two forms of rebellion are different if the

191   cost of inefficiency c_{ineff} is not zero (see ineqs. (4b) and (4c)). The different conditions for the evolution

192   of acquiescence and helping efficiency can cause conflicting selection within first-brood offspring.

193   Thus, helping efficiency may evolve even though acquiescence is not favored.

194   Conditions (4) do not specify the conditions for conflict resolution because the benefit b and cost c

195   evolve as helping efficiency y changes. Consequently, whether or not conditions (4) are met varies with

196   the evolution of helping efficiency. In order to determine the conditions for conflict resolution, a

197   dynamic analysis is necessary (see §2 in the online Supporting Information (SI)).

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198 **Conditions for conflict resolution**

199 The system evolves either to a state where manipulation disappears ($p^* = 0$), to a state where resistance

200 is complete ($q^* = 1$), or to induced behavior where manipulation, acquiescence, and helping efficiency

201 are established [$(p^*, q^*, y^*) = (1, 0, 1)$].

202   The evolution of induced behavior requires two conditions regarding resistance. First, acquiescence

203 must be favored when first-brood offspring help at their maximum efficiency, which occurs if

$$b_{\max} r > c_{\mathrm{eff}}. \tag{5}$$

When condition (5) holds, the coevolutionary dynamics of resistance q and helping efficiency y are as

described in Fig. 4A. Acquiescence can be disfavored at the start of the process, and the evolution of

helping efficiency can render acquiescence favored if the population starts in the dark gray area in Fig.

4A. The population starts in the either the gray or dark gray area in Fig. 4A if the next condition is met.

Second, induced behavior requires that the probability of resistance is initially small enough, which

occurs if

$$b_0 r + (1 - q_0) S \sqrt{\frac{V_y}{V_q}} > c_0, \tag{6a}$$

204 where

$$S = b_{\max} r - (c_{\mathrm{eff}} - c_{\mathrm{ineff}}). \tag{6b}$$

205 The variables with subscript "0" refer to the value of the variable at the initial time. The quantity S

206 measures selection for helping efficiency, which is positive when condition (5) holds. V_q and V_y are the

207 additive genetic variances for resistance and helping efficiency respectively.

208   Condition (6a) is related to Hamilton's rule (Hamilton, 1964, 1970). Hamilton's rule states that

209 acquiescence is favored at the initial time if $b_0 r > c_0$ (from ineq. (4b)). The additional term in condition

210 (6a) measures the speed of increase in helping efficiency relative to that of resistance ($S\sqrt{V_y/V_q}$) and

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211 the opportunity that helping efficiency has to render acquiescence favored $(1 - q_0)$. Because this

212 additional term is positive when ineq. (5) holds, condition (6a) requires less stringent conditions

213 (smaller b/c ratios) to be met than those required for acquiescence to be favored at the initial time

214 $(b_0 r > c_0)$. Condition (6a) may then be seen as defining a relaxed Hamilton's rule, which rather than

215 giving the direction of selection specifies when acquiescence can be obtained in the long run.

216   The evolution of induced behavior also requires two conditions regarding manipulation. First,

217 manipulation must be favored when first-brood offspring help at their maximum efficiency (ineq.

218 (S25a) in the SI). Second, the evolution of helping efficiency must be able to render manipulation

219 favored (ineq. (S25c) in the SI). If the probability of manipulation is initially small, the second condition

220 regarding manipulation simply states that manipulation must be favored initially.

   Four conditions are then necessary and sufficient for induced behavior (ineqs. (S25) in the SI). If

manipulation p and resistance q are initially small, induced behavior $(p^*, q^*, y^*) = (1, 0, 1)$ evolves if all

the following conditions hold:

$$b_{\max} r_{2m} > c_{\text{eff}} r_{1m} \tag{7a}$$

$$b_{\max} r > c_{\text{eff}} \tag{7b}$$

$$b_0 r_{2m} > c_0 r_{1m} \tag{7c}$$

$$b_0 r + S \sqrt{V_y / V_q} > c_0. \tag{7d}$$

221 Conditions (7a) and (7b) respectively state that both manipulation and acquiescence must be favored

222 when helping efficiency is maximal; condition (7c) states that manipulation must be initially favored;

223 and condition (7d) guarantees that acquiescence becomes favored as the population evolves.

224   The evolutionary resolution of manipulation conflict occurs when induced behavior is obtained and

225 acquiescence is not initially favored (i.e., conditions (7) are met but condition (4b) is not met initially).

226 The region of parameter space in which the conflict is resolved is narrow (black regions in Fig. 5).

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227   However, the region for conflict resolution can be wider than the region in which first-brood offspring

228   are favored to stay from the beginning of the process (i.e., non-conflicting acquiescence; dark gray

229   regions in Fig. 5). In this simple model, where the mother equally manipulates both sexes, both sexes

230   are equally efficient, and the sex ratio is equal in both broods, the region of conflict resolution can be

231   the same for both diploids and haplodiploids (Fig. 5).

232   **Spontaneous behavior**

233   The evolution of helping efficiency could render spontaneous (i.e., unmanipulated) helping favored just

234   as it does for induced behavior. In §1 of the SI, I build an analogous model in which the probability x_1

235   that a first-brood individual stays in the maternal patch is fully under control of the staying individual.

236   A spontaneously staying first-brood individual expresses alloparental care toward the second brood

237   with probability y_1. The population averages of the spontaneous behavior and helping efficiency are x

238   and y respectively.

239   The coevolutionary dynamics of the spontaneous behavior x and helping efficiency y are a mirror

240   image of those of resistance q and helping efficiency y (Fig. 4B). As a result, if staying spontaneously is

241   initially disfavored, the evolution of helping efficiency can render it favored. Two conditions must be

242   satisfied for efficient spontaneous behavior to be obtained $[(x^*, y^*) = (1, 1)]$. First, spontaneous

243   behavior must be favored when helping efficiency is maximal (same condition (5) as for acquiescence).

244   Second, the probability of staying spontaneously must be initially *large* enough (condition (6a) after

245   changing $1 - q_0$ for x_0 and V_q for the additive genetic variance for staying spontaneously V_x). Hence, the

246   opportunity for helping efficiency to render spontaneous behavior favored is x_0. If the initial probability

247   x_0 of staying spontaneously is small (as is expected to be the case for altruistic traits), then the second

248   condition for efficient spontaneous behavior simply requires that the spontaneous behavior is favored

249   at the initial time. Hence, if the ancestral probability of spontaneously staying is small, the evolution of

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250 helping efficiency cannot not render the spontaneous behavior favored if it is not favored initially.

251 Consequently, induced behavior $(p^*, q^*, y^*) = (1, 0, 1)$ can be obtained under less stringent

252 conditions (smaller initial b/c ratios) than spontaneous behavior $(x^*, y^*) = (1, 1)$. In particular, suppose

253 that the initial benefit b_0 and cost c_0 are the same under manipulated and spontaneous behavior.

254 Assume also that the relatedness r of first- to second brood is the same under manipulated and

255 spontaneous behavior. Then, if manipulation, resistance, and staying spontaneously are all initially

256 unlikely (i.e., $p_0, q_0, x_0 \approx 0$), induced behavior can be obtained (condition (7d) is met) while

257 spontaneous behavior is not obtained ($b_0 r < c_0$) if

$$0 < c_0 - b_0 r < S\sqrt{\frac{V_y}{V_q}}. \tag{8}$$

258 Condition (8) specifies when induced behavior can be expected but spontaneous behavior fails to

259 evolve. This condition summarizes that the evolution of helping efficiency allows induced behavior to

260 require less stringent conditions than spontaneous behavior since condition (8) cannot be satisfied if

261 helping efficiency cannot evolve (i.e., if $SV_y = 0$).

262 Because induced and spontaneous behavior can evolve under different conditions, predictions may

263 be derived to test whether or not advanced eusociality in a given taxon is the result of manipulation.

Discerning whether advanced eusociality stems from manipulation

265 The ancestral conditions give a distinction between induced and spontaneous behavior. Induced

266 behavior requires ancestrally imperfect resistance probability (black line in Fig. 6A). Under the same

267 ecological conditions and if the ancestral benefit b_0 and the ancestral cost c_0 are the same under

268 manipulated and spontaneous behavior, spontaneous behavior requires a sufficiently large ancestral

269 probability of staying spontaneously (dashed gray line in Fig. 6A).

270 Although it is not possible to directly determine ancestral conditions except when experimental

271 evolution is feasible, indirect estimation of ancestral conditions may be possible. Consider an advanced

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272 eusocial population A of interest. Assume there is an extant population B satisfying the following

273 requirements. 1) The population B is not advanced eusocial; 2) it is very close phylogenetically to

274 population A and it has not been exposed to the manipulation mechanism that could have brought

275 population A to advanced eusociality; and 3) it has the following life-history properties: offspring are

276 produced in two subsequent broods, first-brood individuals are maternally manipulated in a detectable

277 way (e.g., via coercion), and some of the first-brood offspring stay as adults in the maternal patch. Then,

278 the ancestral probability of resistance (q_0) and of staying spontaneously (x_0) for population A can be

279 estimated in population B (Fig. 6B). The ancestral probability of resistance (q_0) is given by the fraction

280 of the manipulated first brood that leave the maternal patch (gray area on the left side of Fig. 6B). In

281 contrast, the ancestral probability of spontaneously staying (x_0) corresponds to the fraction of the first

282 brood that stay without being manipulated (white area on the right side of Fig. 6B).

283   A large resistance probability in population B rejects the hypothesis that the advanced eusociality in

284 population A arose from the resolution of a conflict caused by the manipulation mechanism evaluated

285 in B. An imperfect resistance probability in B is consistent with advanced eusociality via resolution of

286 manipulation conflict in A (black line in Fig. 6A). Similarly, a small probability of staying spontaneously

287 in population B rejects the hypothesis that the advanced eusociality in population A arose because the

288 evolution of helping efficiency rendered spontaneous behavior favored. A substantial probability of

289 staying spontaneously in population B is consistent with advanced eusociality in A arising because the

290 evolution of helping efficiency rendered staying spontaneously favored (dashed gray line in Fig. 6A).

291 However, these conclusions are very difficult to draw in practice, particularly because of requirement 2)

292 according to which the population must be naive to the manipulation mechanism evaluated.

Discussion

294 Manipulation allows unlikely behaviors to evolve (Dawkins, 1982, Hughes *et al.*, 2012). A puzzle with

295 manipulation is that the evolution of resistance to manipulation can reduce or eliminate the

296 manipulated behaviors (e.g., Parker and Macnair, 1979, Clutton-Brock and Parker, 1995, Gavrilets and

297 Hayashi, 2006, Reuter and Keller, 2001, Kawatsu, 2013). However, the benefits and costs of the

298 manipulated behavior can evolve if they have a genetic basis (Charlesworth, 1978, Worden and Levin,

299 2007, Akçay and Roughgarden, 2011). Benefits and costs of a manipulated behavior can have a genetic

300 basis since they depend on the extent with which the manipulated behavior is expressed. Yet, how the

301 evolution of payoffs can affect the nature and outcome of the conflict is not known. I have shown that

302 the manipulation conflict can disappear as a result of the evolution of payoffs released by manipulation.

303 The reason is that manipulation can simultaneously favor resistance and the efficiency with which the

304 manipulated behavior is expressed. Since the conflict disappears, I refer to the resulting behavior as

305 being induced rather than as being manipulated. The resolution of conflict has implications for our

306 understanding of the evolution of advanced eusociality in particular, and for the evolution of

307 manipulated behavior in general.

Ancestrally imperfect resistance and costly inefficiency allow for conflict resolution

309 The conflict can be eliminated if two key factors occur. First, inefficiency at expressing the manipulated

310 behavior must be costly ($c_{\text{ineff}} > 0$). When manipulated, an individual has two options for rebelling: it

311 can either refrain from performing the manipulated behavior (i.e., referred to as resistance), or it can

312 perform the behavior inefficiently. The evolution of these two forms of rebellion can be decoupled

313 because one can be costlier than the other. For simplicity, I have assumed that resistance is costless,

314 and have focused on the effect of costly inefficiency. Inefficiency is costly if the cost of being delayed in

315 the maternal patch is larger than the benefit of exploiting the maternal patch ($c_d > b_e$). That is,

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316 inefficiency is costly if the fraction of reproductive opportunities missed by having delayed dispersal is

317 greater than the increased probability to reproduce due to exploiting the maternal patch. If inefficiency

318 is costly, then helping efficiency can increase even if resistance is also favored (compare conditions (4b)

319 and (4c)). Acquiescence becomes favored if helping efficiency becomes large enough. Once

320 acquiescence is favored, the conflict disappears. After the conflict is resolved, both inducing and

321 induced individuals favor the induced behavior, even if the cost of inefficiency disappears.

322   Second, for the conflict to be eliminated, resistance must be initially imperfect. I have assumed that

323 the manipulated behavior is performed entirely by the subjects of manipulation. So, if they resist with

324 full probability, no manipulated behavior is expressed regardless of how hard manipulators try. In

325 consequence, acquiescence can only be obtained if the probability of resistance is ancestrally imperfect

326 (González-Forero and Gavrilets, 2013). Ancestrally imperfect resistance allows induced behavior to be

327 obtained under more lax conditions than spontaneous behavior. The reason stems from the

328 observation that the evolution of helping efficiency can render both acquiescence and spontaneous

329 behavior favored if they are already present ancestrally. Spontaneous behavior is unlikely to be present

330 ancestrally because it is selected against before ecological conditions make it favorable. In contrast,

331 acquiescence is more likely to be present ancestrally because of the absence of selection for resistance

332 before manipulation arises.

333   Acquiescence is likely to be present ancestrally depending on how manipulation is executed. Before

334 manipulation starts evolving, there is no initial selection pressure for resistance. Hence, if manipulation

335 is ancestrally executed in a way that subjects of manipulation have not evolved the means to detect,

336 ancestrally imperfect resistance can be expected. Subtle forms of manipulation can then be particularly

337 likely to yield induced behavior.

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Major transitions via conflict resolution

The outcome of conflict resolution is consistent with requirements for a major evolutionary transition in general and for advanced eusociality in particular. Major evolutionary transitions involve the evolution of high levels of cooperation and low levels of conflict (Queller and Strassmann, 2009). Conflict resolution yields here an efficient helping behavior that is induced by the mother and over which there is no conflict between inducing and induced individuals. The high helping efficiency corresponds to high levels of cooperation, while the elimination of conflict produces the required low levels of conflict, thereby fulfilling these requirements for a major transition. On the other hand, advanced eusociality involves 1) maternally induced workers, 2) high levels of specialization of workers and reproductives, and 3) relatively minor conflict in workers regarding their helping role (Wilson, 1971, Michener, 1974, Sherman *et al.*, 1991, Crespi and Yanega, 1995, Hölldobler and Wilson, 2009, Bignell *et al.*, 2011). Maternal manipulation results in 1) maternally induced helping, 2) high helping efficiency, and 3) elimination of conflict between inducing and induced individuals, which directly relate to each of the three mentioned characteristics of advanced eusociality. However, the high maternal fertility observed in the specialization of reproductives is not a consequence of the present model (Figs. S5 and S6 in the SI).

Conflict resolution reinterprets the role of parental manipulation in advanced eusociality. The hypothesis of eusociality via parental manipulation indicates that offspring evolve helping behaviors because of parental influence (Alexander, 1974). Parental manipulation is thought to be relevant for primitive eusociality where the small colony sizes allow the mother to coerce offspring into helping (West, 1967, Michener and Brothers, 1974, Brand and Chapuisat, 2012). However, whether or not parental manipulation is relevant for the evolution of advanced eusociality is less clear, because the large colony sizes would make it impracticable for the mother to coerce offspring into helping (Keller and Nonacs, 1993).

18

362   There are at least two kinds of predictions available to assess whether or not parental manipulation

363   occurs in advanced eusocial taxa. A first kind of prediction assumes that the manipulation conflict

364   results in arms races. Predictions of the first kind indicate that the manipulation mechanism (e.g.,

365   queen pheromones, and cuticular hydrocarbons) should evolve fast, be highly divergent among species

366   (Brunner *et al.*, 2011), and should not honestly signal the queen's condition (Keller and Nonacs, 1993). A

367   second kind of prediction assumes that there is a single winner of the manipulation conflict.

368   Predictions of the second kind indicate that if the mother wins the conflict, the maternal preference is

369   satisfied and the fraction of rebellious workers (e.g., those activating their ovaries) should be

370   independent of sister-sister relatedness because the mother is equally related to her female offspring. In

371   contrast, if offspring win the conflict, the offspring preference is satisfied and the fraction of rebellious

372   workers should covary with sister-sister relatedness (Wenseleers *et al.*, 2004, van Zweden *et al.*, 2013).

373   The empirical evidence has not been conclusive, but parental manipulation is only weakly supported in

374   some species (Heinze and d'Ettorre, 2009, Brunner *et al.*, 2011, van Zweden *et al.*, 2013).

375   The assumptions of the available predictions for testing whether or not parental manipulation

376   occurs in advanced eusociality do not apply if the manipulation conflict is eliminated. After the conflict

377   disappears, evolutionary arms races between inducing and induced individuals are not expected.

378   Instead, the mother and offspring agree on the offspring's helping role, and should thereafter coevolve

379   in a mutualistic manner. In addition, after the conflict disappears, there is not a single winner of the

380   conflict in the sense of whose preferred outcome is more satisfied, because in this sense both parties

381   win. The resolution of conflict aligns the fitness interests of mother and offspring and both attain their

382   maximum inclusive fitness for their current circumstances. The fraction of rebelling workers after the

383   manipulation conflict is resolved may thus covary with sister-sister relatedness since workers are still

384   able to pursue their own inclusive fitness interests. In addition, large colony sizes are compatible with

385   ancestral manipulation because after the conflict is resolved the mother need not coerce offspring into

19

386 helping. However, conflict may arise again if the mother evolves multiple mating as it may increase her

387 productivity (Mattila and Seeley, 2007). Finally, the prediction that manipulation mechanisms should

388 not constitute honest signals is not expected after conflict resolution since it is possible that ancestral

389 manipulation is co-opted into honest signaling after the conflict is eliminated (see below).

Manipulation could either be lost or be co-opted as communication after conflict resolution

391 Conflict resolution could either eliminate selection for manipulation or it could co-opt manipulation

392 into communication. After conflict resolution, manipulation may become disfavored. Since induced

393 individuals are now favored to express the induced behavior, they may be selected to express it even if

394 manipulation is not present. Suppose that first-brood individuals receive environmental cues (e.g.,

395 temperature or humidity) that inform them that they belong to the first brood rather than to the second

396 one. In that case, manipulation becomes unnecessary and first-brood offspring develop as workers

397 following environmental cues. Hence, manipulation could decrease and disappear. Even in the absence

398 of manipulation, the behavior is maintained since the attained helping efficiency renders the behavior

399 favored by selection. However, the behavior is not socially induced anymore, and it becomes

400 environmentally induced instead.

401   Alternatively, manipulation may continue to be favored after the conflict is eliminated. Now suppose

402 that first brood individuals receive no reliable cues to inform them of the brood they belong to. If

403 manipulation is reduced, helpers may develop in the second brood. Since second-brood helpers do not

404 have recipients of their help, the possibility of second-brood helpers makes manipulation still favored

405 in order to prevent second brood helpers. Manipulation is then maintained after the conflict

406 disappears. In this case, manipulation is maintained to inform first-brood offspring about the brood

407 they belong to. Manipulation is thus co-opted as communication.

408   The co-option of manipulation as communication also suggests a hypothesis for the evolution of

20

409 royal jelly in honey bees. In honey bees, royal jelly is given to individuals which induces them to develop

410 into reproductives. That is, individuals are induced to become reproductive rather than workers. The

411 existence of royal jelly is puzzling because individuals should attempt to become reproductive by

412 default. Indeed, it is further puzzling that royal jelly enhances the reproductive abilities of *Drosophila*

413 females (Kamakura, 2011). Why are not these enhanced reproductive abilities in *Drosophila* females

414 present in nature? If manipulation informs offspring about the brood they are in, it may become

415 cheaper to inform reproductives rather than workers. In particular, if the mother starts to produce more

416 workers than reproductives, it may become less expensive to inform reproductives-to-be rather than

417 workers-to-be because there are fewer reproductives. In such a case, induction of reproductives rather

418 than workers would be selected. A mechanism such as royal jelly could then evolve. If reproductives

419 become highly specialized so that they require helpers to survive, their enhanced reproductive abilities

420 triggered by royal jelly are only of use if helpers are available. Then, the enhanced reproductive abilities

421 in *Drosophila* females would be useless in the solitary species.

Assessing whether a behavior stems from ancestral manipulation

423 Two analytical conditions specify when a behavior can result from the resolution of manipulation

424 conflict but not from spontaneous behavior. First, the ancestral resistance probability must be

425 sufficiently small (condition (6a) is met). Second, spontaneous behavior must be ancestrally disfavored

426 or, more generally, its ancestral probability must be sufficiently small (condition (S15b) in the SI is not

427 met). Although ancestral conditions cannot be directly estimated except in experimental evolution,

428 indirect estimation of ancestral conditions in extant populations may be possible (Fig. 6B). In addition,

429 estimation of costs, benefits, and relatednesses is very difficult in practice. However, the model defines

430 costs and benefits in a specific manner which may help address this difficulty.

431 The model presented here is deliberately simple so that complete analytical treatment is possible.

21

432 Enhancing its realism necessarily affects many of its properties. For example, I assumed that

433 manipulation and resistance are costless. However, costs of manipulation and resistance that are either

434 constant or functions of manipulation and resistance can qualitatively change the dynamics (Reuter

435 *et al.*, 2004). When comparing induced and spontaneous behavior, I assumed that the ancestral benefit

436 b_0 and the ancestral cost c_0 are the same under both scenarios. Yet, the ancestral helping efficiency can

437 be different between these scenarios because individuals may help more or less depending on whether

438 or not and how they were manipulated. I also assumed competition to be global, so the effects of local

439 competition in the conflict resolution remain to be elucidated. In addition, I ignored the effect of

440 genetic drift, which can take the evolutionary trajectories out of the basin of attraction toward induced

441 behavior. Finally, I assumed that the mother manipulates both sexes equally and that both sexes are

442 equally efficient. Although sexually unbiased manipulation and sexually unbiased efficiency are

443 realistic assumptions for diploid genetic systems with ancestral biparental care, they are not proper

444 assumptions for haplodiploids where only maternal care is expected to occur ancestrally. An extension

445 of the model to include sex-differential manipulation and sex-differential efficiency is more appropriate

446 to assess conflict resolution in haplodiploids.

447 **Conflict resolution in broader contexts**

448 Conflict resolution may similarly occur in other settings where manipulation and resistance coevolve.

449 The model was built for a specific mother-offspring setting so that dynamic analysis is possible.

450 However, the key factors of the process are independent of the mother-offspring setting. Manipulation,

451 resistance, and the efficiency of the manipulated behavior are properties that occur across biological

452 and cultural systems. The necessary factors for conflict elimination, namely ancestrally imperfect

453 resistance and inefficiency costs, can occur widely in evolving systems as well.

454   Although the manipulation conflict in this model only resolves if the subjects of manipulation and

22

455 the targets of the manipulated behavior are related (in the model, the "targets" are second-brood

456 offspring; see condition (7b)), the process is in principle not limited to family settings. The conflict may

457 also resolve if subjects and targets are unrelated for at least three reasons. First, relatedness may be

458 unnecessary if resistance is costlier than acquiescence (González-Forero and Gavrilets, 2013). Second,

459 in the model, relatednesses measure the correlation in the heritable components of the traits between

460 actors and recipients of the traits (Frank, 1998, 2013). These correlations may arise from at least six

461 different processes, only one of which requires a family setting. Those processes are: 1) kinship (as in

462 kin selection) (Hamilton, 1964, 1970); 2) conditional response to partner's behavior (e.g., help only if

463 helped; as in reciprocity) (Queller, 1985, Frank, 1994, Fletcher and Zwick, 2006); 3) biased assortment

464 among groups (e.g., helpers being more common in some groups than in others; as in group selection)

465 (Queller, 1985, Fletcher and Doebeli, 2009); 4) manipulation (e.g., by changing partner's behavior to

466 match yours); 5) punishment (e.g., by changing payoffs so that the partner changes its behavior); or 6)

467 partner choice (e.g., by changing partner) (Queller, 2011). Third, if relatedness is negative, induced

468 behaviors that harm the targets of the induced behavior could be obtained (which may be modeled by

469 letting $b_{\max} < 0$, causing $b < 0$) (González-Forero and Gavrilets, 2013).

470   The resolution of conflict as a result of the evolutionary process released by manipulation itself

471 renders manipulation both more likely to be important in nature and more difficult to detect.

472 Increasing the testability of manipulation becomes then a potentially rewarding challenge.

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23

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Appendix

Dynamic equations

The time is discrete. The number of individuals in class i at the current time step is $N_i(t)$. The number of individuals in class i in the next time step is $N_i(t+1)$, which is given by the i-th entry in the column vector $\mathbf{N}(t+1) = \mathbf{W}\mathbf{N}(t)$. For simplicity, fathers can be disregarded and it is enough to keep track of mothers only. Letting the class order in the vector $\mathbf{N}$ be mothers, first brood, and second brood, the transition matrix is

$$\mathbf{W} = \begin{pmatrix} 0 & s_1 & s_2 \\ f_1 & 0 & 0 \\ f_2 & 0 & 0 \end{pmatrix}, \tag{9}$$

where s_k is the survival of k-th-brood offspring (i.e., the probability that k-th-brood offspring become mothers) and f_k is the maternal fertility through k-th-brood offspring (i.e., the number of offspring produced as brood k).

For simplicity, I assume that the fraction of female offspring produced is the same in the first and second broods. Let σ be the fraction of offspring that are female. Because for first- and second-brood offspring to become mothers they must be female, then the survival of first-brood offspring is

$$s_1 = \sigma[p_m(1-q_1)(s_0 - c) + p_m q_1 s_0 + (1 - p_m)s_0] \tag{10a}$$

$$= \sigma[s_0 - c p_m(1 - q_1)]. \tag{10b}$$

Let Q be the average resistance probability among manipulated first-brood offspring in the maternal patch. Then, the survival of second-brood offspring is

$$s_2 = \sigma[p_m(1-Q)(s_0 + b) + p_m Q s_0 + (1 - p_m)s_0] \tag{11a}$$

$$= \sigma[s_0 + b p_m(1 - Q)]. \tag{11b}$$

30

Let α be the fraction of offspring that belong to the first brood, and let n be the total number of offspring that a mother produces. Each offspring must be weighted by the genetic contribution towards it (Taylor, 1990). The genetic contribution of the mother toward offspring of sex i is η_i (i.e., for sexual diploids, $\eta_i = 1/2$; for haplodiploids, $\eta_{\female} = 1/2$ while $\eta_{\male} = 1$). The genetic contribution of a mother to her offspring is thus on average $\eta = \sigma\eta_{\female} + (1-\sigma)\eta_{\male}$. Hence, maternal fertility through first and second broods is

$$f_1 = \eta\alpha n \tag{12a}$$

$$f_2 = \eta(1-\alpha)n. \tag{12b}$$

From eq. (29) in Taylor and Frank (1996) and eqs. (6) and (2) in Frank (1997), assuming weak selection and weak mutation, the evolutionary change in the population-average value trait value z ($= p, q, y$) can be approximated by

$$\frac{dz}{dt} = V_z \sum_{ij} v_i \frac{dw_{ij}}{dg_z} u_j \Bigg|_{\mathbf{z}_a=\mathbf{z}} \tag{13a}$$

$$= V_z \left(v_m \frac{ds_1}{dg_z} u_1 + v_m \frac{ds_2}{dg_z} u_2 \right. \tag{13b}$$

$$\left. + v_1 \frac{df_1}{dg_z} u_m + v_2 \frac{df_2}{dg_z} u_m \right) \Bigg|_{\mathbf{z}_a=\mathbf{z}}, \tag{13c}$$

600   where w_{ij} is the ij-th entry in the transition matrix $\mathbf{W}$, g_z is the breeding value for trait z in the actor, V_z

601   is the additive genetic variance for trait z, v_i is the individual reproductive value for class-i individuals,

602   u_j is the equilibrium frequency of class j individuals, and traits are evaluated at the population-average

603   value [i.e., $\mathbf{z}_a = (p_m, q_1, Q, y, Y) = \mathbf{z} = (p, q, q, y, y)$].

Equilibrium class frequencies u_i and individual reproductive values v_i can be respectively obtained from the equations

$$\lambda\mathbf{N} = \mathbf{W}\mathbf{N} \tag{14a}$$

$$\lambda\mathbf{N}^T = \mathbf{N}^T\mathbf{W}, \tag{14b}$$

31

where T denotes transposition and the equations are evaluated at the population averages. The equilibrium frequencies u_i are obtained by solving for N_i in eq. (14a) and dividing the solution by $\sum N_i$. The individual reproductive values v_i are obtained by solving for N_i in eq. (14b) together with the condition that the sum of class reproductive values is 1 (i.e., $\sum u_i v_i = 1$, where $u_i v_i$ is the reproductive value of class i). The quantity λ is the dominant eigenvalue of the transition matrix $\mathbf{W}$, which gives the asymptotic growth rate of the population. These calculations yield the equilibrium class frequencies

$$u_m = \frac{\lambda}{\lambda + f_1 + f_2} \tag{15a}$$

$$u_1 = \frac{f_1}{\lambda + f_1 + f_2} \tag{15b}$$

$$u_2 = \frac{f_2}{\lambda + f_1 + f_2}, \tag{15c}$$

the individual reproductive values

$$v_m = \frac{\lambda + f_1 + f_2}{2\lambda} \tag{16a}$$

$$v_1 = \frac{s_1}{\lambda} v_m \tag{16b}$$

$$v_2 = \frac{s_2}{\lambda} v_m. \tag{16c}$$

and the asymptotic growth rate

$$\lambda = \sqrt{f_1 s_1 + f_2 s_2} \tag{17a}$$

$$= \sqrt{\eta \sigma n \left\{ s_0 + p(1-q)\left[(1-\alpha)b - \alpha c\right]\right\}}. \tag{17b}$$

604   Because the available resources for offspring production only allow the mother to produce a number

605   of offspring that maintains the population size constant, the number of offspring is

$$n = \frac{1}{\eta \sigma \left\{ s_0 + p(1-q)\left[(1-\alpha)b - \alpha c\right]\right\}}, \tag{18}$$

606   in which case the asymptotic growth rate is $\lambda = 1$. Since competition is global, the number of offspring

607   n depends on the population-average trait values p, q, and y rather than on local average trait values.

32

608   Hence, because the breeding values of actors are uncorrelated with population averages, the derivatives

609   of fertility in line (13c) are zero.

Therefore, the dynamic equations specified by eq. (13) are

$$\frac{dp}{dt} = V_p v_m u_m \sigma (1 - q) (b r_{2m} - c r_{1m}) \tag{19a}$$

$$\frac{dq}{dt} = -V_q v_m u_1 \sigma p (b r_{21} - c) \tag{19b}$$

$$\frac{dy}{dt} = V_y v_m u_1 \sigma p (1 - q) [b_{\max} r_{21} - (c_{\text{eff}} - c_{\text{ineff}})], \tag{19c}$$

610   where $r_{ji} = \rho_{ji} u_j / u_i$. The quantity $\rho_{ji} = dg_{z_j} / dg_{z_i}$ is the regression relatedness of an actor in class i

611   toward a recipient in class j, where g_{z_j} is the breeding value for z in the recipient and g_{z_i} is that in the

612   actor. Hence, r_{ji} is an equilibrium relatedness.

33

613 **Figure legends**
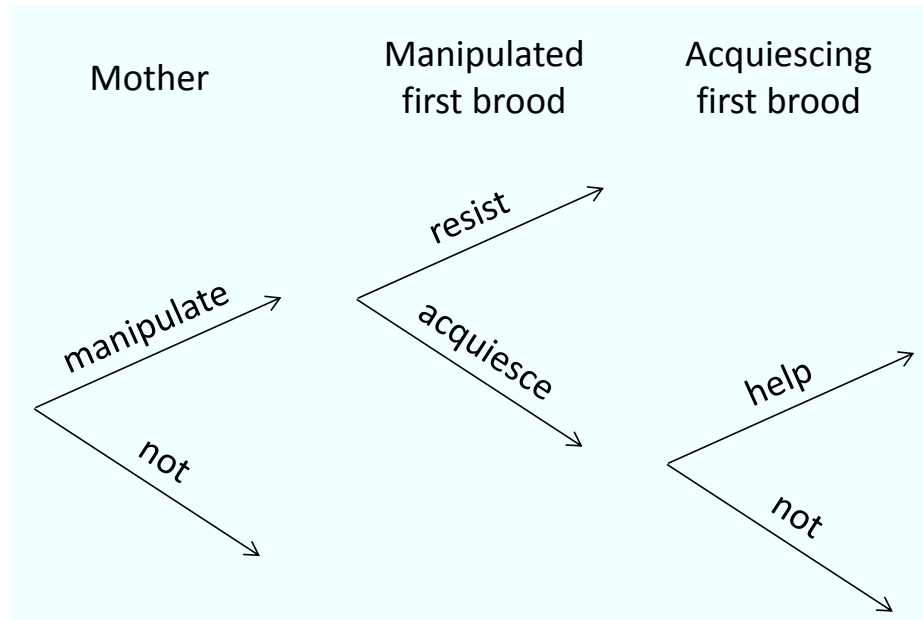
Figure 1: The three decisions individuals can make. Mothers manipulate with probability p first-brood offspring to stay as adults. Manipulated first-brood offspring resist with probability q and leave without delay. Otherwise, they acquiesce with probability $1 - q$ and stay for some period. Acquiescing individuals help with probability y to raise the second brood.
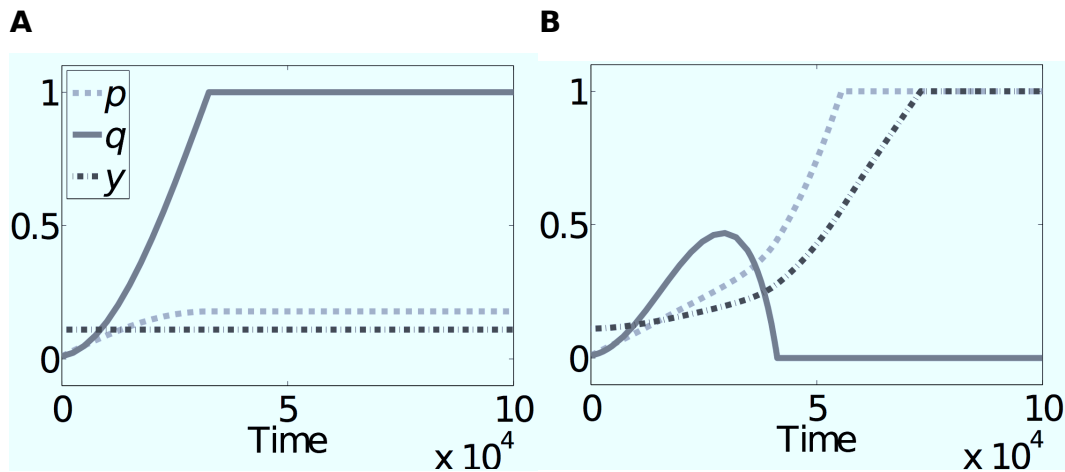
Figure 2: Coevolution of manipulation p, resistance q, and helping efficiency y. Numerical solutions of eqs. (19) are shown. (A) There is no genetic variation for helping efficiency ($V_y = 0$). Resistance evolves and eliminates the manipulated behavior (i.e., the probability that first-brood offspring stay in the maternal patch is $p^*(1 - q^*) = 0$ at the end). (B) Same conditions as in (A), but there is genetic variation for helping efficiency ($V_y = 0.001$). Helping efficiency increases and after $\approx 30 \times 10^3$ generations, resistance decreases and is eliminated. The remaining parameter values for both panels are $p_0 = q_0 = 0.01$, $y_0 = 0.11$, $\rho = \rho_{1m} = \rho_{2m} = 1/2$, $V_p = 0.001$, $V_q = 0.1$, $\alpha = \sigma = \eta = s_0 = 1/2$, $c_{\text{eff}} = 0.2$, and $c_{\text{ineff}} = 0.012$.
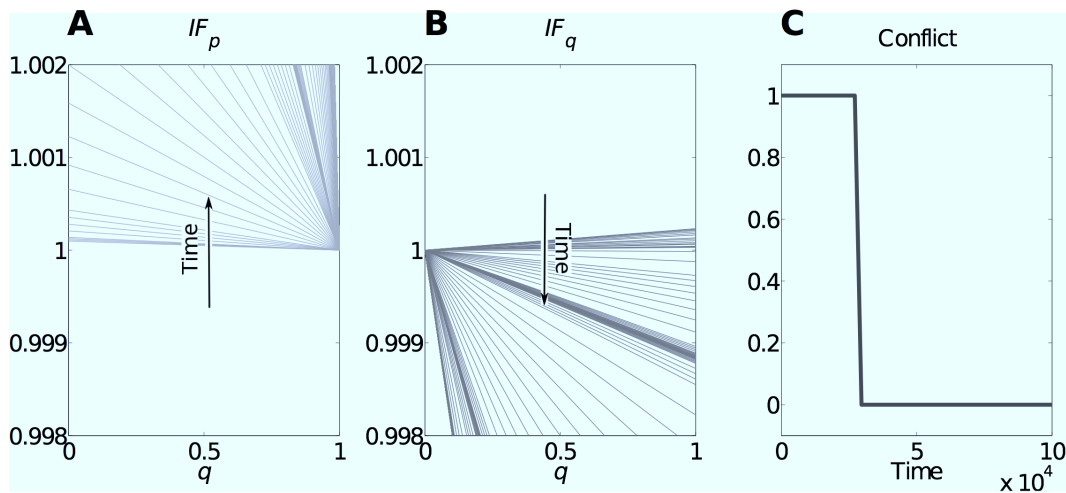
Figure 3: Evolutionary resolution of manipulation conflict. (A) Mother's inclusive fitness through manipulation IF_p vs. possible values of resistance q during the process in Fig. 2B. The lowest line is mother's inclusive fitness at time 1 in Fig. 2B, and the lines further up correspond to mother's inclusive fitness as time increases. (B) First-brood offspring's inclusive fitness through resistance IF_q vs. possible values of resistance during the process in Fig. 2B. The highest line is offspring's inclusive fitness at time 1 in Fig. 2B, and the lines further down correspond to offspring's inclusive fitness as time increases. In (A), the optimum inclusive fitness for the mother is at $q = 0$ throughout, while in (B) the optimum inclusive fitness for first-brood offspring is initially at $q = 1$ and later at $q = 0$. (C) The level of conflict over time. The level of conflict is the distance between the preferred trait values of the two parties. After $\approx 30 \times 10^3$ generations, the conflict disappears. For the three panels, the same parameter values are used as in Fig. 2B. The inclusive fitness through trait i $(= p, q)$ is $IF_i = IF_0 + i h_i$, where the baseline inclusive fitness (IF_0) is set to 1, and the inclusive fitness effect of trait i (h_i) is given by the right-hand side of eqs. (19a) or (19b) divided by V_i respectively. The level of conflict is $C = |\max_q(IF_p) - \max_q(IF_q)|$, where $\max_q(x)$ gives the resistance q that maximizes x.
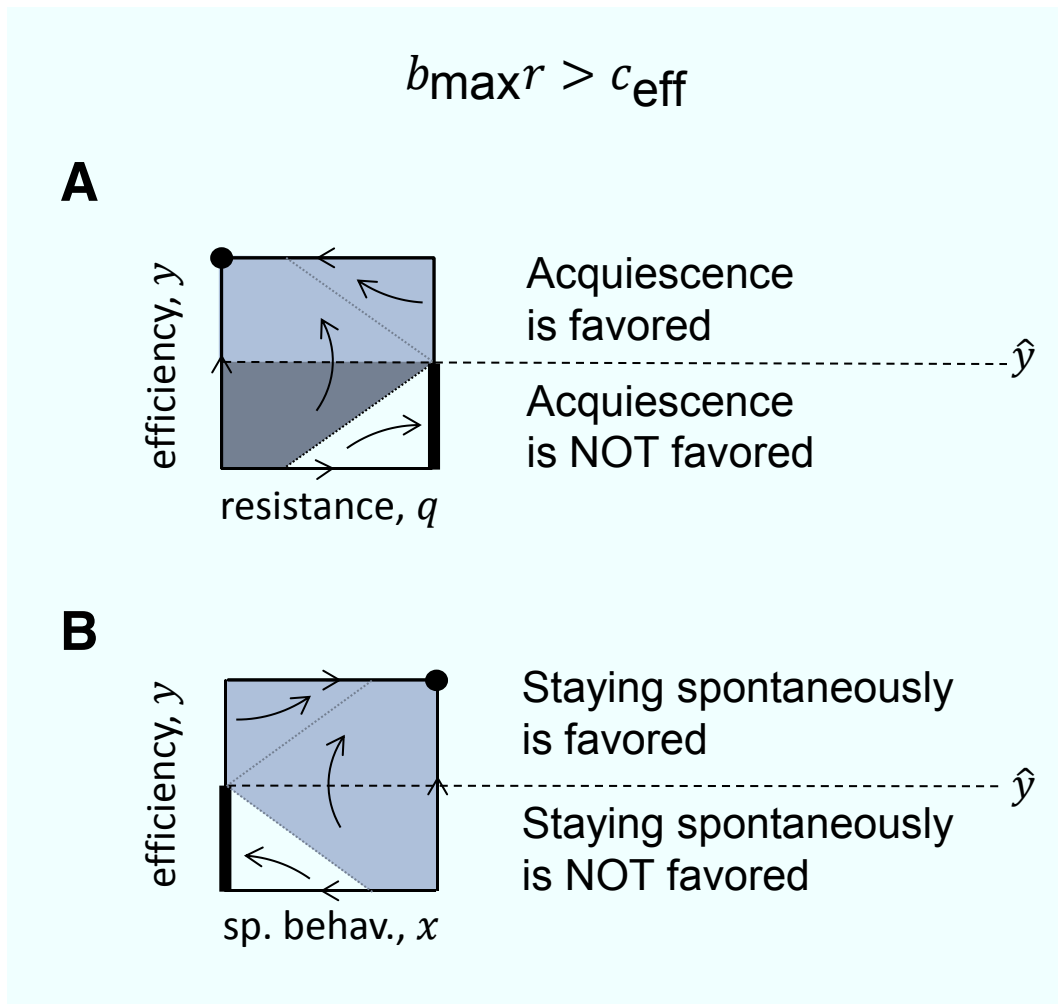
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Figure 4: Coevolutionary dynamics of resistance q and spontaneous behavior x with helping efficiency y when $b_{max}r > c_{eff}$. The arrows indicate the direction of change (the arrows at the boundaries indicate the partial change with respect to the direction of the boundary). Thick strokes indicate stable equilibria. (A) Coevolution of resistance q and helping efficiency y. Acquiescence is disfavored below the dashed line and is favored above it. The dashed line is the critical helping efficiency $\hat{y} = c_{ineff}/S$ (obtained from ineq. (4b)). If the population starts in the gray areas, it converges to acquiescence and maximum helping efficiency (large dot). Thus, for final acquiescence, acquiescence need not be favored initially if the probability of resistance is initially sufficiently small (i.e., if the population starts in the dark gray area). (B) Coevolution of spontaneous behavior x and helping efficiency y. If the population starts in the gray area, it converges to spontaneous behavior and maximum helping efficiency (large dot).
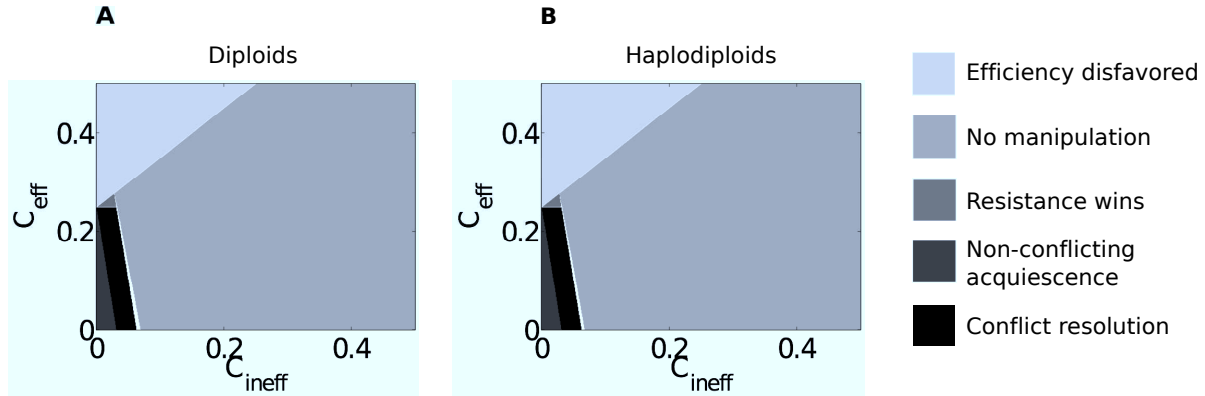
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Figure 5: Conflict resolution across values of efficiency and inefficiency costs. (A) Diploids. (B) Haplodiploids. For both panels, in the lightest gray area, helping efficiency is disfavored. For the other shades, helping efficiency is favored. In addition, for light gray: manipulation does not evolve; for gray: manipulation evolves, but resistance wins; for dark gray: manipulation evolves but acquiescence is favored from the start and it is established at the end; and for black: manipulation and resistance evolve, but resistance is eliminated by the evolution of helping efficiency. Specifically, each region satisfies the following. For the lightest gray, $y(0) > y(1)$; for the other shades $y(0) < y(1)$. In addition, light gray: $p(0) > p(1)$, and $p(\text{end}) < 0.1$; gray: $p(0) < p(1)$, $q(0) < q(1)$, and $q(\text{end}) > 0.9$; dark gray: $p(0) < p(1)$, $q(0) > q(1)$, and $q(\text{end}) < 0.1$; and black: $p(0) < p(1)$, $q(0) < q(1)$, $y(0) < y(1)$, $p(\text{end}) > 0.9$, $y(\text{end}) > 0.9$, and $q(\text{end}) < 0.1$. White areas do not satisfy any of these conditions. The end is at 10^6 generations. Parameter values are as in Fig. 2 except that $V_p, V_q, V_y = 0.01$ and in (B) $\eta_\female = 1/2$, $\eta_\male = 1$, $\eta = \sigma\eta_\female + (1-\sigma)\eta_\male = 3/4$, $\rho = \sigma[\sigma 3/4 + (1-\sigma)1/2] + (1-\sigma)[\sigma/4 + (1-\sigma)/2] = 1/2$, and $\rho_{1m} = \rho_{2m} = \sigma/2 + (1-\sigma) = 3/4$ (regression relatedness values are taken from Bulmer (1994)).
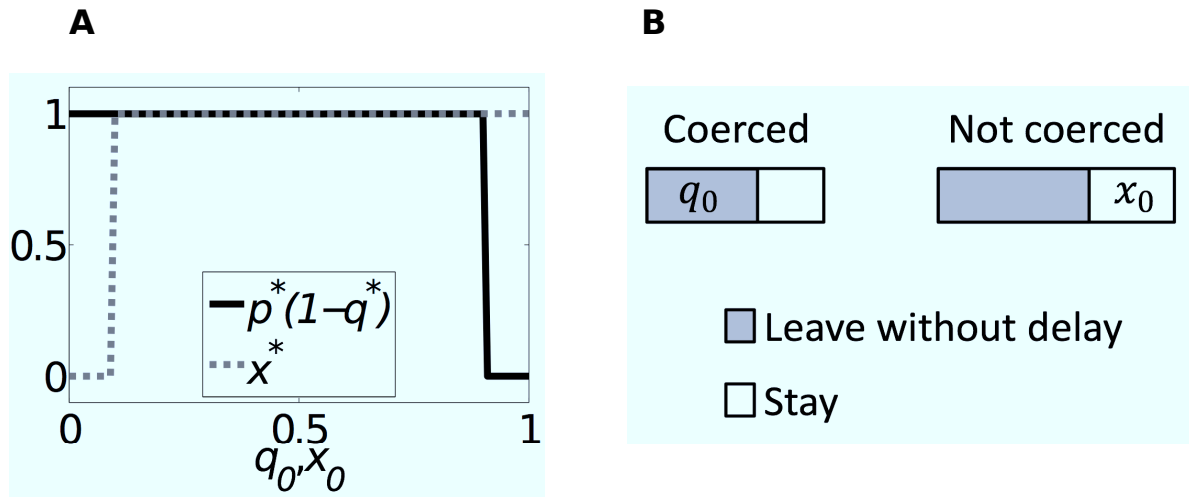
A

B

Figure 6: Discerning between manipulation and spontaneous helping. (A) Equilibrium values for induced and spontaneous behavior. The black line shows the predicted fraction of first brood that stay under manipulation vs. the ancestral resistance probability (q_0). The dashed gray line shows the predicted fraction of first brood that stay under spontaneous behavior vs. the ancestral probability of staying spontaneously (x_0). For advanced eusociality from manipulation, the ancestral resistance probability (q_0) must be small enough. In contrast, for advanced eusociality from spontaneous behavior and the same ecological conditions, the ancestral probability of staying spontaneously (x_0) must be large enough. Parameter values are as in Fig. 2 except that $V_p, V_q, V_x, V_y = 0.01$, $c_{\text{eff}} = 0.06$, and $c_{\text{ineff}} = 0.05$. (B) Estimation of the ancestral probabilities of resistance (q_0) and of staying spontaneously (x_0). A fraction of the first-brood individuals in the ancestral population is maternally coerced. The ancestral probability of resistance (q_0) is given by the fraction of coerced first brood that leave without delay. The ancestral probability of staying spontaneously (x_0) is given by the fraction of non-coerced first brood that stay in the maternal patch for a sufficiently large portion of their adulthood so that their reproductive success is decreased.