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Multiple coexistence equilibria in a two parasitoid-one host model

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HIGHLIGHTS

- A stage structured model for two parasitoids with a common host is reanalyzed.
- Maturation delays of the host are randomly distributed.
- Depending on these distributions multiple coexistence equilibria can arise.
- Multiple coexistence equilibria can be simultaneously stable.
- Stable coexistence does not necessarily require mutual invasibility.

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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 analyze 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.

1. Introduction

It is known that parasitoid species of the same host can coexist (Force, 1970; Price, 1970; Harvey et al., 2009). This observation seems to contradict a principle in ecology which predicts that competing species cannot coexist on the same limiting resource (Gause and Witt, 1935), though it has been shown that the principle holds under very stringent equilibrium conditions (Chesson and Case, 1986) and that competitors can coexist on the same biological resource along periodic solutions (Hsu et al., 1977; Armstrong and McGehee, 1980). Parasitoid species are a particularly interesting case, as various mechanisms that can promote parasitoid coexistence on the same host have been suggested (Price, 1970; Lane et al., 2006; Hackett-Jones et al., 2009). Briggs (1993) started to investigate under which conditions parasitoids can coexist when they attack different juvenile stages of a common host. This investigation was continued by Briggs et al. (1993), who found that in their model coexistence at equilibrium is possible only when there is sufficient variability in the maturation delays of the juvenile stages. They suggested that when the variability is large enough, different host individuals can be interpreted as different resources: individuals with a relatively long egg phase support the egg parasitoid, and individuals with a relatively long larva phase support the larva parasitoid. In the present paper, we reanalyze the model by Briggs et al. (1993) and find more complex patterns than those already identified: there may be multiple coexistence equilibria, and, contrary to conventional wisdom, stable coexistence does not require mutual invasibility. The model is presented in Section 2. In Sections 3–5, we formulate the original results in our somewhat different notation and, in Section 6, we show that coexistence equilibria are not unique for many distributions of the maturation delays. Finally, in Section 7, we set our results in the

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context of other works, discuss their relevance for biological pest control, and propose questions for further investigation. A general introduction to parasitoid–host systems can be found, for instance, in the text book by Godfray (1994).

2. The model

The model describes a host with two juvenile stages E and L, and an adult stage A. We refer to the first juvenile stage as eggs and to the second juvenile stage as larvae but they can also represent other developmental stages as pupae or different instars. The egg stage is attacked by an egg parasitoid (whose density is denoted by P) while the larva stage is attacked by a larva parasitoid (density denoted by Q) with attack rates a_P and a_Q, respectively. Non-infected host juveniles have random maturation delays which are distributed with probability density functions w_E and w_L. Infected hosts do not progress to the next stage but give rise to new parasitoids a constant time T_{JP} or T_{JQ} after the infection. Unlike the original paper, we do not explicitly introduce survival probabilities for the juvenile parasitoids, since these can be absorbed in the parameters c_P and c_Q for the expected number of parasitoids emerging from an infected host. All other host and parasitoid stages have constant (background) death rates d_E, d_L, d_A, d_P and d_Q. Adult hosts have a life time fecundity ρ (so ρd_A is the rate with which an adult produces offspring).

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

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

where

$R_E(t) = \rho d_A A(t)$	Host egg recruitment rate
$M_E(t) = \int_0^\infty R_E(t-x_E)S_E(x_E,t)w_E(x_E)dx_E$	Host egg maturation rate = host larva recruitment rate
$M_L(t) = \int_0^\infty M_E(t-x_L)S_L(x_L,t)w_L(x_L)dx_L$	Host larva maturation rate = host adult recruitment rate
with	
$S_E(x_E,t) = \exp\left(-\int_{t-x_E}^t (a_P P(y) + d_E)dy\right)$	Probability for host eggs to survive from time $t - x_E$ to t
$S_L(x_L,t) = \exp\left(-\int_{t-x_L}^t (a_Q Q(y) + d_L)dy\right)$	Probability for host larvae to survive from time $t - x_L$ to t

and

Parameter	Description
ρ	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
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
T_{JQ}	Duration of juvenile larva parasitoid stage

and

Function	Description
w_E	probability density function for host egg maturation delay
w_L	probability density function for host larva maturation delay

3. Preliminaries

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

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

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

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

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

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

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

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

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

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

$$\Gamma_3 = \frac{1}{d_A}. \tag{6}$$

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