

# Multiple coexistence equilibria in a two parasitoid-one host model

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## Abstract

Briggs et al. (1993) introduced a host-parasitoid model for the dynamics of a system with two parasitoids that attack different juvenile stages of a common host. Their main result was that coexistence of the parasitoids is only possible when there is sufficient variability in the maturation delays of the host juvenile stages. Here we analyse the phenomenon of coexistence in that model more deeply. We show that with some distribution families for the maturation delays, the coexistence equilibrium is unique, while with other distributions multiple coexistence equilibria can be found. In particular we find that stable coexistence does not necessarily require mutual invasibility.

*Keywords:* Population dynamics, Parasitoid-Host Interaction, Delay Differential Equations, Multiplicity of coexistence equilibria

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## 1. Introduction

2 It is known that parasitoid species of the same host can coexist (Force, 1970;  
3 Price, 1970; Harvey et al., 2009). This observation seems to contradict a  
4 principle in ecology which predicts that competing species cannot coexist on  
5 the same limiting resource (Gause and Witt, 1935), though it has been shown

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6 that the principle holds under very stringent equilibrium conditions (Ches-  
7 son and Case, 1986) and that competitors can coexist on the same biological  
8 resource along periodic solutions (Hsu et al., 1977; Armstrong and McGehee,  
9 1980). Parasitoid species are a particularly interesting case, as various mech-  
10 anisms that can promote parasitoid coexistence on the same host have been  
11 suggested (Price, 1970; Lane et al., 2006; Hackett-Jones et al., 2009). Briggs  
12 (1993) started to investigate under which conditions parasitoids can coexist  
13 when they attack different juvenile stages of a common host. This investi-  
14 gation was continued by Briggs et al. (1993), who found that in their model  
15 coexistence at equilibrium is possible only when there is sufficient variability  
16 in the maturation delays of the juvenile stages. They suggested that when  
17 the variability is large enough, different host individuals can be interpreted  
18 as different resources: individuals with a relatively long egg phase support  
19 the egg parasitoid, and individuals with a relatively long larva phase support  
20 the larva parasitoid. In the present paper we re-analyse the model by Briggs  
21 et al. (1993) and find more complex patterns than those already identified:  
22 there may be multiple coexistence equilibria, and, contrary to conventional  
23 wisdom, stable coexistence does not require mutual invasibility. The model  
24 is presented in Section 2. In Sections 3, 4 and 5 we formulate the original  
25 results in our somewhat different notation and in Section 6 show that co-  
26 existence equilibria are not unique for many distributions of the maturation  
27 delays. Finally, in Section 7 we set our results in the context of other works,  
28 discuss their relevance for biological pest control, and propose questions for  
29 further investigation. A general introduction to parasitoid-host systems can  
30 be found, for instance, in the text book by Godfray (1994).

## 31 **2. The model**

32 The model describes a host with two juvenile stages  $E$  and  $L$ , and an adult  
33 stage  $A$ . We refer to the first juvenile stage as eggs and to the second  
34 juvenile stage as larvae but they can also represent other developmental  
35 stages as pupae or different instars. The egg stage is attacked by an egg  
36 parasitoid (whose density is denoted by  $P$ ) while the larva stage is attacked  
37 by a larva parasitoid (density denoted by  $Q$ ) with attack rates  $a_P$  and  $a_Q$   
38 respectively. Non-infected host juveniles have random maturation delays  
39 which are distributed with probability density functions  $w_E$  and  $w_L$ . Infected  
40 hosts do not progress to the next stage but give rise to new parasitoids a  
41 constant time  $T_{JP}$  or  $T_{JQ}$  after the infection. Unlike the original paper, we

42 do not explicitly introduce survival probabilities for the juvenile parasitoids,  
 43 since these can be absorbed in the parameters  $c_P$  and  $c_Q$  for the expected  
 44 number of parasitoids emerging from an infected host. All other host and  
 45 parasitoid stages have constant (background) death rates  $d_E$ ,  $d_L$ ,  $d_A$ ,  $d_P$  and  
 46  $d_Q$ . Adult hosts have a life time fecundity  $\rho$  (so  $\rho d_A$  is the rate with which  
 47 an adult produces offspring).

48 The population dynamics are described by delay differential equations shown  
 49 below. We adopt the notation used in the original paper but extend it when  
 50 needed. For simplicity, the term maturing is used for eggs transforming to  
 51 larvae as well as for larvae transforming to adults, although for eggs the  
 52 term hatching might be more appropriate. The balance equations for the  
 53 population densities are

$$54 \quad \begin{cases} \frac{dE(t)}{dt} = R_E(t) - M_E(t) - a_P P(t)E(t) - d_E E(t) \\ \frac{dL(t)}{dt} = M_E(t) - M_L(t) - a_Q Q(t)L(t) - d_L L(t) \\ \frac{dA(t)}{dt} = M_L(t) - d_A A(t) \\ \frac{dP(t)}{dt} = a_P c_P E(t - T_{JP})P(t - T_{JP}) - d_P P(t) \\ \frac{dQ(t)}{dt} = a_Q c_Q L(t - T_{JQ})Q(t - T_{JQ}) - d_Q Q(t) \end{cases} \quad (1)$$

55 where

$$56 \quad \begin{array}{l} R_E(t) = \rho d_A A(t) \\ M_E(t) = \int_0^\infty R_E(t - x_E) S_E(x_E, t) w_E(x_E) dx_E \\ M_L(t) = \int_0^\infty M_E(t - x_L) S_L(x_L, t) w_L(x_L) dx_L \end{array} \quad \left| \begin{array}{l} \text{host egg recruitment rate} \\ \text{host egg maturation rate} \\ = \text{host larva recruitment} \\ \text{rate} \\ \text{host larva maturation rate} \\ = \text{host adult recruitment} \\ \text{rate} \end{array} \right.$$

57 with

$$S_E(x_E, t) = \exp\left(-\int_{t-x_E}^t (a_P P(y) + d_E) dy\right) \quad \left| \begin{array}{l} \text{probability for host eggs to} \\ \text{survive from time } t - x_E \text{ to} \\ t \end{array} \right.$$

$$S_L(x_L, t) = \exp\left(-\int_{t-x_L}^t (a_Q Q(y) + d_L) dy\right) \quad \left| \begin{array}{l} \text{probability for host larvae} \\ \text{to survive from time } t - x_L \\ \text{to } t \end{array} \right.$$

58

59 and

60

parameter	description
$\rho$	total lifetime fecundity of host adults
$d_E$	background mortality rate of host eggs
$d_L$	background mortality rate of host larvae
$d_A$	background mortality rate of host adults
$d_P$	background mortality rate of egg parasitoids
61 $d_Q$	background mortality rate of larva parasitoids
$a_P$	egg parasitoid attack rate
$a_Q$	larva parasitoid attack rate
$c_P$	expected number of egg parasitoids emerging from infected egg
$c_Q$	expected number of larva parasitoids emerging from infected larva
$T_{JP}$	duration of juvenile egg parasitoid stage
62 $T_{JQ}$	duration of juvenile larva parasitoid stage

63 and

function	description
64 $w_E$	probability density function for host egg maturation delay
65 $w_L$	probability density function for host larva maturation delay

66

67 **3. Preliminaries**

68 In order to investigate equilibrium states, we introduce some quantities that  
69 depend on constant parasitoid densities  $P$  and  $Q$ . Note first that eggs and  
70 larvae can have three different fates: they can die due to the background  
71 death rates  $d_E$  and  $d_L$ , they can be successfully attacked by parasitoids or  
72 they can progress to the next stage. We first state the formulae for the  
73 transition probabilities between the host stages and the expected durations  
74 in the different stages (for the full computations see Appendix A).

75 The probability that a freshly emerged egg hatches into a larva is

$$\Pi_1(P) = \int_0^\infty w_E(\tau) e^{-(a_P P + d_E)\tau} d\tau \quad (2)$$

76 and the probability that a freshly hatched larva emerges as an adult is

$$\Pi_2(Q) = \int_0^\infty w_L(\tau) e^{-(a_Q Q + d_L)\tau} d\tau. \quad (3)$$

77 As shown in Appendix A.2, the expected duration of the egg stage is

$$\Gamma_1(P) = \frac{1 - \Pi_1(P)}{a_P P + d_E}, \quad (4)$$

78 the expected duration of the larva stage (given that this stage is reached) is

$$\Gamma_2(Q) = \frac{1 - \Pi_2(Q)}{a_Q Q + d_L}, \quad (5)$$

79 and the expected duration of the adult stage (given that this stage is reached)  
80 is

$$\Gamma_3 = \frac{1}{d_A}. \quad (6)$$

81 We now can state the following relations, valid when the related population  
82 densities are constant:

83 The rate of eggs emerging, given constant adult density  $A$ , is by definition

$$R_E = \rho d_A A. \quad (7)$$

84 The constant egg density  $E$  is the product of the rate of eggs emerging and  
85 the expected duration of the egg stage (to verify set  $\frac{dE}{dt} = 0$ ),

$$E = R_E \Gamma_1(P). \quad (8)$$

86 The constant larva density  $L$  is the product of three factors, viz., the rate  
87 of eggs emerging, the probability for an egg to mature to a larva and the  
88 expected duration of the larva stage, given that it is reached (to verify set  
89  $\frac{dL}{dt} = 0$ ),

$$L = R_E \Pi_1(P) \Gamma_2(Q). \quad (9)$$

90 The constant adult density  $A$  is the product of four factors, viz., the rate of  
91 eggs emerging, the probability for an egg to mature to a larva, the probability  
92 for a larva to mature to an adult and the expected life length of an adult (to  
93 verify set  $\frac{dA}{dt} = 0$ ),

$$A = R_E \Pi_1(P) \Pi_2(Q) \Gamma_3. \quad (10)$$

94 The average number of offspring from a freshly laid egg (the basic reproduc-  
95 tion number of the host) is the product of the average output of an adult  $\rho$   
96 and the probability for an egg to mature to an adult,

$$R_0 = \rho \Pi_1(P) \Pi_2(Q). \quad (11)$$

97 At a nontrivial equilibrium the basic reproduction number  $R_0$  equals one,  
 98 as can be seen by plugging the definition of  $R_E$  into equation (10). The  
 99 zero growth condition for host eggs (8) and larvae (9) can be combined by  
 100 eliminating  $R_E$ . This yields

$$\frac{\Pi_1(P)\Gamma_2(Q)}{\Gamma_1(P)} = \frac{L}{E}. \quad (12)$$

#### 101 4. Equilibrium states

##### 102 4.1. When only the egg parasitoid is present

103 For the case that only the egg parasitoid is present, its equilibrium density  
 104  $P^*$  can be determined by plugging  $Q = 0$  into the basic reproduction number  
 105  $R_0$ , which is equal to 1 at equilibrium, i.e. by requiring

$$\rho \Pi_1(P^*) \Pi_2(0) = 1. \quad (13)$$

107 Assuming that  $R_0 > 1$  for  $P = 0$  and  $Q = 0$ , this equation has a unique root  
 108 for  $P^*$  since  $R_0$  approaches 0 strictly monotonically with increasing  $P$ .

109 The equilibrium state for the egg density is determined by the requirement  
 110 of zero growth rate for (non-trivial)  $P$ . This, by setting  $dP(t)/dt = 0$  and  
 111 assuming constant population densities, leads to

$$E_P^* = \frac{d_P}{a_P c_P}. \quad (14)$$

112 The equilibrium larva density  $L_P^*$  in presence of only the egg parasitoid can  
 113 be calculated from the relation (12),

$$L_P^* = E_P^* \frac{\Pi_1(P^*)\Gamma_2(0)}{\Gamma_1(P^*)}. \quad (15)$$

114 The host adult density can be obtained for all equilibrium systems by com-  
 115 bining (7) and (8).

##### 116 4.2. When only the larva parasitoid is present

117 In the same way as for the egg parasitoid, we can derive the equilibrium den-  
 118 sities for the case that only the larva parasitoid is present. The equilibrium  
 119 larva parasitoid density  $Q^*$  is determined through the equation

$$\rho \Pi_1(0) \Pi_2(Q^*) = 1 \quad (16)$$

120 and again this equilibrium density is unique. The equilibrium larva density  
 121 is

$$L_Q^* = \frac{d_Q}{a_Q c_Q}, \quad (17)$$

122 and the equilibrium egg density is

$$E_Q^* = L_Q^* \frac{\Gamma_1(0)}{\Pi_1(0)\Gamma_2(Q^*)}. \quad (18)$$

123 *4.3. When both parasitoids are present*

124 According to equation (11) the host adult density is in equilibrium when the  
 125 parasitoid densities satisfy

$$Q = \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) \quad (19)$$

126 where  $\Pi_2^{-1}$  is the inverse function of  $\Pi_2$ . Plugging (19) into (12) yields a  
 127 condition for all host stages to be in equilibrium

$$f(P) = \frac{L}{E} \quad (20)$$

128 where  $f : [0, P^*] \rightarrow \mathbb{R}^+$  is defined by

$$f(P) = \frac{\Pi_1(P)}{\Gamma_1(P)} \Gamma_2 \left( \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) \right). \quad (21)$$

129 When both parasitoids coexist, the equilibrium egg and larva densities are  
 130 determined by the requirement of zero growth rate for the egg and larva  
 131 parasitoid respectively. Hence they are given by  $E_P^*$  and  $L_Q^*$ , and thus the  
 132 egg parasitoid coexistence equilibrium  $P^{**}$  is determined by the condition

$$f(P^{**}) = \frac{L_Q^*}{E_P^*}. \quad (22)$$

133 The corresponding larva parasitoid density  $Q^{**}$  can be obtained by equation  
 134 (19).

135 Note that in the same way one can derive an equivalent function  $g(Q) = L/E$

136 which determines coexistence equilibria by  $g(Q^{**}) = \frac{L_Q^*}{E_P^*}$ , where

$$\begin{aligned}
 g(Q) &= \frac{\Pi_1 \left( \Pi_1^{-1} \left( \frac{1}{\rho \Pi_2(Q)} \right) \right)}{\Gamma_1 \left( \Pi_1^{-1} \left( \frac{1}{\rho \Pi_2(Q)} \right) \right)} \Gamma_2(Q) \\
 &= \frac{\Gamma_2(Q)}{\Pi_2(Q)} \frac{1}{\rho \Gamma_1 \left( \Pi_1^{-1} \left( \frac{1}{\rho \Pi_2(Q)} \right) \right)}
 \end{aligned} \tag{23}$$

137 with  $\Pi_1^{-1}$  being the inverse function of  $\Pi_1$ . All further analysis could be car-  
 138 ried out with either  $f$  or  $g$  but for simplicity we stick with the function  $f$ .  
 139 Turning back to the function  $f$ , we see that the shape of the function con-  
 140 tains information on the multiplicity of coexistence equilibria. According to  
 141 equation (22), multiple coexistence equilibria cannot arise if  $f$  is strictly  
 142 monotonic. If on the other hand for some parameters  $f$  is not mono-  
 143 tonic, we can always find values of the parameters  $c_P$ ,  $c_Q$ ,  $d_P$  or  $d_Q$  that  
 144 give rise to multiple coexistence equilibria by shifting the critical horizontal  
 145  $L_Q^*/E_P^* = d_Q a_P c_P / d_P a_Q c_Q$  until the graph of the function  $f$  (which does not  
 146 depend on those parameters) is intersected multiple times. Each intersec-  
 147 tion yields a coexistence equilibrium. Similarly, the critical horizontal can  
 148 be shifted using those parameters until there are no coexistence equilibria.

## 149 5. Invasibility of stable equilibria

150 When in the absence of parasitoids  $R_0 > 1$ , either parasitoid can establish  
 151 a population. Often, a stable host-parasitoid equilibrium will be reached  
 152 with  $R_0$  set at 1 (Murdoch et al., 1987) and we follow Briggs et al. (1993) in  
 153 examining when this equilibrium can be invaded by the other parasitoid. A  
 154 case where the host and parasitoid populations settle into a periodic solution  
 155 is examined numerically in the next Section.

156 It is not difficult to show that a stable equilibrium population with only the  
 157 larva parasitoid can be invaded by the egg parasitoid when the egg parasitoid  
 158 alone reduces the egg density more than the larva parasitoid alone, that is  
 159 when

$$E_P^* < E_Q^*. \tag{24}$$

160 To demonstrate this, we compute the Malthusian parameter  $\lambda = \lambda_P(E)$  for  
 161 the egg parasitoid at constant egg density  $E$ . Namely, we linearise system



162 (1) around the equilibrium, obtaining

$$\frac{dP(t)}{dt} = a_P c_P E P(t - T_{JP}) - d_P P(t) \quad (25)$$

163 where  $E = E_Q^*$ . We then assume

$$P(t) = e^{\lambda t} P(0) \quad (26)$$

164 and obtain

$$\begin{aligned} \lambda P(t) &= a_P c_P E P(t) e^{-\lambda T_{JP}} - d_P P(t) \\ \lambda &= E a_P c_P e^{-\lambda T_{JP}} - d_P. \end{aligned} \quad (27)$$

165 The egg parasitoid can invade a stable equilibrium community of the larva  
 166 parasitoid and the host when this equation has a positive real root for  
 167  $E = E_Q^*$ , that is  $\lambda_P(E_Q^*) > 0$ . The claim that this requires  $E_P^* < E_Q^*$   
 168 follows because the unique real root  $\lambda_P(E)$  increases strictly monotonically  
 169 with  $E$  and  $\lambda_P(E_P^*) = 0$ . (Note that we do not have to consider complex  
 170 roots for  $\lambda$  since their real parts cannot exceed the real root.)

171 In the same way it can be seen that the larva parasitoid can invade a stable  
 172 equilibrium population with only the egg parasitoid when

$$L_Q^* < L_P^*. \quad (28)$$

173 We speak of mutual invasibility of stable equilibria when

$$E_P^* < E_Q^* \text{ and } L_Q^* < L_P^*. \quad (29)$$

174 The value of the function  $f$  defined in (21) at the boundary of its domain, re-  
 175 lative to the right hand side of (22), turns out to be related to the invasibility  
 176 conditions. Indeed,

$$\begin{aligned} f(0) &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left( \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(0)} \right) \right) \\ &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 (\Pi_2^{-1} (\Pi_2(Q^*))) \\ &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 (Q^*) \\ &= \frac{L_Q^*}{E_Q^*} \end{aligned} \quad (30)$$

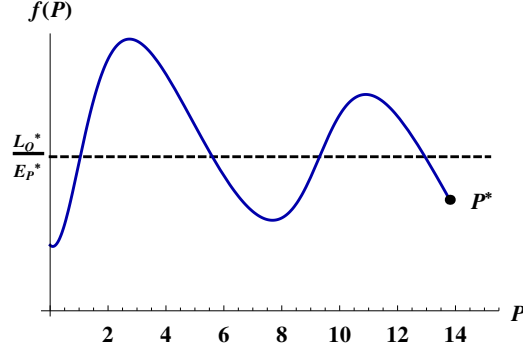


Figure 1: The graph of the function  $f$  which intersects the level  $L_Q^*/E_P^*$  when the egg parasitoid density corresponds to a coexistence equilibrium. The maturation delays are distributed with two discrete values each (see Appendix B.2). Parameter values are  $T_{E_1} = 0.2$ ,  $T_{E_2} = 1.35$ ,  $T_{L_1} = 0.75$ ,  $T_{L_2} = 5$ ,  $r_E = 0.5$ ,  $r_L = 0.3$ ,  $a_P = 2$ ,  $a_Q = 0.2$ ,  $d_E = 0$ ,  $d_L = 0$ ,  $\rho = 500$ ,  $d_P = 8$ ,  $d_Q = 0.175$ ,  $c_P = 0.5$  and  $c_Q = 0.5$

177 and

$$\begin{aligned}
 f(P^*) &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left( \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P^*)} \right) \right) \\
 &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left( \Pi_2^{-1} (\Pi_2(0)) \right) \\
 &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2(0) \\
 &= \frac{L_P^*}{E_P^*},
 \end{aligned} \tag{31}$$

178 which implies that the egg parasitoid can invade a stable equilibrium  
 179 with the larva parasitoid alone when  $f(0) < L_Q^*/E_P^*$  and the larva para-  
 180 sitoid can invade a stable equilibrium with the egg parasitoid alone when  
 181  $f(P^*) > L_Q^*/E_P^*$ .

182

## 183 6. Applying distributions for the maturation delays

184 We apply several distributions for the maturation delays in order to analyze  
 185 their influence on the multiplicity of coexistence equilibria. Among those  
 186 are the constant-duration distribution, (shifted) exponential distribution and  
 187 (shifted) gamma distribution, which have been introduced in the original pa-  
 188 per of Briggs et al. (1993). Here the term 'shifted' refers to including minimal

189 values for the maturation delays. Additionally we introduce a two-value dis-  
190 tribution where the maturation delays assume one of two discrete values with  
191 certain probabilities.

192 It turns out that, among these distributions, only the constant-duration and  
193 the (non-shifted) exponential distribution yield at most one coexistence equi-  
194 librium. For those two distributions the function  $f$  is monotonic and therefore  
195 the critical horizontal  $L_Q^*/E_P^*$  can be crossed at most once. Elementary rep-  
196 resentations for  $f$  in those cases are shown in Appendix B. For the case of  
197 constant maturation delays,  $f$  is decreasing and hence there is a coexistence  
198 equilibrium only if  $f(0) > L_Q^*/E_P^* > f(P^*)$ , implying that neither parasitoid  
199 can invade a stable equilibrium of the other parasitoid and the host. For  
200 the case of exponentially distributed maturation delays,  $f$  is increasing and  
201 hence, in the other way around, there must be mutual invasibility of stable  
202 equilibria for a coexistence equilibrium to exist.

203 For all the other distributions (two-value distribution, shifted exponential  
204 distribution and (normal or shifted) gamma distribution), we could numer-  
205 ically find parameters so that the graph of  $f$  crosses the critical horizontal  
206 line multiple times, giving rise to multiple equilibria. Fig. 1 shows an exam-  
207 ple where the graph of  $f$  crosses the critical horizontal line four times with  
208 two-value distributions for the maturation delays (see caption).

### 209 6.1. Simulations and stability

210 To see how the system behaves after a small perturbation from an equilib-  
211 rium, we computed time plots with the software *Mathematica* shown in Fig.  
212 2. The plots reveal that coexistence equilibria can be stable or unstable,  
213 possibly giving rise to oscillations around the equilibrium after perturbation.  
214 Bifurcation diagrams are shown in Fig. 3. The left panel shows how the  
215 parameter  $a_P$  shifts the horizontal in Fig. 1 without changing the function  
216  $f$ , and thus we can observe how coexistence equilibria appear and disappear  
217 in pairs when changing the parameter. The right panel shows how the adult  
218 mortality  $d_A$  affects stability without changing the equilibrium values (since  
219 this parameter does not occur in the function  $f$  or in the level of the critical  
220 horizontal line). Low values for  $d_A$  seem to stabilize some equilibria while  
221 high values for  $d_A$  appear to destabilize all equilibria.

222 We further analyzed the dynamics for low values of the host adult death  
223 rate  $d_A$ . We show some simulations for that case in the  $(P, Q)$ -plane in Fig.  
224 4. There we see that the population densities lie on the curve of equation

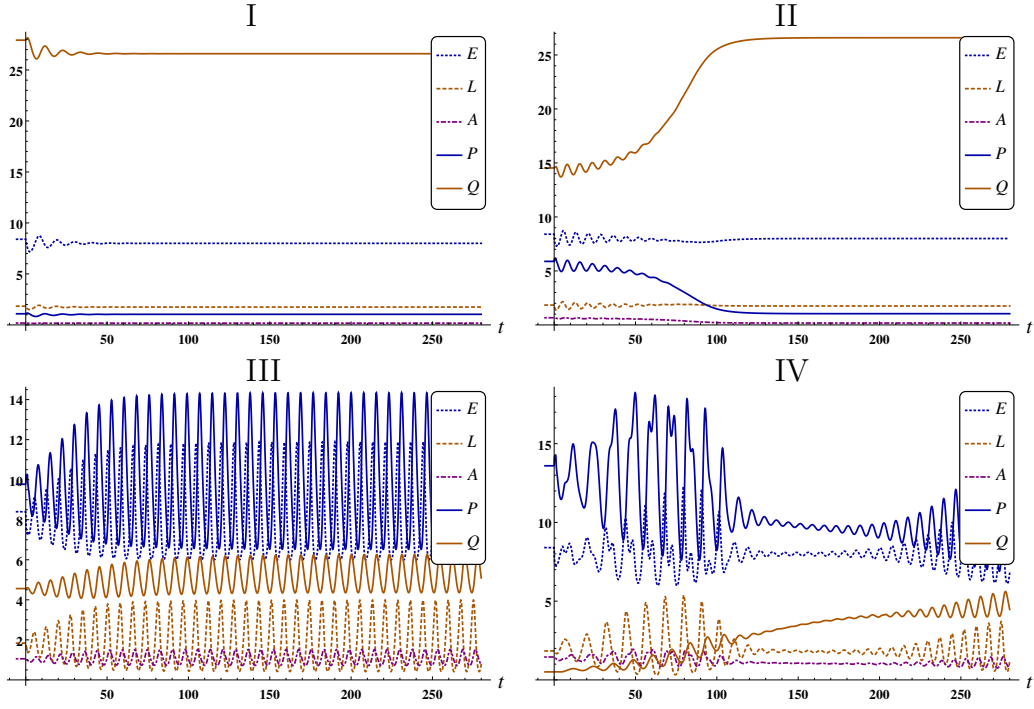


Figure 2: Time plots of population dynamics after small perturbations from equilibrium densities. The initial densities for  $t \leq 0$  are constant and correspond to perturbations from the equilibrium densities indicated by the first (I), second (II), third (III) and fourth (IV) intersection of the graph of  $f$  with the critical horizontal in Fig. 1. The perturbations consist of increasing all equilibrium densities by 5%. Note that in plot (IV) the same attractor as in plot (III) seems to be approached. Distributions and parameter values are the same as in Fig. 1. Additionally  $T_{JP} = 1$ ,  $T_{JQ} = 1$  and  $d_A = 0.3$

225  $\Pi_1(P) \frac{\Gamma_2(Q)}{\Gamma_1(P)} = \frac{L_Q^*}{E_P^*}$  and move in a direction depending on the relative po-  
 226 sition of this curve and the curve  $\rho \Pi_1(P) \Pi_2(Q) = 1$ . This can be justified  
 227 through a time-scale argument that we just sketch here, leaving details to  
 228 future work. For the argument note that  $A(t)$  is a slow variable when  $d_A$   
 229 is low, what can be seen from the models definition (1); thus in the fast  
 230 time-scale  $E(t)$ ,  $L(t)$ ,  $P(t)$  and  $Q(t)$  will evolve under a constant value for  
 231 the rate of eggs emerging, see equation (7). Numerical evidence suggests  
 232 that this reduced system always quickly converges to its (quasi)-equilibrium,  
 233 where  $E = E_P^*$ ,  $L = L_Q^*$  and equations (8) and (9) hold, corresponding to  
 234 the solid curve in the  $(P, Q)$ -plane in Fig. 4. Thus, on the slow time-scale,

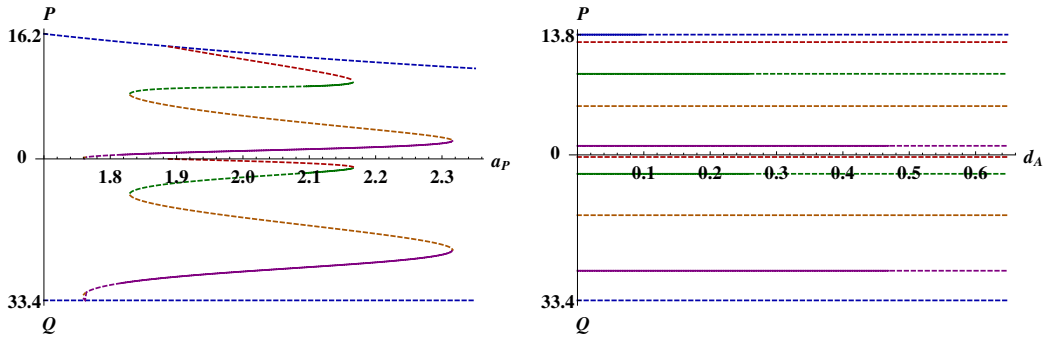


Figure 3: Bifurcation diagrams showing the equilibrium values for both parasitoid species. The upper vertical axis represents values for  $P$  and the lower vertical axis represents values for  $Q$ . The outermost lines represent equilibria with only one parasitoid species while the inner equilibria are true coexistence equilibria. Values for  $P$  and  $Q$  corresponding to the same coexistence equilibrium are drawn with the same color in the online version of the article. Stability is indicated by solid (stable) and dashed (unstable) lines. For the stability analysis the eigenvalues of the characteristic equation were calculated with the MATLAB package eigAM/eigTMN by Breda et al. (2014). Parameter values are the same as in Fig. 1 and Fig. 2 (except axis parameters)

235  $A(t)$  changes according to the third equation of the system (1) with all other  
 236 state variables at the quasi-equilibrium. It can be easily verified that  $A(t)$   
 237 will increase or decrease according to whether the basic reproduction num-  
 238 ber  $R_0$  from equation (11) is greater or smaller than 1, thus according to  
 239 whether  $(P, Q)$  is above or below the dashed curve in Fig. 4. As at the quasi-  
 240 equilibrium  $A$  and  $P$  are related by relation (8) with  $E = E_P^*$ , an increase  
 241 [decrease] of  $A(t)$  corresponds to an increase [decrease] of  $P(t)$ . This explains  
 242 why the dynamics in the  $(P, Q)$ -plane is towards the right when the dashed  
 243 curve is above the solid curve ( $R_0 > 1$ ) and towards the left when the dashed  
 244 curve is below. Since the intersections between the two curves correspond  
 245 to values of  $(P, Q)$  where all state variables are at equilibrium, the previous  
 246 graphical argument shows that, in the limit of  $d_A \rightarrow 0$ , an equilibrium is  
 247 stable when the dashed curve crosses the solid curve from above, while it is  
 248 unstable when the curves cross in the opposite way.

249 These findings can be transferred to the shape of the function  $f(P)$ . Indeed,  
 250 it can be easily verified that the solid curve is below the dashed curve if  
 251 and only if  $f(P)$  is below  $L_Q^*/E_P^*$ . Therefore the findings above imply that  
 252 coexistence equilibria are stable, for  $d_A$  sufficiently small, when  $f'(P^{**}) > 0$ ,

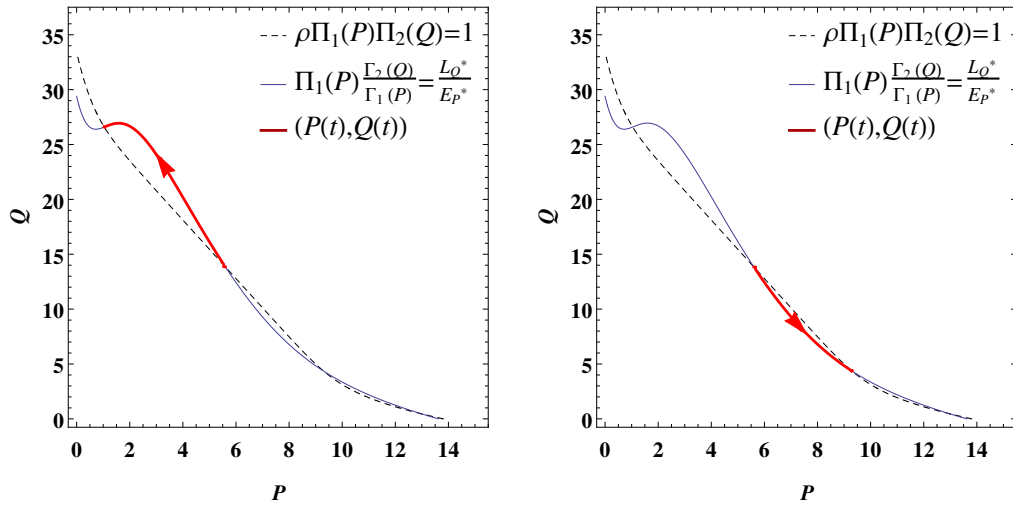
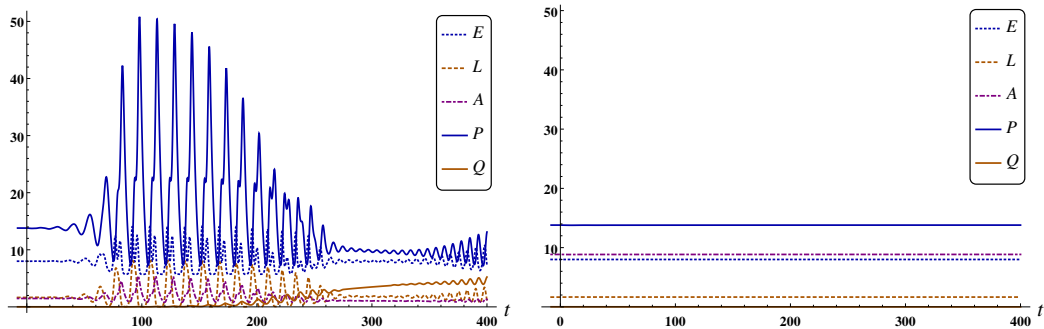


Figure 4: Parasitoid phase plane with time dynamics. Initial population densities (for  $t \leq 0$ ) correspond to the second coexistence equilibrium from left in Fig. 1. Perturbation is introduced via the host adult densities, which are respectively to its equilibrium value decreased by 1% in the left panel and increased by 1% in the right panel. Host adult mortality rate is very low,  $d_A = 0.001$ . All other parameter values are as in Fig. 1 and 2

253 while they are unstable when  $f'(P^{**}) < 0$ . The second statement appears to  
 254 be true for all  $d_A > 0$  but we give a formal proof only for the scenario with  
 255 constant maturation delays in Appendix C.2.

256 Further investigations of invasibility are illustrated with time plots in Fig. 5,  
 257 where the larva parasitoid is introduced at very low density into an equilib-  
 258 rium system of egg parasitoid and host. This numerical example has impor-  
 259 tant implications concerning invasion and coexistence which go beyond what  
 260 was found by Briggs et al. (1993). One point is that the invasibility criteria  
 261 stated in Section 5 do hold only for constant equilibria. If a single-parasitoid  
 262 equilibrium is unstable with respect to the interaction of this parasitoid and  
 263 the host, it has no sense to investigate its invasibility by the other parasitoid.  
 264 Instead one should (numerically) find the single parasitoid-host attractor and  
 265 investigate its invasibility (Metz et al., 1992). One may actually do this in  
 266 one go by using the introduction of the second parasitoid as a way to perturb  
 267 the unstable equilibrium as done in Fig. 5. As this figure reveals, oscillations  
 268 may facilitate successful invasion in the sense that the second parasitoid is  
 269 successful when the single parasitoid equilibrium is unstable ( $d_A = 0.3$ ),  
 270 while being unsuccessful in case it is stable ( $d_A = 0.05$ ) since  $L_P^* < L_Q^*$ . By



(a) For  $d_A = 0.3$  the equilibrium of host and egg parasitoid is unstable and the larva parasitoid can invade through oscillations

(b) For  $d_A = 0.05$  the equilibrium of host and egg parasitoid is stable and the larva parasitoid cannot invade

Figure 5: Time plots of population dynamics after introducing the larva parasitoid into an equilibrium system of egg parasitoid and host. The system is started with constant population densities for  $t \leq 0$  corresponding to the equilibrium densities of egg parasitoid and host with additional a low density  $Q = 0.01$  of the larva parasitoid. Distributions and parameter values are the same as in Fig. 1 and 2 with exception of a lower value for  $d_A$  in the right panel

271 combining Fig. 5b with the right panel of Fig. 3 another conclusion emerges:  
 272 non-invasibility of a stable single-parasitoid equilibrium does not exclude the  
 273 possibility of stable equilibrium coexistence of the two parasitoids (indeed,  
 274 for  $d_A = 0.05$  we observe in Fig. 3 that simultaneously the equilibrium with  
 275 only the egg parasitoid, and two coexistence equilibria are stable).

276

## 277 7. Discussion

278 We found multiple (non-trivial) coexistence equilibria in a model for the  
 279 population dynamics of two parasitoids attacking different juvenile stages  
 280 of a common host. The model was introduced by Briggs et al. (1993) and  
 281 it involves distributed maturation delays for the host juvenile stages. We  
 282 have shown that, depending on the distributions of the maturation delays,  
 283 multiple coexistence equilibria can arise. To our knowledge, this is the first  
 284 documented example of multiple coexistence equilibria in a parasitoid-host  
 285 model, as well as the first example for the multiplicity of coexistence equi-  
 286 libria to depend on the distribution of maturation delays.

287 Non steady-state attractors in parasitoid-host systems, in contrast, have re-  
288 ceived considerable attention before. Already the dynamics of the classical  
289 discrete-time model by Nicholson and Bailey (1935) are known to be os-  
290 cillatory: one or both species go extinct after diverging oscillations around  
291 the unstable coexistence equilibrium. In a continuous-time parasitoid-host  
292 model by Murdoch et al. (1987), stability of a steady-state coexistence at-  
293 tractor can be facilitated by an invulnerable host stage. For modifications of  
294 this model, multiple non steady-state attractors have been found by Murdoch  
295 et al. (1992, 1997), Briggs (1993) and Briggs et al. (1999). Particularly Briggs  
296 (1993) shows that such non steady-state attractors can lead to parasitoid co-  
297 existence in situations where no stable coexistence equilibrium is predicted.  
298 Further Sieber and Hilker (2011) report multiple (non-)equilibrium attractors  
299 in a single host population that is exploited by microparasites and predators.  
300 Beyond that, there is a well-developed body of theory on coexistence in vari-  
301 able environments (deterministic and stochastic), see for example the works  
302 by Abrams (1984), Chesson (1994) and Li et al. (2016). Occurrence of oscil-  
303 lations in real parasitoid populations is documented by Godfray and Hassell  
304 (1989), who offer a review on oscillations of host parasitoid systems in the  
305 tropics and corresponding discrete and continuous models.

306 In our model we found that equilibria can have different properties. Sin-  
307 gle parasitoid equilibria are potentially stable and non-invadable only when  
308 the host stage of the other parasitoid is reduced more strongly than what  
309 would be needed by the competitor to sustain. Similarly we found that two-  
310 parasitoid coexistence equilibria are "potentially stable" only when increasing  
311 a parasitoid species reduces its own host stage relatively to its competitors  
312 host stage when the competing parasitoid species is chosen accordingly so  
313 that the host stays at equilibrium. Coexistence equilibria for which this  
314 is not the case turned out to be always unstable. This can be interpreted  
315 as a manifestation of the principle that coexistence of competitors can be  
316 possible only when intraspecific competition is stronger than interspecific  
317 competition, see for example the review by Chesson (2000). For the poten-  
318 tially stable equilibria we found that stability can be always altered with the  
319 parameter  $d_A$  of host adult mortality (which does not change the equilibrium  
320 values due to the way the model is parameterized). Especially, we found that  
321 low values for  $d_A$  generally stabilize potentially stable equilibria. In the other  
322 way around we found that high values for  $d_A$  are always destabilizing. This is  
323 similar to the observations of Murdoch et al. (1987), who found for a similar  
324 single-parasitoid model that stable equilibria can exist only when there is a



325 sufficiently long invulnerable adult stage of the host.  
326 We made several observations concerning invasibility and single-parasitoid  
327 equilibria in the model. One point is that in the presence of multiple co-  
328 existence equilibria, stable coexistence can occur without mutual invasibil-  
329 ity. We described a situation where the parasitoids can coexist although the  
330 larva parasitoid cannot invade a stable equilibrium of egg parasitoid and host  
331 ( $L_P^* < L_Q^*$ ). This is similar to the findings of Buonomo and Cerasuolo (2014)  
332 in a model for plants and parasites. Our example also shows that host juve-  
333 nile densities can increase when an additional parasitoid is introduced since  
334 the equilibrium larva density with the egg parasitoid alone  $L_P^*$  is lower than  
335 the equilibrium larva density  $L_Q^*$  when both parasitoids coexist. Analogous  
336 examples can be found for situations where introducing the egg parasitoid  
337 increases the equilibrium egg density. These findings differ from those of  
338 other authors including Briggs (1993) and Briggs et al. (1993), who assume  
339 that stable coexistence requires mutual invasibility, and conclude that (in  
340 the absence of other mechanisms such as hyperparasitism) introducing a sec-  
341 ond parasitoid cannot lead to higher equilibrium densities of host juveniles.  
342 This is interesting in the light of the discussion whether single or multiple  
343 parasitoids should be introduced for optimal biological pest control, see for  
344 example the contributions by Ehler (1990) and Pedersen and Mills (2004).  
345 Furthermore we found that the invasibility criterion suggested by Briggs et al.  
346 (1993) is not generally valid when there are multiple coexistence equilibria.  
347 The original criterion states that a parasitoid species can invade only if its  
348 growth rate is positive at the equilibrium host density set by the resident  
349 parasitoid. We found however that if there are multiple coexistence equilib-  
350 ria, and the residents single-parasitoid equilibrium is not stable, invasion of  
351 the other parasitoid can take place through oscillations eventually leading to  
352 coexistence of both parasitoids. This is related to the findings on invasion in  
353 oscillating conditions by Armstrong and McGehee (1980), Bacaër and Guer-  
354 naoui (2006), Greenman and Norman (2007) and Bate and Hilker (2013).  
355 Since in our model such situations occurred only when there are multiple co-  
356 existence equilibria we conjecture that this is indeed a necessary condition.  
357 The question remains of when coexistence equilibria can arise generally and  
358 what is the connection to the maturation delays of the hosts. A literature  
359 search reveals that the occurrence of multiple equilibria in population models  
360 is generally connected to some non-linearity or non-monotonicity in the inter-  
361 action of different species. Evidence for that can be found in several models  
362 based on ordinary differential equations. Pimenov et al. (2015) find that in a

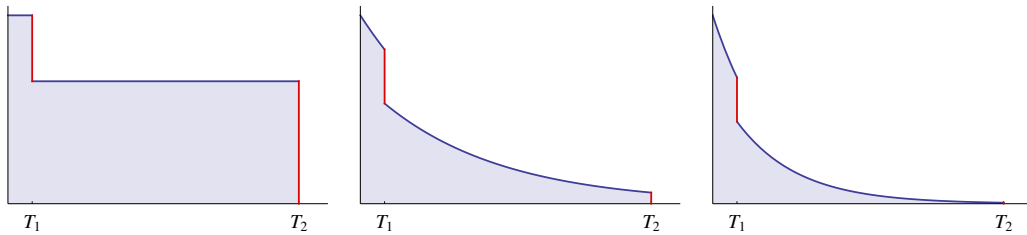


Figure 6: Age distribution of a host juvenile stage subjected to constant parasitism pressure  $a_P P$  or  $a_Q Q$  equal to 0, 0.2 or 0.4 (from left to right; note that there is no background death rate). The maturation delay for the stage is distributed by two discrete values  $T_1$  and  $T_2$  which occur with probabilities  $r$  and  $1 - r$ . The area under the curve represents the expectation value  $\Gamma_i$  for the time in this stage, while the sum of the lengths of the vertical bars at the times  $T_1$  and  $T_2$  represents the probability  $\Pi_i$  to reach the next stage. The ratio  $\Gamma_i/\Pi_i$  equals approximately 8.8, 9.5 and 7.9 from left to right, and thus first increases and then decreases with increasing parasitism. Parameter values are:  $r = 0.35$ ,  $T_1 = 1$ ,  $T_2 = 12$

363 predator-prey model, multiple coexistence equilibria can arise when the prey  
 364 changes its behavior in dependence of the predator density. Similarly Freeze  
 365 et al. (2014) find multiple coexistence equilibria in a three species model  
 366 where a super predator changes feeding behavior in dependence of its prey  
 367 species densities. Buonomo and Cerasuolo (2014) find multiple coexistence  
 368 equilibria in a model with host plants that react to parasitism in a non-linear  
 369 way.

370 We found in our model too that multiple coexistence equilibria can occur  
 371 only when the host larva-egg proportion depends in a non-monotonic way on  
 372 the density of one parasitoid while the other parasitoid density is kept so that  
 373 the host stays at equilibrium. We have seen that this can never happen for  
 374 two important special cases: constant and exponentially distributed maturation  
 375 delays. For constant maturation delays, increasing one parasitoid (and  
 376 decreasing the other parasitoid accordingly) increases its own host stage rel-  
 377 atively to the host stage of the competitor, which additionally implies that  
 378 if there is a coexistence equilibrium, it is unstable and neither parasitoid can  
 379 invade a stable population with the other parasitoid. Conversely for expo-  
 380 nentially distributed maturation delays, increasing a parasitoid (and again  
 381 decreasing the other parasitoid accordingly) reduces its host stage relatively  
 382 to the host stage of the competitor, which additionally implies pairwise inva-  
 383 sibility when there is a coexistence equilibrium. For all other distributions we  
 384 investigated, the parasitoid densities can affect the hosts larva-egg proportion

385 in a non-monotonic fashion giving rise to multiple coexistence equilibria. An  
 386 illustration of how this can happen with the two-value distributions we used  
 387 in our numerical examples is shown in Fig. 6. There we show the expected  
 388 duration  $\Gamma_i$  of a juvenile stage and the probability  $\Pi_i$  to reach the next  
 389 stage, both for different densities of the corresponding parasitoid. We see  
 390 that increasing the parasitoid density first decreases  $\Pi_i$  heavily because only  
 391 a small part of the hosts with long maturation delay reaches maturation,  
 392 while further increasing the parasitoid density decreases  $\Gamma_i$  more strongly  
 393 because parasitism still mainly affects hosts with a long maturation delay  
 394 whose contribution to  $\Pi_i$  was already low. Such mechanisms can lead to a  
 395 non-monotonic relation between the parasitoid densities and the hosts larva-  
 396 egg proportion, what potentially gives rise to multiple coexistence equilibria.  
 397 Note however that the ratio of a parasitoids host stage and the other para-  
 398 sitoids host stage is according to (21) and (23) not only proportional to  
 399  $\Gamma_i/\Pi_i$  but depends also on  $\Gamma_j(\Pi_j^{-1}(\frac{1}{\rho\Pi_i}))$  (where  $j$  refers to the other para-  
 400 sitoids host stage); thus this graphical illustration is incomplete, but still, in  
 401 our view, sheds some light on the mechanisms through which the distribution  
 402 of maturation delays affects coexistence equilibria.

#### 403 **Appendix A. Transition probabilities and expected duration of** 404 **the stages**

405 Here we derive formulas for the transition probabilities from egg to larva  
 406  $\Pi_1(P)$  and from larva to adult  $\Pi_2(Q)$ , and for the expected duration of  
 407 the egg, larva and adult stage,  $\Gamma_1(P)$ ,  $\Gamma_2(Q)$  and  $\Gamma_3$  respectively. The  
 408 calculations are valid for constant parasitoid densities  $P$  and  $Q$ . We use the  
 409 following notations for the various random variables

410

random variable	density	description
$X_E$	$w_E(\tau)$	time needed for egg maturation
$X_L$	$w_L(\tau)$	time needed for larva maturation
$K_E$	$(a_P P + d_E)e^{-\tau(a_P P + d_E)}$	time until an egg dies or is infected (when it does not mature before), distributed exponentially
$K_L$	$(a_Q Q + d_L)e^{-\tau(a_Q Q + d_L)}$	time until a larva dies or is infected (when it does not mature before), distributed exponentially
$K_A$	$d_A e^{-\tau d_A}$	time until an adult dies, distributed exponentially

414 *Appendix A.1. Transition probabilities  $\Pi_1(P)$  and  $\Pi_2(Q)$*

415 When the parasitoid densities are constant, the probability for a freshly laid  
416 egg to mature to a larva is

$$\begin{aligned}
\Pi_1(P) &= \mathbb{P}[X_E < K_E] \\
&= \int_0^\infty \int_\tau^\infty w_E(\tau) (a_P P + d_E) e^{-(a_P P + d_E)\sigma} d\sigma d\tau \\
&= \int_0^\infty w_E(\tau) e^{-(a_P P + d_E)\tau} d\tau,
\end{aligned} \tag{A.1}$$

417 where we use the independence of  $X_E$  and  $K_E$ . Likewise the probability for  
418 a freshly hatched larva to mature to an adult is given by

$$\Pi_2(Q) = \mathbb{P}[X_L < K_L] = \int_0^\infty w_L(\tau) e^{-(a_Q Q + d_L)\tau} d\tau. \tag{A.2}$$

419 Obviously  $\Pi_1$  and  $\Pi_2$  decrease strictly monotonically to 0.

420 *Appendix A.2. Expectation values for the durations of different stages*

421 When the parasitoid densities are constant, the expected duration of the egg  
422 stage (which is either terminated by death of the egg or maturation to a  
423 larva) is for  $a_P P + d_E \neq 0$

$$\begin{aligned}
\Gamma_1(P) &= \mathbb{E}[\min\{K_E, X_E\}] \\
&= \mathbb{E}[K_E|K_E \leq X_E]\mathbb{P}[K_E \leq X_E] + \mathbb{E}[X_E|X_E < K_E]\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E|K_E \leq X_E]\mathbb{P}[K_E \leq X_E] \\
&\quad + (\mathbb{E}[K_E|X_E < K_E] - \mathbb{E}[K_E - X_E|X_E < K_E])\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E|K_E \leq X_E]\mathbb{P}[K_E \leq X_E] \\
&\quad + (\mathbb{E}[K_E|X_E < K_E] - \mathbb{E}[K_E])\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E] - \mathbb{E}[K_E]\mathbb{P}[X_E < K_E] \\
&= \frac{1}{a_P P + d_E}(1 - \Pi_1(P))
\end{aligned} \tag{A.3}$$

424 where we used that  $K_E$  is exponentially distributed.

425 For  $a_P P + d_E = 0$  obviously

$$\Gamma_1(0) = \mathbb{E}[X_E]. \tag{A.4}$$

426 In the same way the expected duration of the larva stage (given that it is  
427 reached) can be calculated for constant parasitoid densities and  $a_Q Q + d_L \neq 0$ ,

$$\Gamma_2(Q) = \mathbb{E}[\min\{K_L, X_L\}] = \frac{1}{a_Q Q + d_L}(1 - \Pi_2(Q)) \tag{A.5}$$

428 and for  $a_Q Q + d_L = 0$

$$\Gamma_2(0) = \mathbb{E}[X_L]. \tag{A.6}$$

429 Note that the expectation values of  $K_E$  and  $K_L$  and thus  $\Gamma_1$  and  $\Gamma_2$  decrease  
430 strictly monotonically with the corresponding parasitoid densities.

431 The expected duration of the adult stage of a freshly emerged adult is

$$\Gamma_3 = \mathbb{E}[K_A] = \frac{1}{d_A}. \tag{A.7}$$

## 432 **Appendix B. Computing $f$ for some distributions**

433 Elementary representations for the function  $f$  from equation (21) can be  
434 found for some distribution families for the maturation delays. To facilitate  
435 the computations, we rearrange  $f$  by using the formulas for  $\Gamma_1$  and  $\Gamma_2$  derived

436 in Appendix A.2 (assuming that  $a_P P + d_E$  and  $a_Q \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) + d_L$  are  
 437 non-zero),

$$\begin{aligned}
 f(P) &= \frac{\Pi_1(P)}{\Gamma_1(P)} \Gamma_2 \left( \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) \right) \\
 &= \frac{\Pi_1(P)}{\frac{1-\Pi_1(P)}{a_P P + d_E}} \frac{1 - \Pi_2 \left( \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) \right)}{a_Q \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) + d_L} \\
 &= (a_P P + d_E) \frac{\Pi_1(P)}{1 - \Pi_1(P)} \frac{1 - \frac{1}{\rho \Pi_1(P)}}{a_Q \Pi_2^{-1} \left( \frac{1}{\rho \Pi_1(P)} \right) + d_L}.
 \end{aligned} \tag{B.1}$$

438 Now the following formulas for  $f$  in the special cases can be easily verified.

439 *Appendix B.1. Constant durations*

440 The maturation from egg to larva and from larva to adult takes a constant  
 441 time  $T_E$  and  $T_L$  respectively. For this distribution

$$\begin{aligned}
 \Pi_1(P) &= e^{-(a_P P + d_E) T_E} \\
 \Pi_2(Q) &= e^{-(a_Q Q + d_L) T_L}
 \end{aligned} \tag{B.2}$$

442 and (for  $d_E > 0$  and  $d_L > 0$ )

$$f(P) = \frac{T_L (a_P P + d_E) (\rho e^{-(a_P P + d_E) T_E} - 1)}{\rho (\log(\rho) - (a_P P + d_E) T_E) (1 - e^{-(a_P P + d_E) T_E})}. \tag{B.3}$$

443 The function  $f(P)$  decreases strictly monotonically in its domain  $P \in [0, P^*]$   
 444 with  $P^* = (\log(\rho) - d_L T_L - d_E T_E) / (T_E a_P)$  obtained by solving (13).<sup>1</sup> There-  
 445 fore the arguments of Section 4.3 and 5 show that a coexistence equilibrium  
 446 is necessarily unique and arises only when none of the parasitoids can invade  
 447 an equilibrium population of the other parasitoid and the host. To prove  
 448 the monotonicity of  $f(P)$  we define  $\gamma = (a_P P + d_E) T_E$  and  $q = \log(\rho)$ . The

---

<sup>1</sup>Note that for  $d_E = 0$  or  $d_L = 0$ , the stated representation of  $f(P)$  is undefined at the boundary of its domain but our result on monotonicity stays generally valid for the original function defined in (21). This can be verified by a simple limit argument.

449 domain for  $P$  implies that  $0 < \gamma < q$ . Obviously  $f(P)$  is decreasing if the  
 450 following function  $g(\gamma)$  is decreasing,

$$g(\gamma) = e^q \frac{T_E}{T_L} f(P) = \frac{\gamma(e^\gamma - e^q)}{(\gamma - q)(e^\gamma - 1)}. \quad (\text{B.4})$$

451 To prove the desired monotonicity of  $g(\gamma)$ , we take the derivative by  $\gamma$  and  
 452 show that  $g_\gamma(\gamma) < 0$  for  $0 < \gamma < q$ . Differentiation yields

$$g_\gamma(\gamma) = \frac{e^\gamma (q + q\gamma - \gamma^2) + e^{q+\gamma} (q - q\gamma + \gamma^2) - qe^{2\gamma} - e^q q}{(\gamma - q)^2 (e^\gamma - 1)^2} \quad (\text{B.5})$$

453 and the numerator (now interpreted as a function of  $q$  for any  $\gamma > 0$ )

$$k(q) = e^\gamma (q + q\gamma - \gamma^2) + e^{q+\gamma} (q - q\gamma + \gamma^2) - qe^{2\gamma} - e^q q \quad (\text{B.6})$$

454 determines the sign of  $g_\gamma(\gamma)$ . The first two derivatives of  $k(q)$  by  $q$  are

$$\begin{aligned} k_q(q) &= e^{q+\gamma} (q - q\gamma + \gamma^2 + 1 - \gamma) - e^q(1 + q) - e^{2\gamma} + e^\gamma(\gamma + 1) \\ k_{qq}(q) &= e^q (e^\gamma (q - q\gamma + \gamma^2 - 2\gamma + 2) - q - 2). \end{aligned} \quad (\text{B.7})$$

455 It can be easily seen that the equation  $k_{qq}(q) = 0$  has only one solution for  
 456  $q$ . Therefore  $k_q(q) = 0$  has at most two solutions and  $k(q)$  has at most two  
 457 (local) extrema.

458 Moreover, we see that  $k(0) = k(\gamma) = 0$ , that  $k(q) \xrightarrow{q \rightarrow -\infty} \infty$  (the dominant  
 459 term being  $qe^\gamma$  with coefficient  $1 + \gamma - e^\gamma$ ), and that  $k(q) \xrightarrow{q \rightarrow \infty} -\infty$  (the  
 460 dominant term being  $qe^q$  with coefficient  $e^\gamma(1 - \gamma) - 1$ ). Since  $k_q(\gamma) = 0$ , this  
 461 implies  $k(q) < 0$  for  $q > \gamma$  (and actually  $k(q) \leq 0$  for  $q \geq 0$ ). This completes  
 462 the proof that  $f(P)$  decreases strictly monotonically.

### 463 *Appendix B.2. Two-value distribution*

464 The maturation delay from egg to larva and from larva to adult are each  
 465 distributed with two distinct values that occur with certain probabilities.  
 466 The transformation from egg to larva has length  $T_{E_1}$  with probability  $r_E$  and  
 467 length  $T_{E_2}$  with probability  $1 - r_E$ . The transformation from larva to adult  
 468 has length  $T_{L_1}$  with probability  $r_L$  and length  $T_{L_2}$  with probability  $1 - r_L$ .  
 469 For this distribution

$$\begin{aligned} \Pi_E(P) &= r_E e^{(a_P P + d_E) T_{E_1}} + (1 - r_E) e^{(a_P P + d_E) T_{E_2}} \\ \Pi_L(Q) &= r_L e^{(a_Q Q + d_L) T_{L_1}} + (1 - r_L) e^{(a_Q Q + d_L) T_{L_2}}. \end{aligned} \quad (\text{B.8})$$

470  $\Pi_L^{-1}$  and therefore  $f$  have no elementary representations. The numerical  
 471 example presented in Fig. 1 shows however that  $f$  can be non-monotonic  
 472 and that therefore multiple coexistence equilibria can occur.

473 *Appendix B.3. Exponential distribution*

474 The maturation delays from egg to larva and from larva to adult are expo-  
 475 nentially distributed with expectation  $1/\lambda_E$  and  $1/\lambda_L$  respectively. For this  
 476 distribution

$$\begin{aligned}\Pi_1(P) &= \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\ \Pi_2(Q) &= \frac{\lambda_L}{a_Q Q + d_L + \lambda_L}\end{aligned}\tag{B.9}$$

477 and

$$f(P) = \frac{a_P P + d_E + \lambda_E}{\rho \lambda_L}.\tag{B.10}$$

478 Obviously  $f(P)$  increases strictly monotonically in this case. Therefore the  
 479 arguments of Section 4.3 and 5 state that a coexistence equilibrium is neces-  
 480 sarily unique and arises only in the case of mutual invasibility.

481 *Appendix B.4. Shifted exponential distribution*

482 The maturation delay from egg to larva and from larva to adult have shifted  
 483 exponential distributions. They have a minimum duration of  $m_E$  and  $m_L$   
 484 respectively, followed by an additional time which is distributed exponentially  
 485 with expectation  $1/\lambda_E$  and  $1/\lambda_L$  respectively. For this distribution

$$\begin{aligned}\Pi_E(P) &= e^{-(a_P P + d_E)m_E} \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\ \Pi_L(Q) &= e^{-(a_Q Q + d_L)m_L} \frac{\lambda_L}{a_Q Q + d_L + \lambda_L}.\end{aligned}\tag{B.11}$$

486  $\Pi_L^{-1}$  and therefore  $f$  have no elementary representations. Numerical cal-  
 487 culations show that  $f$  can become non-monotonous and therefore multiple  
 488 equilibria can arise.



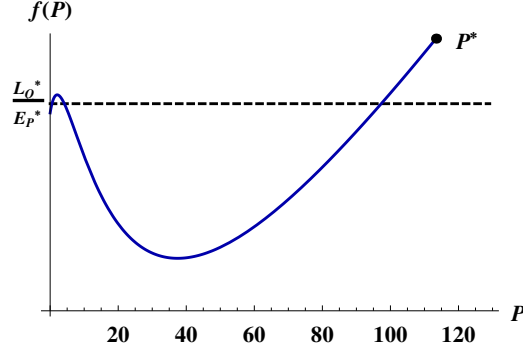


Figure B.7: The graph of the function  $f$  with gamma distributed maturation delays. Parameter values are  $p_E = 2$ ,  $p_L = 5$ ,  $\lambda_E = 1$ ,  $\lambda_L = 1$ ,  $a_P = 0.198$ ,  $a_Q = 1$ ,  $d_E = 0$ ,  $d_L = 0$ ,  $\rho = 550$ ,  $d_P = 1$ ,  $d_Q = 1$ ,  $c_P = 1$  and  $c_Q = 1$

489 *Appendix B.5. Gamma distribution*

490 The maturation delay from egg to larva and from larva to adult have gamma  
 491 distributions with shape parameter  $p_E$  and  $p_L$  respectively and inverse scale  
 492 parameter  $\lambda_E$  and  $\lambda_L$  respectively. For this distribution

$$\begin{aligned} \Pi_E(P) &= \left( \frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\ \Pi_L(Q) &= \left( \frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L} . \end{aligned} \quad (\text{B.12})$$

493  $\Pi_L^{-1}$  and therefore  $f$  have elementary representations,

$$f(P) = \frac{(a_P P + d_E) \left( (a_P P + d_E + \lambda_E)^{p_E} - \rho \lambda_E^{p_E} \right) \left( \frac{\lambda_E^{-p_E} (a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L}}{\lambda_L \rho \left( (a_P P + d_E + \lambda_E)^{p_E} - \lambda_E^{p_E} \right) \left( \left( \frac{\lambda_E^{-p_E} (a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L} - 1 \right)} . \quad (\text{B.13})$$

494 Numerical calculations show that  $f$  can become non-monotonous and there-  
 495 fore multiple equilibria can arise, see Fig. B.7.

496 *Appendix B.6. Shifted gamma distribution*

497 The maturation delay from egg to larva and from larva to adult have shifted  
 498 gamma distributions. They have a minimum duration of  $m_E$  and  $m_L$  re-  
 499 spectively, followed by an additional time which is gamma distributed with

500 shape parameter  $p_E$  and  $p_L$  respectively and inverse scale parameter  $\lambda_E$  and  
 501  $\lambda_L$  respectively. For this distribution

$$\begin{aligned}\Pi_E(P) &= e^{-(a_P P + d_E)m_E} \left( \frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\ \Pi_L(Q) &= e^{-(a_Q Q + d_L)m_L} \left( \frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L}.\end{aligned}\tag{B.14}$$

502  $\Pi_L^{-1}$  and therefore  $f$  have no elementary representations. As with the non-  
 503 shifted gamma distribution,  $f$  can become non-monotonous and therefore  
 504 multiple equilibria can arise.

### 505 Appendix C. Characteristic equation

506 Here we derive a characteristic equation by considering a small perturbation  
 507 from an equilibrium  $(\bar{E}, \bar{L}, \bar{A}, \bar{P}, \bar{Q})$ ,

$$\begin{aligned}E(t) &= \bar{E} + e(t), \quad L(t) = \bar{L} + l(t), \quad A(t) = \bar{A} + a(t) \\ P(t) &= \bar{P} + p(t), \quad Q(t) = \bar{Q} + q(t)\end{aligned}\tag{C.1}$$

508 and assume that

$$\begin{aligned}e(t) &= h_E e^{\lambda t}, \quad l(t) = h_L e^{\lambda t}, \quad a(t) = h_A e^{\lambda t} \\ p(t) &= h_P e^{\lambda t}, \quad q(t) = h_Q e^{\lambda t}.\end{aligned}\tag{C.2}$$

509 The aim of the characteristic equation is to investigate stability of an equi-  
 510 librium by the complex roots for  $\lambda$ . An equilibrium is stable when all roots  
 511 have negative real parts while it is unstable when there are roots with positive  
 512 real part, see (Diekmann et al., 1995). In order to derive the characteristic  
 513 equation, we define

$$\begin{aligned}\bar{R}_E &:= \rho d_A \bar{A} \\ \gamma_E &:= a_P \bar{P} + d_E \\ \gamma_L &:= a_Q \bar{Q} + d_L \\ \bar{M}_E &:= \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} w_E(x_E) dx_E \\ \bar{M}_L &:= \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} w_L(x_L) dx_L\end{aligned}\tag{C.3}$$

514 and

$$\begin{aligned}
r_E(t) &:= R_E(t) - \bar{R}_E \\
&= \rho d_A A(t) - \bar{R}_E \\
&= \rho d_A (\bar{A} + a(t)) - \bar{R}_E \\
&= \rho d_A a(t)
\end{aligned} \tag{C.4}$$

515 and

$$\begin{aligned}
m_E(t) &:= M_E(t) - \bar{M}_E \\
&= \int_0^\infty R_E(t - x_E) S_E(x_E, t) w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} e^{-a_P \int_{t-x_E}^t p(y) dy} w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} \left( 1 - a_P \int_{t-x_E}^t p(y) dy \right) w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty r_E(t - x_E) e^{-x_E \gamma_E} w_E(x_E) dx_E \\
&\quad - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E}^t p(y) dy w_E(x_E) dx_E
\end{aligned} \tag{C.5}$$

516 where we use that  $e^x \approx 1 + x$  for small  $x$  and that  $r_E(t - x_E)p(y) \approx 0$ . In  
517 the same way

$$\begin{aligned}
m_L(t) &:= M_L(t) - \bar{M}_L \\
&= \int_0^\infty m_E(t - x_L) e^{-x_L \gamma_L} w_L(x_L) dx_L \\
&\quad - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L \\
&= \int_0^\infty \left( \int_0^\infty r_E(t - x_E - x_L) e^{-x_E \gamma_E} w_E(x_E) dx_E \right. \\
&\quad \left. - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E-x_L}^{t-x_L} p(y) dy w_E(x_E) dx_E \right) \cdot e^{-x_L \gamma_L} w_L(x_L) dx_L \\
&\quad - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L.
\end{aligned} \tag{C.6}$$

518 Now we can state the derivatives

$$\begin{aligned}
\dot{e}(t) &= \dot{E}(t) = R_E(t) - M_E(t) - a_P E(t)P(t) - d_E E(t) \\
&= \bar{R}_E + r_E(t) - (\bar{M}_E + m_E(t)) - a_P(\bar{E} + e(t))(\bar{P} + p(t)) - d_E(\bar{E} + e(t)) \\
&= r_E(t) - m_E(t) - a_P(\bar{E}p(t) + e(t)\bar{P}) - d_E e(t)
\end{aligned} \tag{C.7}$$

519 where we use that  $\bar{R}_E - \bar{M}_E - a_P \bar{E}\bar{P} - d_E \bar{E} = 0$  and  $e(t)p(t) \approx 0$ . In the  
520 same way

$$\begin{aligned}
\dot{l}(t) &= m_E(t) - m_L(t) - a_Q(\bar{L}q(t) + l(t)\bar{Q}) - d_L l(t) \\
\dot{a}(t) &= m_L(t) - d_A a(t) \\
\dot{p}(t) &= c_P a_P(\bar{E}p(t - T_{JP}) + e(t - T_{JP})\bar{P}) - d_P p(t) \\
\dot{q}(t) &= c_Q a_Q(\bar{L}q(t - T_{JQ}) + l(t - T_{JQ})\bar{Q}) - d_Q q(t).
\end{aligned} \tag{C.8}$$

521 We introduce the notation

$$\begin{aligned}
\bar{\Pi}_1 &:= \Pi_1(\bar{P}) = \int_0^\infty e^{-x_E \gamma_E} w_E(x_E) dx_E \\
\bar{\Pi}_2 &:= \Pi_2(\bar{Q}) = \int_0^\infty e^{-x_L \gamma_L} w_L(x_L) dx_L \\
\bar{\Pi}_1(\lambda) &:= \Pi_1\left(\bar{P} + \frac{\lambda}{a_P}\right) = \int_0^\infty e^{-x_E(\gamma_E + \lambda)} w_E(x_E) dx_E \\
\bar{\Pi}_2(\lambda) &:= \Pi_2\left(\bar{Q} + \frac{\lambda}{a_Q}\right) = \int_0^\infty e^{-x_L(\gamma_L + \lambda)} w_L(x_L) dx_L
\end{aligned} \tag{C.9}$$

522 and obtain the following by plugging (C.2) into (C.7) and (C.8)

$$\begin{aligned}
\lambda h_E &= \rho d_A \left( h_A - h_A \bar{\Pi}_1(\lambda) + \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right) - a_P(\bar{E}h_P + h_E \bar{P}) - d_E h_E \\
\lambda h_L &= \rho d_A \left( h_A \bar{\Pi}_1(\lambda) - \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} - h_A \bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) + \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \bar{\Pi}_2(\lambda) \right. \\
&\quad \left. + \bar{A} a_Q h_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right) - a_Q(\bar{L}h_Q + h_L \bar{Q}) - d_L h_L \\
\lambda h_A &= \rho d_A \left( h_A \bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) - \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \bar{\Pi}_2(\lambda) - \bar{A} a_Q h_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right) - d_A h_A \\
\lambda h_P &= a_P c_P e^{-\lambda T_{JP}} (\bar{E}h_P + h_E \bar{P}) - d_P h_P \\
\lambda h_Q &= a_Q c_Q e^{-\lambda T_{JQ}} (\bar{L}h_Q + h_L \bar{Q}) - d_Q h_Q
\end{aligned} \tag{C.10}$$

523 where we divide on both sides by  $e^{\lambda t}$  and use that  $\overline{M}_E = \rho d_A \overline{A} \overline{\Pi}_1$ . From the  
 524 last two equations of (C.10) we can express  $h_p$  and  $h_q$  explicitly in terms of  
 525  $h_e$  and  $h_l$  as

$$\begin{aligned} h_P &= h_E \Phi_P(\lambda) \quad \text{where} \quad \Phi_P(\lambda) = \frac{\overline{P} a_P c_P e^{-\lambda T_{JP}}}{\lambda + d_P - a_P c_P \overline{E} e^{-\lambda T_{JP}}} \\ h_Q &= h_L \Phi_Q(\lambda) \quad \text{where} \quad \Phi_Q(\lambda) = \frac{\overline{Q} a_Q c_Q e^{-\lambda T_{JQ}}}{\lambda + d_Q - a_Q c_Q \overline{L} e^{-\lambda T_{JQ}}}. \end{aligned} \quad (\text{C.11})$$

526 Using the solutions from (C.11) and the first two equations in (C.10) we can  
 527 express  $h_E$  and  $h_L$  in the following form,

$$\begin{aligned} h_E &= h_A \Phi_E(\lambda) \\ \text{where} \quad \Phi_E(\lambda) &= \frac{\rho d_A (1 - \overline{\Pi}_1(\lambda))}{\lambda + d_E + a_P \overline{P} + \Phi_P(\lambda) (a_P \overline{E} - \rho d_A \overline{A} a_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda})} \\ h_L &= h_A \Phi_L(\lambda) \\ \text{where} \quad \Phi_L(\lambda) &= \frac{\rho d_A (\overline{\Pi}_1(\lambda) (1 - \overline{\Pi}_2(\lambda)) - \Phi_E(\lambda) \Phi_P(\lambda) \overline{A} a_P (1 - \overline{\Pi}_2(\lambda)) \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda})}{\lambda + d_L + a_Q \overline{Q} + \Phi_Q(\lambda) (a_Q \overline{L} - \rho d_A \overline{A} a_Q \overline{\Pi}_1 \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda})}. \end{aligned} \quad (\text{C.12})$$

528 Plugging  $h_P$ ,  $h_Q$ ,  $h_E$  and  $h_L$  in the third equation of (C.10) we have the  
 529 characteristic equation in the form  $G(\lambda) = 1$ ,

$$\begin{aligned} G(\lambda) &= \\ &= \frac{\rho d_A}{\lambda + d_A} \left( \overline{\Pi}_1(\lambda) \overline{\Pi}_2(\lambda) - \overline{A} a_P \overline{\Pi}_2(\lambda) \Phi_P(\lambda) \Phi_E(\lambda) \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} - \overline{A} a_Q \overline{\Pi}_1 \Phi_Q(\lambda) \Phi_L(\lambda) \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda} \right). \end{aligned} \quad (\text{C.13})$$

### 530 *Appendix C.1. A sufficient condition for instability*

531 The following observation can be helpful for proving instability of an equilib-  
 532 rium. It is easily verified that  $G(\lambda) \xrightarrow{\lambda \rightarrow \infty} 0$ . Hence if  $G(0) > 1$  then there is  
 533 a positive real root for the characteristic equation and the coexistence equi-  
 534 librium is unstable. Therefore we investigate the structure of  $G(0)$ . First we  
 535 see that

$$\begin{aligned} \lim_{\lambda \rightarrow 0} \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} &= -\frac{d\overline{\Pi}_1/d\overline{P}}{a_P} \\ \lim_{\lambda \rightarrow 0} \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda} &= -\frac{d\overline{\Pi}_2/d\overline{Q}}{a_Q}. \end{aligned} \quad (\text{C.14})$$

536 We will denote  $\bar{\Pi}'_1 = d\bar{\Pi}_1/d\bar{P}$  and  $\bar{\Pi}'_2 = d\bar{\Pi}_2/d\bar{Q}$ . Then we calculate

$$\begin{aligned}\Phi_P(\lambda)\Phi_E(\lambda) &= \Phi_P(\lambda) \frac{\rho d_A(1 - \bar{\Pi}_1(\lambda))}{\lambda + d_E + a_P\bar{P} + \Phi_P(\lambda) \left( a_P\bar{E} - \rho d_A\bar{A}a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)} \\ &= \frac{\rho d_A(1 - \bar{\Pi}_1(\lambda))}{\frac{\lambda + d_E + a_P\bar{P}}{\Phi_P(\lambda)} + \left( a_P\bar{E} - \rho d_A\bar{A}a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}.\end{aligned}\tag{C.15}$$

537 Since  $1/\Phi_P(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$ ,

$$\lim_{\lambda \rightarrow 0} \Phi_P(\lambda)\Phi_E(\lambda) = \frac{\rho d_A(1 - \bar{\Pi}_1)}{a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1}.\tag{C.16}$$

538 In the same way

$$\begin{aligned}\Phi_Q(\lambda)\Phi_L(\lambda) &= \Phi_Q(\lambda) \frac{\rho d_A \left( \bar{\Pi}_1(\lambda)(1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\bar{A}a_P(1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\lambda + d_L + a_Q\bar{Q} + \Phi_Q(\lambda) \left( a_Q\bar{L} - \rho d_A\bar{A}a_Q\bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)} \\ &= \frac{\rho d_A \left( \bar{\Pi}_1(\lambda)(1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\bar{A}a_P(1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\frac{\lambda + d_L + a_Q\bar{Q}}{\Phi_Q(\lambda)} + \left( a_Q\bar{L} - \rho d_A\bar{A}a_Q\bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)}.\end{aligned}\tag{C.17}$$

539 Since  $1/\Phi_Q(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$ ,

$$\lim_{\lambda \rightarrow 0} \Phi_Q(\lambda)\Phi_L(\lambda) = \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}'_1)}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}'_2)(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1)}.\tag{C.18}$$

540 Now  $G(0)$  can be simplified,

$$\begin{aligned}G(0) &= \rho \left( \bar{\Pi}_1\bar{\Pi}_2 + \bar{A}\bar{\Pi}_2\bar{\Pi}'_1 \frac{\rho d_A(1 - \bar{\Pi}_1)}{a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1} + \bar{A}\bar{\Pi}_1\bar{\Pi}'_2 \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}'_1)}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}'_2)(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1)} \right) \\ &= \rho \left( \frac{\bar{\Pi}_2(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}'_1)}{a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1} + \bar{A}\bar{\Pi}_1\bar{\Pi}'_2 \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}'_1)}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}'_2)(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1)} \right) \\ &= \rho \frac{(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}'_1)(a_Q\bar{L}\bar{\Pi}_2 + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}'_2)}{(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}'_1)(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}'_2)}.\end{aligned}\tag{C.19}$$

541

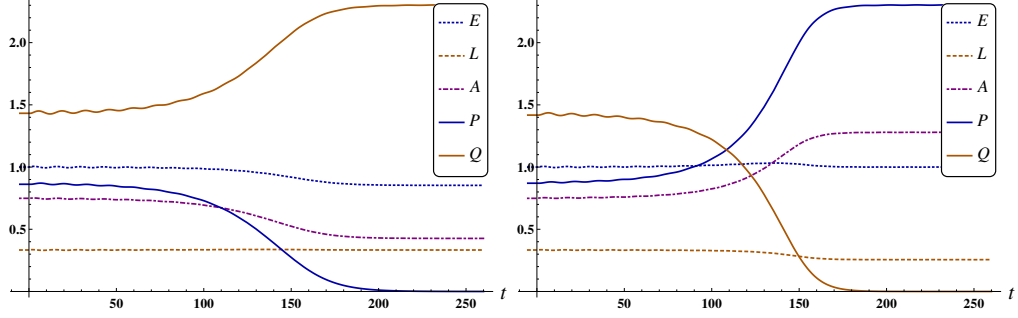


Figure C.8: Time plots of population dynamics after small perturbations from equilibrium densities. Both maturation delays, from egg to larva and from larva to adult, have constant lengths  $T_E$  and  $T_L$  respectively. The initial densities for  $t \leq 0$  are constant and correspond to perturbations from the unique set of coexistence equilibrium densities. In the left panel, the egg parasitoid density  $P$  is decreased by 1% and the larva parasitoid wins the competition. In the right panel, the larva parasitoid density  $Q$  is decreased by 1% and the egg parasitoid wins the competition. Parameter values are  $T_E = 1$ ,  $T_L = 1$ ,  $a_P = 1$ ,  $a_Q = 1$ ,  $d_E = 0$ ,  $d_L = 0$ ,  $d_A = 0.2$ ,  $\rho = 10$ ,  $d_P = 1$ ,  $d_Q = 1$ ,  $c_P = 1$ ,  $c_Q = 3$ ,  $T_{JP} = 1$  and  $T_{JQ} = 1$

542 *Appendix C.2. Instability of the coexistence equilibrium when maturation de-*  
543 *lays are constant*

544 We have seen in Appendix B.1, that with constant maturation delays at  
545 most one coexistence equilibrium exists, and that if it exists, none of the  
546 parasitoids can invade an equilibrium population of the other parasitoid and  
547 the host. This observation and the simulations shown in Fig. C.8 suggest that  
548 the coexistence equilibrium is unstable. We will now prove this conjecture  
549 by using the criteria from Appendix C.1, which states that an equilibrium  
550 is unstable when the corresponding  $G(0) > 1$ . Using the formulations of  
551 Appendix B.1 and Appendix C.1, it is easily verified that with constant  
552 maturation delays  $\bar{\Pi}'_1 = -a_P T_E \bar{\Pi}_1$  and  $\bar{\Pi}'_2 = -a_Q T_L \bar{\Pi}_2$ . Plugging into (C.19)  
553 yields with the notation  $\Gamma_1(\bar{P}) = \bar{\Gamma}_1$  and  $\Gamma_2(\bar{Q}) = \bar{\Gamma}_2$ ,

$$\begin{aligned}
G(0) &= \rho \frac{(a_P \bar{E} \bar{\Pi}_1 - a_P T_E \rho d_A \bar{A} \bar{\Pi}_1)(a_Q \bar{L} \bar{\Pi}_2 - a_Q T_L \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Pi}_2)}{(a_P \bar{E} - a_P T_E \rho d_A \bar{A} \bar{\Pi}_1)(a_Q \bar{L} - a_Q T_L \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Pi}_2)} \\
&= \frac{\bar{\Gamma}_1 - T_E}{\bar{\Gamma}_1 - T_E \bar{\Pi}_1} \frac{\bar{\Gamma}_2 - T_L}{\bar{\Gamma}_2 - T_L \bar{\Pi}_2}, \tag{C.20}
\end{aligned}$$

554 where we use  $\bar{E} = \rho d_A \bar{A} \bar{\Gamma}_1$ ,  $\bar{L} = \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Gamma}_2$  and  $\rho \bar{\Pi}_1 \bar{\Pi}_2 = 1$  according to  
555 equation (7), (8), (9) and (11). For both fractions in the last line of (C.20),  
556 the numerator is positive and the denominator is negative. To verify this,  
557 we deduce from equation (A.3) that

$$\begin{aligned}\bar{\Gamma}_1 &= \mathbb{E}[\min\{K_E, T_E\}] < T_E \text{ and} \\ \bar{\Gamma}_1 &= \bar{\Pi}_1 T_E + (1 - \bar{\Pi}_1) \mathbb{E}[K_E | K_E \leq T_E] > \bar{\Pi}_1 T_E,\end{aligned}\tag{C.21}$$

558 where  $K_E$  is an exponentially distributed random variable. In the same way  
559  $\bar{\Gamma}_2 < T_L$  and  $\bar{\Pi}_2 T_L < \bar{\Gamma}_2$ . To prove  $G(0) > 1$ , it is therefore enough to show  
560 that  $\bar{\Gamma}_1 - T_E \bar{\Pi}_1 < T_E - \bar{\Gamma}_1$  and  $\bar{\Gamma}_2 - T_L \bar{\Pi}_2 < T_L - \bar{\Gamma}_2$ . To verify the first –and  
561 in the same way the second– inequality, we use  $\bar{\Gamma}_1 = (1 - \bar{\Pi}_1)/(a_P \bar{P} + d_E)$   
562 from equation (A.3), and argue

$$\begin{aligned}\bar{\Gamma}_1 - T_E \bar{\Pi}_1 < T_E - \bar{\Gamma}_1 &\Leftrightarrow \\ \frac{1 - \bar{\Pi}_1}{a_P \bar{P} + d_E} - T_E \bar{\Pi}_1 < T_E - \frac{1 - \bar{\Pi}_1}{a_P \bar{P} + d_E} &\Leftrightarrow \\ 1 - \bar{\Pi}_1 - \bar{\Pi}_1 (a_P \bar{P} + d_E) T_E < (a_P \bar{P} + d_E) T_E - 1 + \bar{\Pi}_1 &\Leftrightarrow \\ 1 - e^{-\gamma} - \gamma e^{-\gamma} < \gamma - 1 + e^{-\gamma} &\Leftrightarrow \\ \int_0^\gamma (x e^{-x}) dx < \int_0^\gamma (1 - e^{-x}) dx &\Leftrightarrow \\ x e^{-x} < 1 - e^{-x} \quad \forall x > 0 &\Leftrightarrow \\ 1 + x < e^x \quad \forall x > 0,\end{aligned}\tag{C.22}$$

563 where  $\gamma = (a_P \bar{P} + d_E) T_E$ . The last line of (C.22) is obviously true. This  
564 completes the proof that the coexistence equilibrium is unstable when the  
565 maturation delays are constant.

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