

1 One problem, too many solutions: How costly is
2 honest signalling of need?

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21 Abstract

22 The “cost of begging” is a prominent prediction of costly signalling theory, suggesting that
23 offspring begging has to be costly in order to be honest. More specifically, it predicts that there
24 is a single cost function for the offspring (depending on e.g. offspring quality) that maintains
25 honesty and it must be proportional to parent’s fitness loss. Here we show another
26 interpretation of the cost. We demonstrate that cost, proportional to the fitness gain of the
27 offspring, also results in honest signalling. Since the loss of the parent does not necessarily
28 coincide with the gain of the offspring, it is provable that any linear combination of the two cost
29 functions (one proportional to parent’s loss, one to offspring’s gain) also leads to honest
30 signalling. Our results, applied for a specific model, support the previous general conclusion that
31 signalling games have different cost functions for different equilibria. Consequently, costly
32 signalling theory cannot predict a unique equilibrium cost in signalling games especially in case
33 of parent-offspring conflicts. As an important consequence, any measured equilibrium cost in
34 real cases has to be compared both to the parent’s fitness loss and to the offspring’s fitness gain
35 in order to provide meaningful interpretation.

36

37 **Keywords:** parent-offspring conflict, communication, honesty, costly signalling, cost of begging

38

39 Background

40 Parent-offspring communication is a hotly debated topic, continuously in the forefront of
41 behavioural sciences [1-4]. Its appeal stems from the seemingly controversial interests of
42 involved parties. Despite the obvious conflict of interest between parent and offspring [5],
43 offspring frequently solicit food from the parents. In general, this solicitation is found to be
44 honest as more needy offspring begs more intensively [6]. Game theoretical explanations of
45 begging behaviour have gained much attention over the years [7-16]. Most of these game
46 theoretical models predicted costly signalling [7], which became the dominant expectation in
47 past decades.

48 Nöldeke and Samuelson [17] offered an enlightening account of the cost of honest
49 signalling of need. They have demonstrated that at equilibrium (where honest signalling
50 exists), the signalling cost of the offspring is proportional to the fitness loss of the parent
51 resulting from the transfer of resources. They also showed that the factor of proportionality
52 is solely determined by the degree of relatedness between parent and offspring.
53 Consequently, they claimed that the offspring's condition (and its expected benefit due to the
54 received resource) influences the signalling cost only to the extent that it influences the
55 parent's loss of fitness. Here we extend their model and prove that their solution is not unique
56 and that there is another equilibrium with honest signalling where their claim does not apply,
57 but which can be readily derived from their equations [17]. At this second equilibrium, the
58 cost of signalling is proportional to the expected fitness benefit of the offspring, and
59 (analogously to the other case) the parent's fitness loss affects the signalling cost only to the
60 extent it affects the offspring's gain. Moreover, any linear combination of these two cost
61 functions provides an equilibrium with honest signalling. Thus, there is an infinite number of
62 distinct equilibria where honest signalling exists.

63 Methods

64 Nöldeke and Samuelson [17] designed their model based on the seminal work of Godfray [7].
65 They have calculated the fitness functions of the two parties, parent and offspring. The parent is
66 interested in the condition of the offspring to transfer the least amount of resource to maximize
67 its own inclusive fitness (all future offspring included) whereas the offspring is interested in

68 receiving the most amount of resource possible to maximize its own inclusive fitness (all future
69 siblings included). The offspring's condition is described by a strictly positive continuous variable
70 (c). The requirement for signalling stems from the fact that the parent cannot assess this condition
71 directly. The offspring, however, can opt to engage in communication with a (costly) signal (x).
72 In the original model of Nöldeke and Samuelson, x denoted both the level (intensity) and the
73 cost of the signal [17]. Here, we introduce function $f(x)$ as the cost of the signal, and reserve x to
74 denote only the intensity of the signal (depending on the condition c) in order to avoid potential
75 confusion.

76 The parent has control over Z amount of resource that it has to divide between the
77 offspring and itself, where offspring receives part z of Z and parent retains part $y = Z - z$. The
78 inclusive fitness functions of offspring and parent (v and u , respectively, after [17]) are:

$$79 \quad v(c, x, z) = h(c, z) - f(x) + \psi g(Z - z), \quad (\text{Eq. 1})$$

$$80 \quad u(c, x, z) = \gamma(h(c, z) - f(x)) + g(Z - z), \quad (\text{Eq. 2})$$

81 where $h(c, z)$ and $g(Z - z)$ are the direct fitness gains of offspring and parent, respectively, when
82 z amount of resource is transferred to offspring. Both h and g are assumed to be continuously
83 differentiable and increasing functions (accordingly strictly decreasing with z). ψ is the coefficient
84 of relatedness between current offspring (and any future siblings from the parent); and γ is the
85 coefficient of relatedness of the parent to its current (and future) offspring. The offspring
86 strategy is the level of solicitation (x) as function of the offspring's quality (c), whereas the
87 parental strategy is the level of shared resource (z) as a function of offspring solicitation (x).
88

89 Conditions of the honest signalling equilibrium

90 A stable equilibrium of honest signalling requires three conditions to be met: (i) signals must be
91 honest, (ii) parents have to respond to signals and (iii) the equilibrium must be evolutionarily
92 stable. The latter condition implies that there is a pair of optimal parent and offspring strategies
93 ($z^*(x)$, $x^*(c)$) from which it does not worth departing unilaterally for any of the participants [17].
94 At an honest equilibrium, parents know the condition of the offspring as their signal of need
95 directly corresponds to their level of need. Thus, the parent's equilibrium strategy has to
96 maximize the parent's inclusive fitness u for any given c , i.e. the following inequality must hold
97 [17]:

98
$$u(c, x^*(c), z^*(x^*(c))) \geq u(c, x^*(c), z(x^*(c))), \quad (\text{Eq. 3})$$

99 where x^* is the equilibrium signal by the offspring, depending on its own quality and z^* is the
100 parent's equilibrium transfer depending on offspring's signal intensity. Substituting Eq. 2 Into
101 Eq. 3 gives the following condition:

102
$$h(c, z^*(x^*(c))) - f(x^*(c)) + \psi g(Z - z^*(x^*(c))) \geq h(c, z) - f(x^*(c)) + \psi g(Z - z). \quad (\text{Eq. 4})$$

103 Analogously to parent, offspring's equilibrium strategy is to maximize its own inclusive
104 fitness v given the parental equilibrium strategy $z^*(x)$ and the condition of the offspring c .

105 Thus, the following condition must hold for any c and x [17]:

106
$$v(c, x^*(c), z^*(x^*(c))) \geq v(c, x, z^*(x)). \quad (\text{Eq. 5})$$

107 Substituting into Eq. 1 gives the following condition:

108
$$\gamma \left(h(c, z^*(x^*(c))) - f(x^*(c)) \right) + g(Z - z^*(x^*(c))) \geq \gamma \left(h(c, z^*(x)) - f(x) \right) + g(Z - z^*(x)) \quad (\text{Eq. 6})$$

109 In a signalling equilibrium, the parent's transfer must satisfy [17]:

110
$$z^*(x^*(c)) = \tilde{z}(c), \quad (\text{Eq. 7})$$

111 where x^* denotes the offspring's equilibrium signal intensity, z^* the parent's equilibrium transfer,
112 and $\tilde{z}(c)$ the parent's optimal transfer.

113 Results

114 The argument of Nöldeke and Samuelson [17] is as follows: the cost of signal at equilibrium
115 has to dispense the conflict of interest between parent and offspring. Accordingly, the two
116 solution functions of h and g of the optimization problems of parent and offspring have to
117 give the same result (see [18] for more general results). In the absence of signalling cost, at
118 the maximum of the offspring's inclusive fitness, the following conditions must be met:

119
$$h_z(c, z) - \psi g_y(Z - z) = 0, \quad (\text{Eq. 8})$$

120
$$h_z(c, z) - \frac{1}{\gamma} g_y(Z - z) = 0, \quad (\text{Eq. 9})$$

121 where subscripts denote derivatives with respect to the variable. At the optimum, the
122 derivatives of the two components of the fitness gain must equal:

123
$$h_z(c, z) = \psi g_y(Z - z), \quad (\text{Eq. 8a})$$

124
$$h_z(c, z) = \frac{1}{\gamma} g_y(Z - z). \quad (\text{Eq. 9a})$$

125 Clearly, the marginal fitness gain of the offspring (in the absence of signal cost) is different from

126 the offspring's point of view (Eq. 8a) than from the parent's point of view (Eq. 9a), hence they
 127 maximize different functions. Thus, there is a clear conflict of interest between parent and
 128 offspring. An illustration of this conflict and the corresponding trade-off can be seen on Figure 1.
 129 The shape of these trade-offs is different since the weights of the parental fitness component
 130 (g) and the offspring fitness component (h) are different for the offspring and the parent. The
 131 fitness components of the inclusive fitness of the offspring and the parents change alongside the
 132 blue and yellow curve respectively with increasing value of z . The trade-off implies that one
 133 component cannot be increased without the loss of fitness in the other component. Blue and
 134 yellow star represents optimal resource allocation and blue and yellow dot indicates the position
 135 (fitness) of the offspring and the parent respectively when the resource allocation is optimal for
 136 the other party. Clearly the dots do not overlap with the stars, hence the optimal resource
 137 allocation of one party is not optimal for the other.

138 Nöldeke and Samuelson [17] proposed that the cost of signals should resolve this conflict in the
 139 honest signalling equilibrium. They [17] proposed the following cost function:

$$140 \quad L_1(z) = g(Z - z^0) - g(Z - z), \quad (\text{Eq. 10})$$

141 where z^0 is the resource requirement of the offspring in the least needy condition, that is $z^0 =$
 142 $\min_c \tilde{z}(c)$ [17]. The cost at equilibrium is:

$$143 \quad f_1(x^*(c)) = \left(\frac{1}{\gamma} - \psi\right) (g(Z - z^0) - g(Z - \tilde{z}(c))) = \left(\frac{1}{\gamma} - \psi\right) L_1(\tilde{z}(c)), \quad (\text{Eq.11})$$

144 where $\frac{1}{\gamma} - \psi$ defines the magnitude of the parent-offspring conflict. In equilibrium, $z = \tilde{z}(c)$.

145 The relationship between $f(x)$ and $L(*)$ discussed further in *ESM Appendix 1*.

146 So far, we have followed the design of Nöldeke and Samuelson [17]. However, starting from
 147 the same equations (Eqs. 8 and 9), a different cost function of signalling can also be obtained.
 148 Instead of providing the optimality conditions to calculate the offspring's marginal fitness
 149 gain, one can similarly rearrange Eqs. 8 and 9 to calculate the parental marginal fitness gain,
 150 from the offspring's point of view (without signal cost):

$$151 \quad g_z(Z - z) = -\frac{1}{\psi} h_z(c, z), \quad (\text{Eq. 12})$$

152 and from the parent's point of view:

$$153 \quad g_z(Z - z) = -\gamma h_z(c, z). \quad (\text{Eq. 13})$$

154 Clearly, in the absence of signal cost, the marginal fitness gain of the parent (as a function of

155 resource allocation) is different from the offspring's point of view (Eq. 11) than from the parent's
 156 point of view (Eq. 12). This still implies the conflict of interest. Following the same logic as above,
 157 at the honest signalling equilibrium, these equations have to provide the same results. That is,
 158 the parent's optimum has to be the same, viewed either from the offspring's or from the parent's
 159 aspect. Thus, just as before, the difference between the right-hand sides of Eqs. 11 and 12 gives
 160 the cost that has to be subtracted from the offspring fitness so that the two equations result in
 161 the same optimum. The cost function we propose is:

$$162 \quad L_2(c, z) = h(c, z) - h(c, z^0), \quad (\text{Eq. 14})$$

163 and the cost at equilibrium is:

$$164 \quad f_2(x^*(c)) = (1 - \gamma \psi) (h(c, \bar{z}(c)) - h(c, z^0)) = (1 - \gamma \psi) L_2(c, \bar{z}(c)). \quad (\text{Eq. 15})$$

165 The existence of the signalling equilibrium can be proved as before (see *ESM Appendix 2*).

166 So far, we have proved that there are two honest signalling equilibria corresponding to
 167 two different cost functions. Since each of these cost functions can remove the conflict of
 168 interest between parent and offspring, it follows that any linear combination of the functions
 169 is also a solution to the optimization problem. Thus, the general cost function of the optimum
 170 strategies is as follows:

$$171 \quad L(c, z) = \alpha \left(\frac{1}{\gamma} - \psi \right) L_1(z) + (1 - \alpha)(1 - \gamma \psi) L_2(c, z). \quad (\text{Eq. 16})$$

172 The cost at equilibrium is:

$$173 \quad f(x^*(c)) = \alpha \left(\frac{1}{\gamma} - \psi \right) L_1(\bar{z}(c)) + (1 - \alpha)(1 - \gamma \psi) L_2(c, \bar{z}(c)).$$

174

175 Finally, we provide a numerical example using Godfray's [7] equations. Godfray used the
 176 following equations for the offspring's and parent's fitness contributions, respectively [7]:

$$177 \quad h(c, z) = U(1 - \exp(-cz)), \quad (\text{Eq. 15})$$

$$178 \quad g(Z - z) = G(Z - z), \quad (\text{Eq. 16})$$

179 where U and G are constants. From now on, we use the values provided by Godfray [7]: $U = 1$,
 180 $G = 0.08$. Figure 1 shows the actual inclusive fitness values for parent and offspring (u of Eq. 2
 181 and v of Eq. 1, respectively) when there is no cost of signalling, as functions of the quality of the
 182 offspring c and parental resource allocation z . Figure 2 also shows the equilibrium transfer
 183 function for parent and for offspring (red curve), which corresponds to the optimal resource

184 allocation for the offspring and the parent, respectively (as a function of c). Figure 2 clearly
185 demonstrates that the optima are at different z values for the two parties.

186 Substituting Godfray's equation (Eqs. 15, 16) into the cost function defined by L_1 (Eq. 10)
187 results in:

$$188 \quad L_1(z) = \left(\frac{1}{\gamma} - \psi\right) G(z - z^0). \quad (\text{Eq. 17})$$

189 Substituting the same equations into the cost function defined by L_2 (Eq. 13), results in:

$$190 \quad L_2(c, z) = (1 - \gamma\psi)U(\exp(-cz^0) - \exp(-cz)). \quad (\text{Eq. 18})$$

191 Figure 3 show the same trade-off as Figure 1 just with cost function added to the offspring
192 inclusive fitness (Eqs 1,2). Figure 3A show the new cost function, Figure 3C shows the cost
193 function proposed by Nöldeke and Samuelson [17], while Figure 3B shows a linear
194 combination of the two functions ($\alpha=0.5$). The dots overlap with the stars, hence these cost
195 functions indeed remove the conflict of interest between parent and offspring. We provide
196 an interactive version in the *Electronic Supplementary Material (ESM_interactive_figure.nb*
197 *and ESM_interactive_figure.cdf)* that can be used to explore parameter ranges with or
198 without signal cost as well as different linear combinations of these cost functions
199 (*ESM_interactive_figure_video.mp4* shows examples).

200 Figure 4 shows the actual values for the different cost functions L_1 (Figure 4B), L_2 (Figure
201 4D) and their linear combination (Figure 4C), when using Godfray's equation (Eqs. 15, 16).
202 Red, yellow and green curves show the signal cost along the equilibrium path ($f_1(x^*(c))$ and
203 $f_2(x^*(c))$). This cost can be calculated by substituting z with the amount of optimal parental
204 investment $\tilde{z} = \ln\left(\frac{\gamma U c}{G}\right) / c$ into Eqs. 17 and 18. Figure 4A shows how these equilibrium costs
205 compare to each other as a function of offspring quality c . Note, while the absolute value of
206 the equilibrium signal cost is different for each cost function but the partial derivative with
207 respect of z is the same along the equilibrium path (see Figure 4F, G and H). Figure 4E
208 illustrates this effect.

209 Discussion

210 According to Nöldeke and Samuelson [17] (and Eq. 13), based on Godfray's original
211 differential benefit model [7], the cost of honest signalling should be proportional to parent's
212 fitness loss. But is it the only solution that yields honest signalling in equilibrium? While the

213 existence of infinite costly equilibria is known in general [18], no other equilibrium has been
214 calculated yet in terms of Godfray's model. Here, we show that a second extremum exists when
215 the cost is proportional to offspring's fitness gain, which also yields a signalling equilibrium with
216 costly signals. Furthermore, we have demonstrated, that any linear combination of the two
217 extreme cost functions is an equilibrium itself, which effectively proves that an infinite number
218 of honest, evolutionarily stable costly signalling equilibria exist for Godfray's model. While we
219 specifically derived the second extremum cost function for Godfray's model, our results have
220 important theoretical and empirical implications.

221 There are six major theoretical outcomes concerning the signalling of need, which apply
222 generally: (i) the population is not in equilibrium [16]; (ii) there is, on average, a shared
223 interest between parent and offspring, hence partially honest pooling equilibria can exist with
224 cost-free signals [11, 13]; (iii) there is an honest signalling equilibrium in a differential benefit
225 model [7], where the cost of signalling is proportional to the parent's fitness loss [17]; (iv) as
226 we have shown, there exists an honest signalling equilibrium in a differential benefit model
227 [7], where the cost of signalling is proportional to the offspring's expected fitness gain; (v)
228 there is an infinite number of honest signalling equilibria where the cost of signalling is
229 proportional to the linear combination of the cost functions of the previous two cases
230 including equilibria where the cost of signalling is smaller – even negative for some signallers
231 – than in any other equilibria; and finally (vi) it is possible, that a differential cost model offers
232 a better fit for parent-offspring communication (marginally mentioned in [19]). This could
233 open up possibilities for other cost-free [20-22] or even negative cost equilibria [21].

234 Another important implication of our results and the above considerations is that it is not
235 possible to decide in case of a real population (based on game theoretical models alone)
236 which one of the infinite numbers of costly honest equilibria will be achieved (provided that
237 an honest separating equilibrium exists). In order to answer questions of which evolutionary
238 trajectory will be played out (or have been taken), a more dynamic approach is needed [10].
239 Godfray and Johnstone [10] calculate the fitness advantage of the signalling equilibrium to
240 the non-signalling equilibrium using the cost function of Nöldeke and Samuelson [17]. Our
241 results could significantly change the outcome of these types of calculations, affecting
242 seriously the evolutionary consequences. This is left for future work.

243 Since the publication of Godfray's [7] influential model, a lot of empirical research has been

244 carried out to measure the “cost of begging”. It was realized very early that the metabolic cost
245 of begging is not unreasonably high [23-25], and thus it probably does not fit the predictions of
246 costly signalling theory. Attempts to try to measure the cost of increased begging on growth
247 provided mixed results [26-28]. However, several types of other costs were proposed, like
248 predation risk [29-31], immunological [32-34] or oxidative costs [35]; for a review, see [36]. We
249 must emphasize, that measuring any cost *in absolute value* is not enough [22, 37]: the measured
250 costs have to be *compared* to something, i.e. only relative measures are informative. One of the
251 reasons why the current empirical results are inconclusive is that we don’t have any information
252 about how these costs relate to the benefits of the parties, though see Moreno-Rueda and
253 Redondo [34] for an exception. The results of Nöldeke and Samuelson [17] and the results
254 presented here, alongside with other theoretical results [21, 22], give us a guide how one can
255 meaningfully compare the costs of the different parties involved. It follows, that researchers of
256 the field have to take into account (that is: measure) both the potential fitness loss of the parent
257 *and* the potential fitness gain of the offspring in parent-offspring communication when testing
258 the predictions of costly begging models.

259 Author’s contributions

260 Sz.Sz. conceived the idea; Sz.Sz., D.C. and I.Z. analysed the model; I.Z. analysed the numerical
261 examples and created the figures; all three authors contributed to the writing of the paper.

262 Competing interests

263 The authors declare that they have no competing interests.

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273 in life”.

274

275 [Electronic Supplementary Material](#)

276 [ESM Appendix 1-2](#)

277 [ESM Interactive Figure Mathematica notebook](#)

278 [ESM Interactive Figure Mathematica interactive computable document format](#)

279 [ESM Interactive Figure Video](#)

280

281 [Figure legends](#)

282 **Figure 1. Inclusive fitness functions and optima without signalling cost.** **A:** $G = \frac{1}{2}$ (it provides a
283 better layout) ; **B:** $G = 0.08$ (as in [7]). Parent’s (yellow curve, function u according to Eq. 2
284 without signal cost $f(x)$) and offspring (blue curve, function v according to Eq. 1 without signal
285 cost $f(x)$) inclusive fitness functions, parameterized by z . The x coordinate value of parent’s curve
286 is the parent’s own fitness contribution $g(c, z)$, the y coordinate value is the fitness contribution
287 the offspring ($\gamma h(c, z)$); similarly, the x value of the offspring’s curve is the parent’s contribution
288 ($\psi g(z)$), the y value is the offspring’s own fitness $h(c, z)$. The actual inclusive fitness value is the
289 sum of the appropriate coordinate values, both for parent and offspring. Parameters are $Z = 2$,
290 $\gamma = 1/2$, $\psi = \frac{1}{2}$, $U = 1$, $c = 3$. Yellow and blue stars indicate parent’s and offspring’s optimum.
291 Dashed lines are the calculated derivative tangents that touch optima at 45° , indicating
292 maximum fitness. The optimum z value for parent and offspring are not identical: the yellow dot
293 indicates what parent’s fitness at the offspring’s optimum z ; blue dot is the offspring’s fitness in
294 case of parent’s optimum z .

295

296 **Figure 2. Inclusive fitness** depending on offspring condition c and parental investment z . **A:**
297 parental fitness. **B:** offspring fitness. Red line connects the equilibrium z values where $\tilde{z} =$
298 $\ln\left(\frac{\gamma U c}{G}\right) / c$ holds. Parameters are $Z = 10$, $G = 0.08$, $U = 1$, $\gamma = \frac{1}{2}$, $\psi = \frac{1}{2}$.

299

300 **Figure 3. Inclusive fitness functions and optima with signalling cost.** Parent's (yellow curve,
301 function u according to Eq. 2) and offspring (blue curve, function v according to Eq. 1) inclusive
302 fitness functions, parameterized by z . The cost function of Eq. 14 is used with various α and β
303 values. The x coordinate value of parent's curve is the parent's own fitness contribution $g(c, z)$,
304 the y coordinate value is the fitness contribution of all future offspring ($\gamma h(c, z)$); similarly, the x
305 value of the offspring's curve is the parent's contribution (minus cost) ($\psi g(z) - f(\alpha, c, z)$), the y
306 value is the offspring's own fitness $h(c, z)$. The actual inclusive fitness value is the sum of the
307 appropriate coordinate values, both for parent and offspring. Parameters are $Z = 2$, $\gamma = \frac{1}{2}$, $\psi = \frac{1}{2}$,
308 $U = 1$, $G = \frac{1}{2}$, $c = 3$. Yellow and blue stars indicate parent's and offspring's optimum. Dashed lines
309 are the calculated derivative tangents that touch optima at 45° , indicating maximum fitness. The
310 optimum z value for parent and offspring are always identical, regardless of α and β values. **A:**
311 Cost function f_1 of Nöldeke and Samuelson [17] ($\alpha = 1$). **B:** Cost function f_2 introduced in this
312 paper ($\alpha = 0$). **C:** Linear combination of the above two cost functions f_1 and f_2 ($\alpha = \frac{1}{2}$).

313

314 **Figure 4. Signalling cost functions,** depending on offspring condition c and parental transfer z .
315 **A:** equilibrium signal cost ($f(x^*(c))$) for the different cost functions. **B:** Signal cost function L_1
316 (Eq. 10). **C:** Linear combination of $\frac{1}{2} L_1 + \frac{1}{2} L_2$ (Eq. 14) **D:** signal cost function L_2 introduced in this
317 paper (Eq. 13). Red, green and orange curves describe the signal cost ($f(x^*(c))$) along the
318 equilibrium path (which describes the equilibrium transfer function ($\tilde{z}(c)$) for parent as function
319 of c), these curves are shown in panel A. **E:** the partial derivative of the signal cost functions with
320 respect to z along the equilibrium path as a function of c . **F:** the partial derivative of signal cost
321 function L_1 (Eq. 10) with respect to z . **G:** the partial derivative of the linear combination of
322 $\frac{1}{2} L_1 + \frac{1}{2} L_2$ (Eq. 14) **H:** the partial derivative of signal cost function L_2 introduced in this paper
323 (Eq. 13) with respect to z . Red, green and orange curves describe the partial derivative of the
324 respective signal cost functions along the equilibrium path with respect to z , these curves are
325 shown in panel E. Parameters are $Z = 10$, $G = 0.08$, $U = 1$, $\gamma = \frac{1}{2}$, $\psi = \frac{1}{2}$.

326

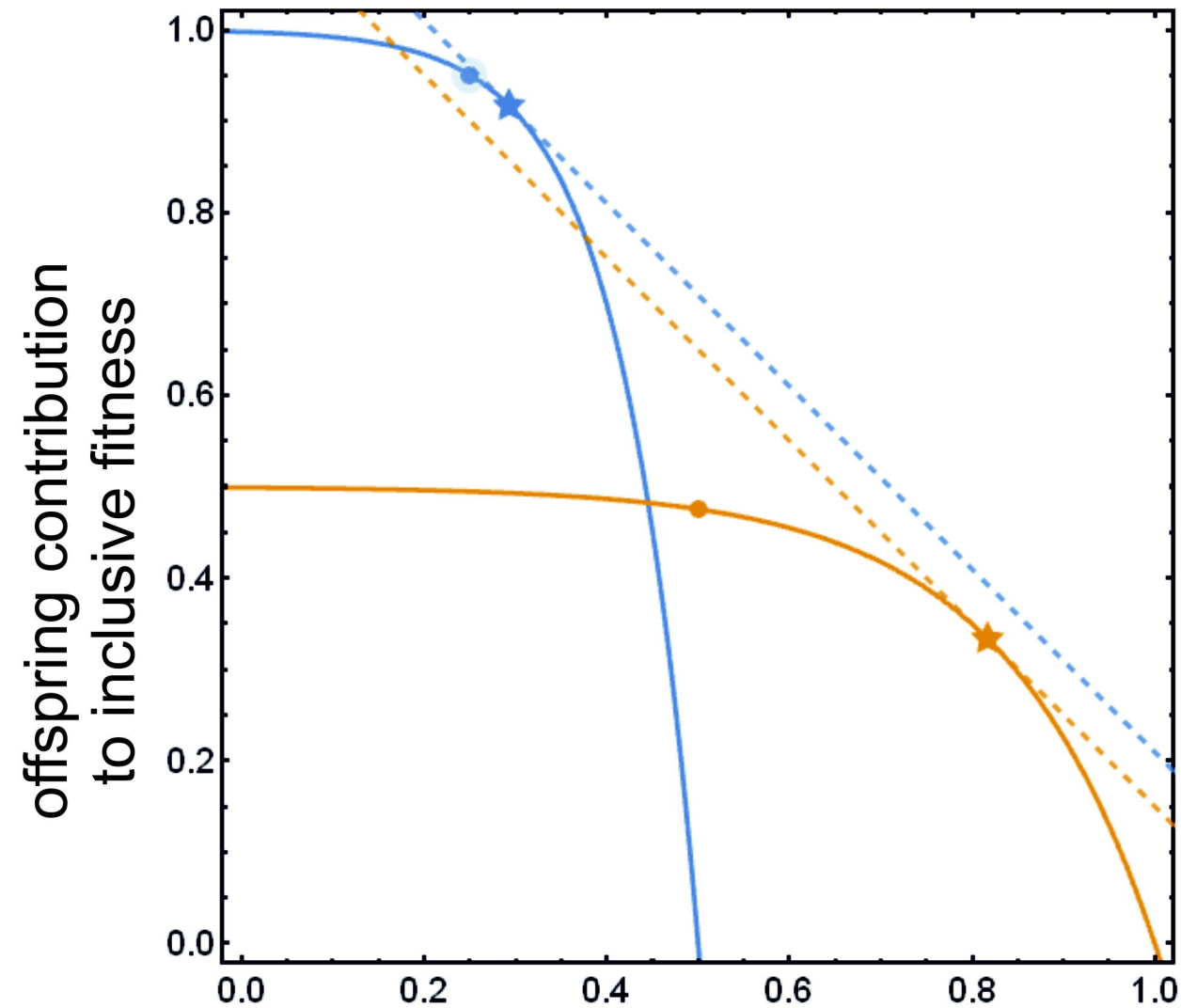
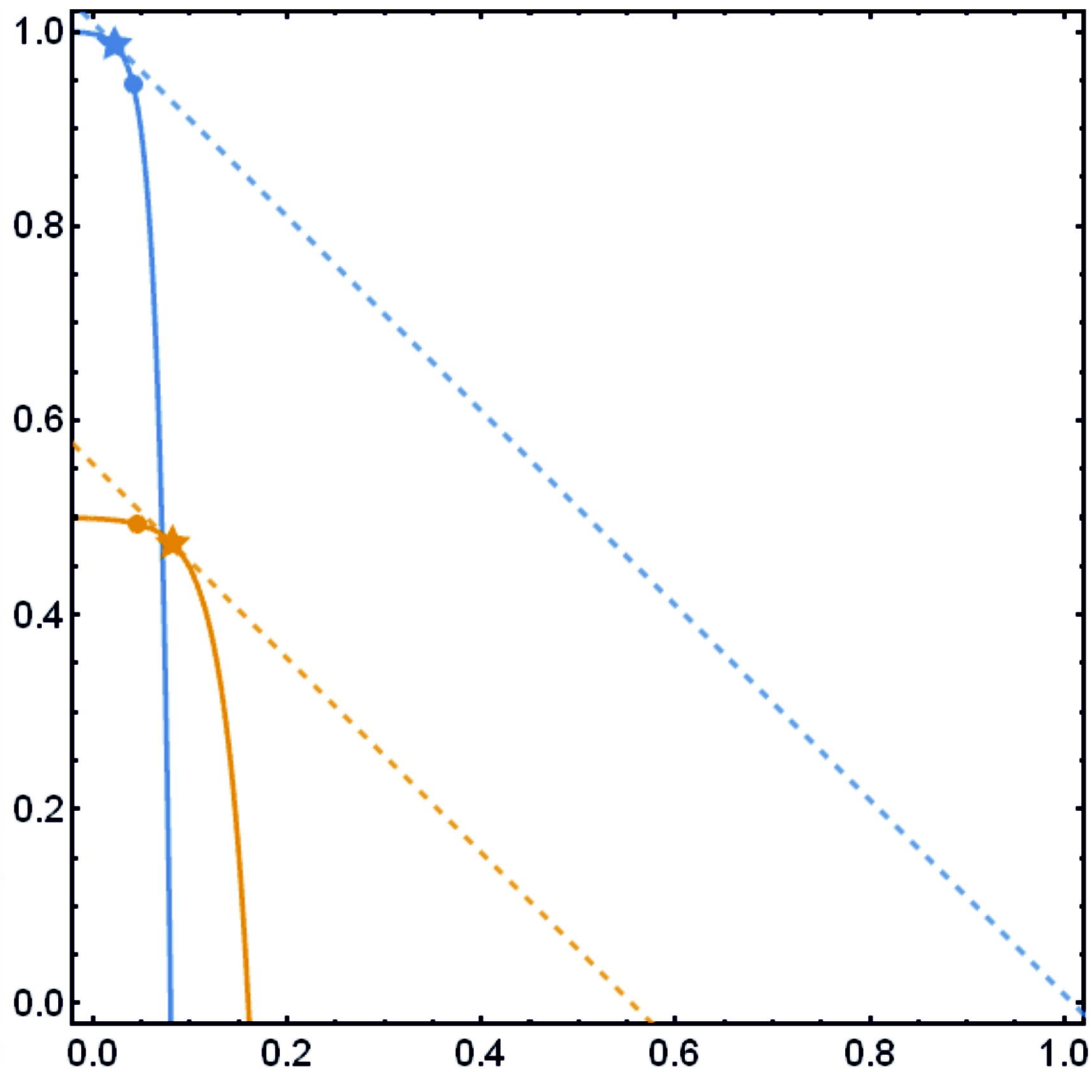
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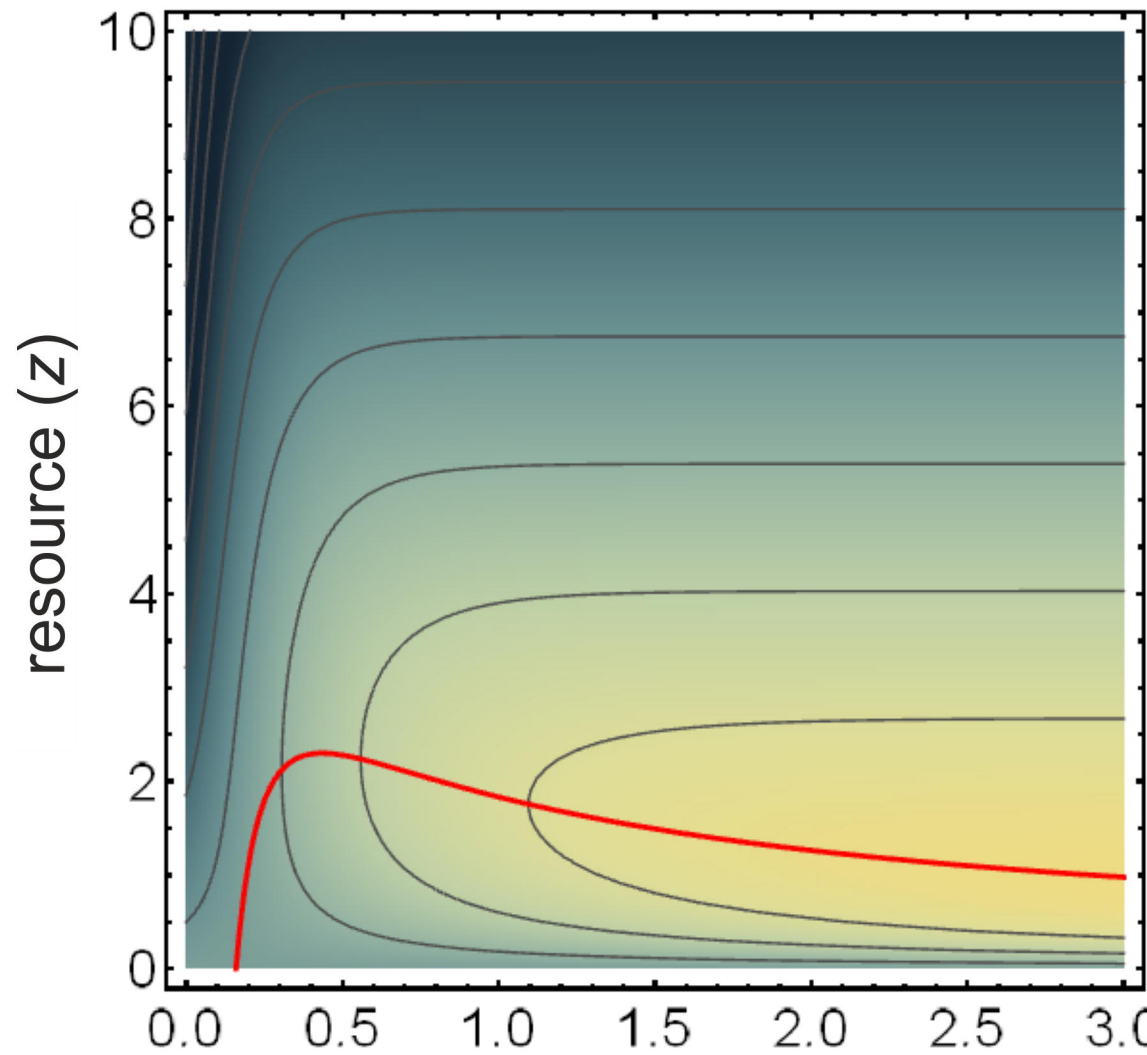
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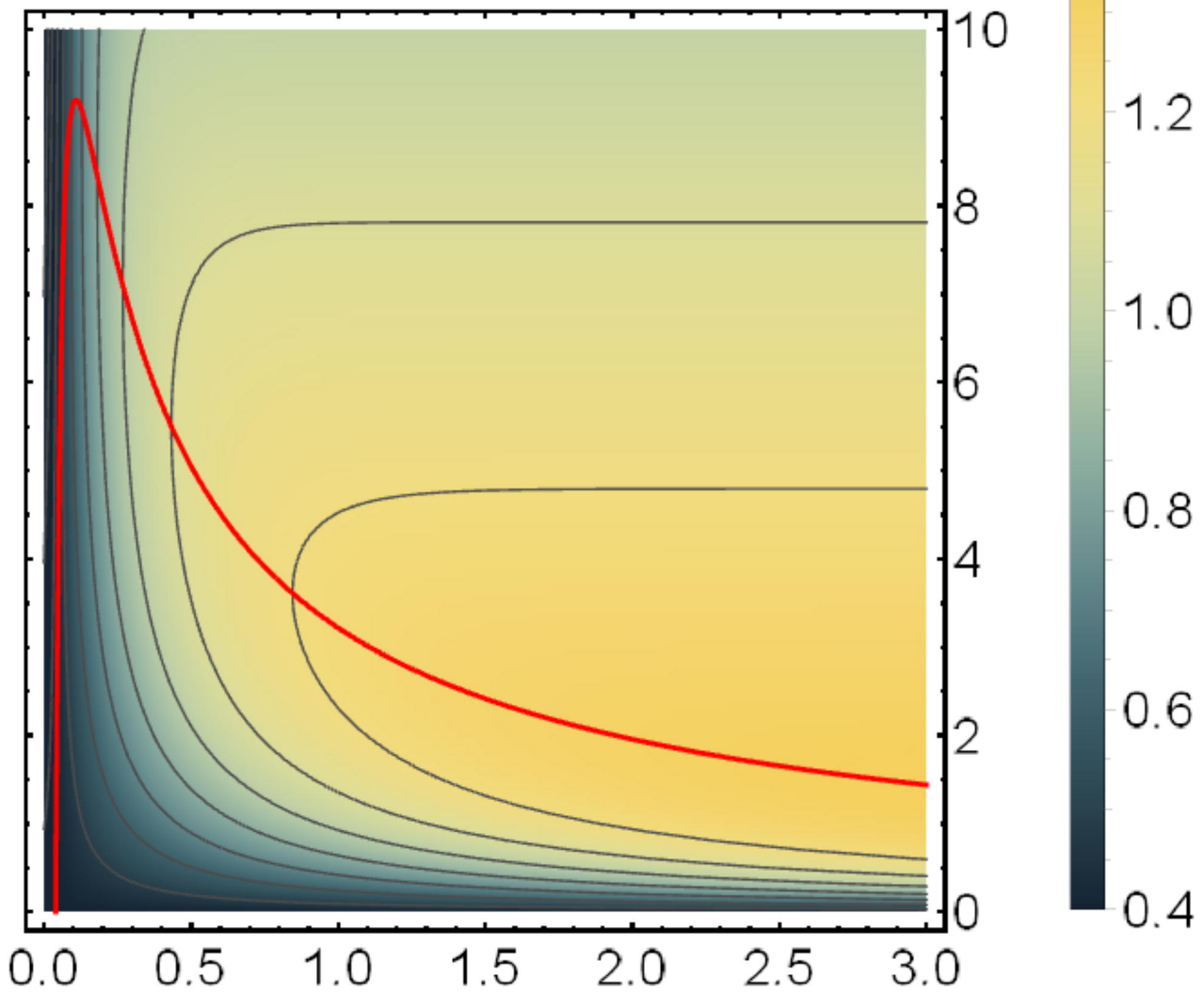
A**B**

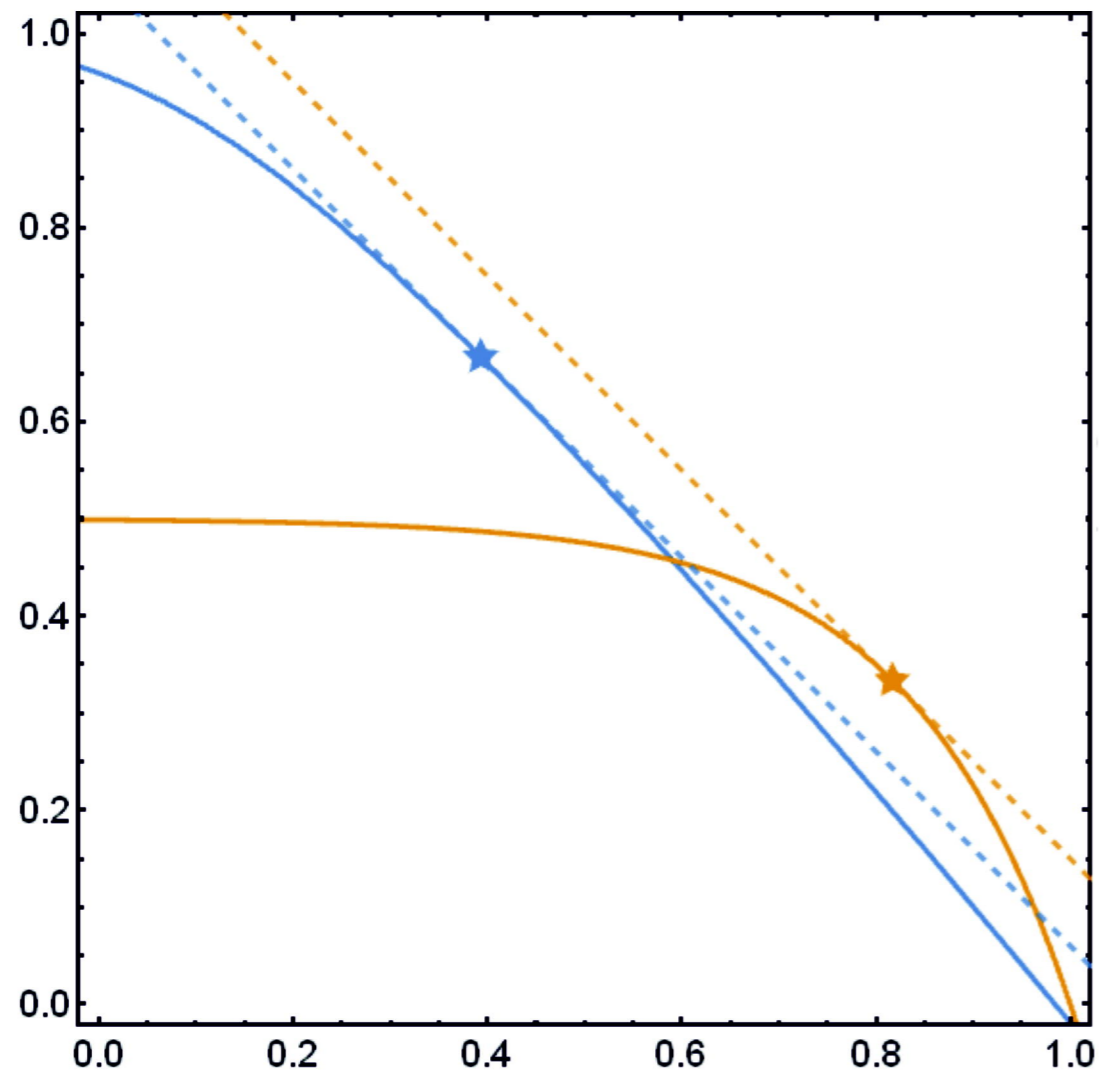
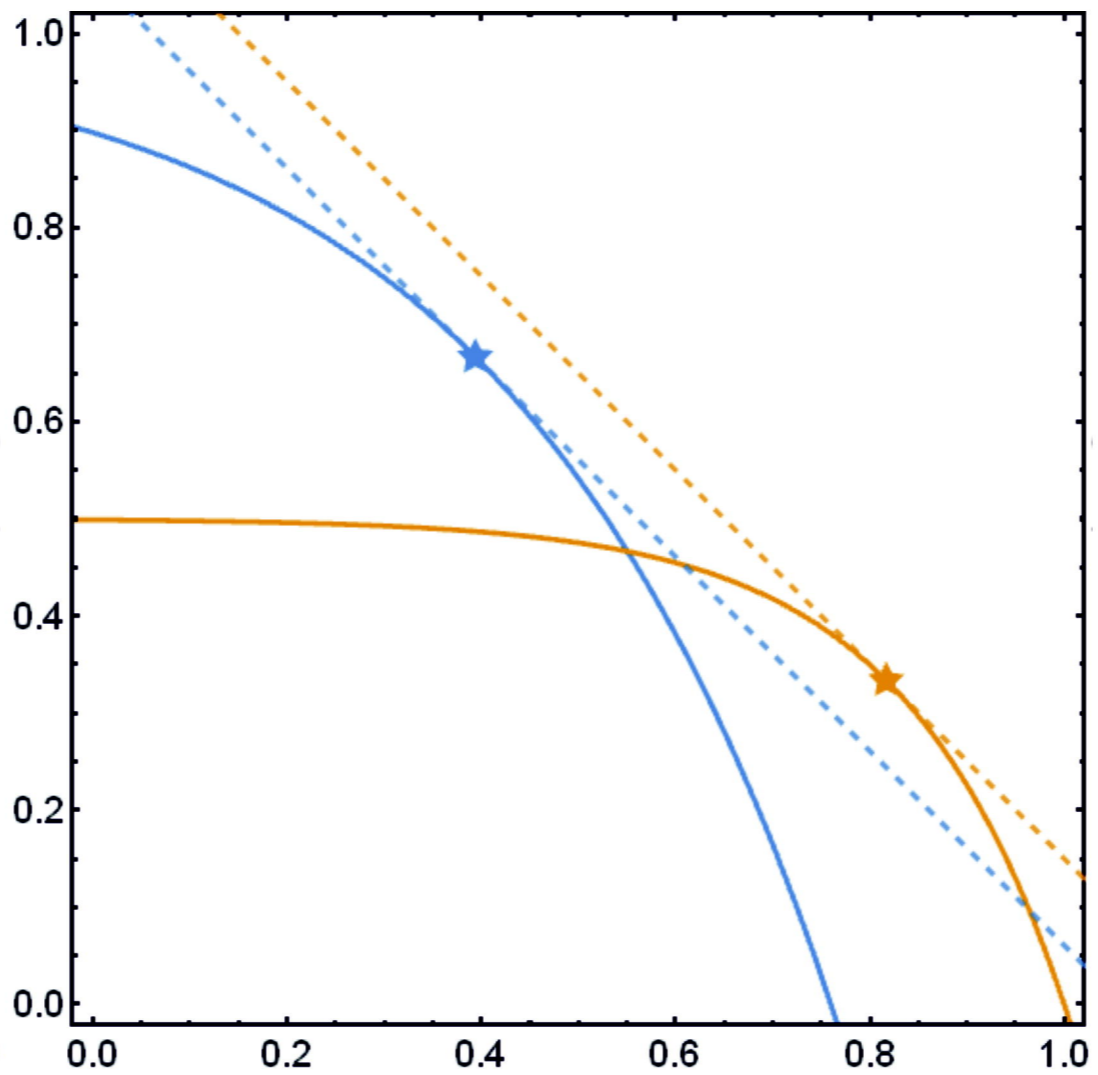
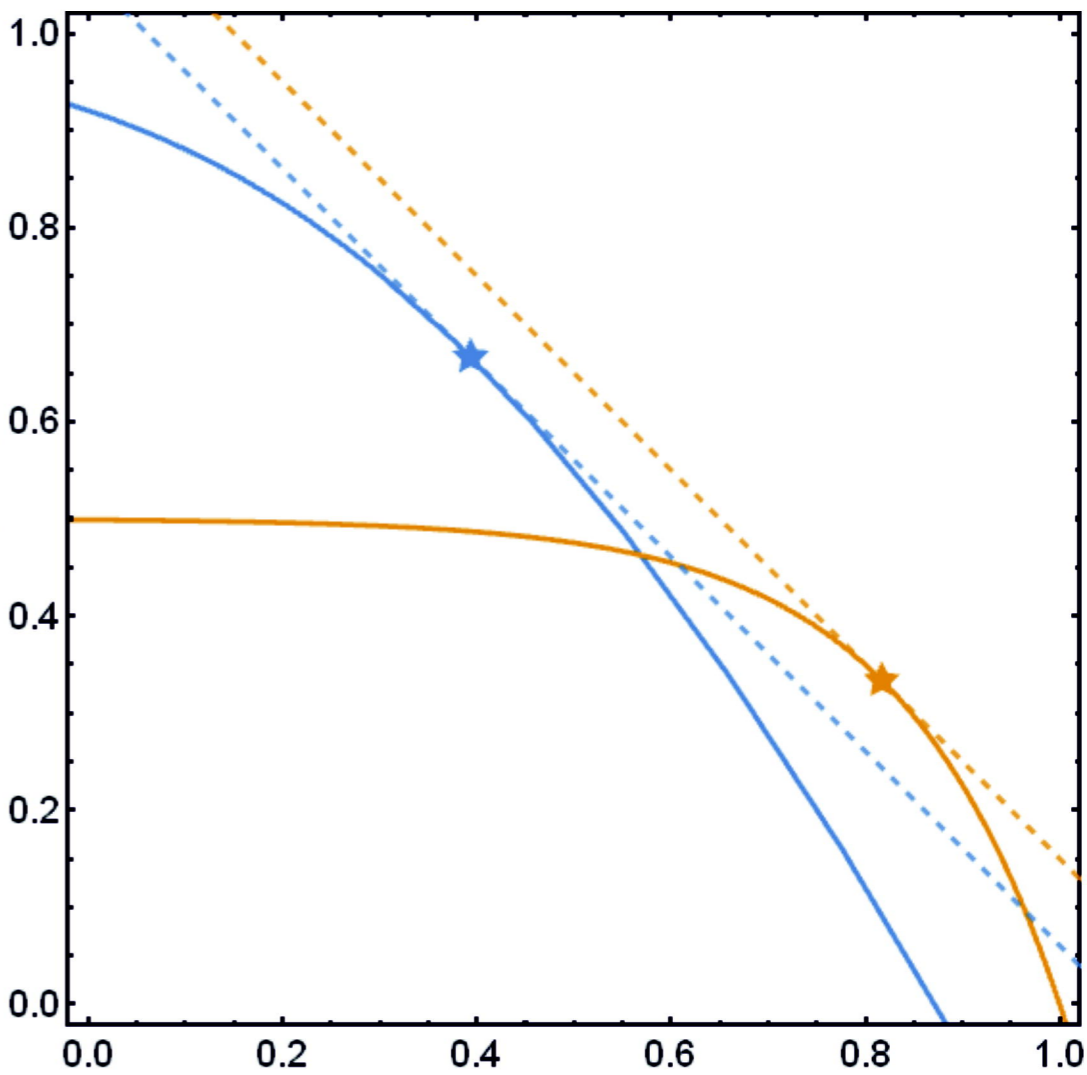
parent contribution to inclusive fitness

A



B

offspring condition (c)

A**B****C**parent contribution
to inclusive fitness

offspring contribution to inclusive fitness

