

PROLONGATION OF PLAGUES BY PARASITIDS WITH MICRO-TYPE EGGS

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Summary

In a theoretical study the interaction is investigated between parasitoids (tachinid flies) with micro-type eggs and their hosts. In case of a plague of the host it is shown that, paradoxically enough, the presence of such parasitoids lengthens the duration of the plague, sometimes even quite dramatically.

INTRODUCTION

It is generally assumed that parasitoids may help controlling high population densities of their phytophagous hosts. Especially at high parasitization rates, one may expect the parasitoids to have a major controlling influence on their hosts. High parasitization rates (30 % or more) are for example known for the tachinid fly *Pales processioneae* (Ratzeburg) in its host *Thaumetopoea processionea* (Linnaeus) (Tschorsch 1996, Zeegers 1997).

In this article, I investigate the influence of a parasitoid on its host in a theoretical study for a class of parasitoid-host couples that includes the *Pales-Thaumetopoea*-example. More generally, I consider the following case:

- *) The phytophagous host occurs in plagues, i.e. it exhibits large growth of its population which ends by overpopulation.
- *) The parasitoid reproduces by micro-type eggs which are eaten by the host. A large and important class of tachinid flies (Diptera: Tachinidae) shows this reproduction strategy.

The second property makes it possible to describe the influence of the parasitoid mathematically virtually without additional assumptions, since the process of finding the host is essentially ruled by statistics. Investigation of such a model will lead to the main conclusions of this article:

- *) A parasitoid cannot exterminate the host. The only way to extinction is by overpopulation of the host.
- *) The presence of a parasitoid slows the rate of growth of the plague and therefore prolongs the presence of the host.
- *) This effect may be quite dramatic in some circumstances, so that even a dynamical stable equilibrium between host and parasitoid may arise.

Derivation of a mathematical model

The reproduction strategy of tachinid flies with micro-type eggs differs from many other parasitoids in that the eggs are not deposited on or near the host. Instead, the eggs are laid

on the food-plants of the host at random. The host swallows the egg while eating, after which the larva hatches inside the host (Herting, 1960). Once in the host, the tachinid larva develops relatively slowly while feeding on non-essential host-tissue. Therefore the host still functions properly and may even grow. A few days before pupation the behaviour of the larva changes radically: it consumes the host rapidly and goes into pupation. More than one fly (up to seven) may evolve from one host (Herting, 1960; author, unpublished).

Based on this biology, we can make the following assumptions necessary to derive a mathematical model:

- *) each species is Orwellian, i.e. all individuals within each species are equal.
- *) the parasitoid is monophagous.
- *) the parasitoid lays her micro-type eggs on the food-plant of the host at random and mutually (stochastically) independently.
- *) the tachinid larva does not alter the behaviour of its host until pupation. (this is an idealization of reality.)
- *) the number of parasitoids that may evolve from one host is not limited (idem).
- *) both parasitoid and host occur in distinct generations.

With these assumptions it is possible to derive a mathematical model for the host-parasitoid dynamics. Here I merely give a sketch of this derivation in the hope to publish the technical details elsewhere.

Consider a food-supply of the food-plant of size V . Let each host-individual need a food-supply v ($\ll V$) during its lifetime in order to be able to pupate successfully. Let M_n denote the number of host-eggs in the n -th generation on this food-supply and let P_n denote the number of micro-type eggs in the n -th generation. How many eggs (on average) are being eaten by the host? Since the eggs are laid at random, we may think of this problem as depicted in figure 1.

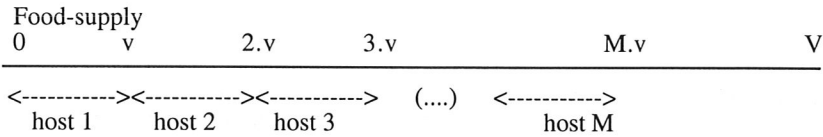


Figure 1: schematic representation of a population of M hosts on a food-supply V . Each host needs a food-supply of size v .

Then clearly the chance for one egg to reach a host is $M_n \cdot v / V$. Since the eggs have been laid independently, the average number of eggs to reach a host out of P_n eggs equals $P_n \cdot M_n \cdot v / V$.

Introducing the 'dimensionless densities' for the eggs as

$$\begin{aligned}
 x_n &\equiv M_n \frac{v}{V} \\
 y_n &\equiv P_n \frac{v}{V}
 \end{aligned}
 \tag{1}$$

we find that the dimensionless average density of eggs in hosts equals $x_n \cdot y_n$. Assuming a fixed number of eggs for each fly, we directly find the (dimensionless) density of parasitoid eggs in the next generation

$$y_{n+1} = \gamma_2 \cdot x_n \cdot y_n \quad (2)$$

where γ_2 is a constant (number of eggs per fly).

Now if each host could carry one egg at the most, the density of affected hosts would be equal to the density of parasitoid-eggs and therefore the density of non-affected hosts would equal

$$x_n - x_n \cdot y_n = x_n \cdot (1 - y_n) \quad (3)$$

However, since two or more eggs can enter the same host, this formula needs to be corrected. The correct formula can indeed be derived exactly and although the mathematics are not especially difficult, they are quite lengthy and cumbersome. Therefore I only give the results here (and hope to publish the details elsewhere):

$$\text{density of non-parasitized hosts} = x_n e^{-y} \quad (4)$$

Observe that this formula is approximated by (3) at low parasitoid-densities. More-over, the correct result (4) is always larger than (3), as it should be (more eggs in one host result in more non-parasitized hosts than initially guessed).

To complete the discussion on the mathematical model, we have to make an assumption on the host-dynamics in the absence of parasitoids. We assume that a density of x eggs leads to $f(x)$ succesful pupations, where $f(x)$ may be any function with the property $f(x) \leq x$. Since there is an overall food shortage for densities $x > 1$, $f(x) = 0$ for $x > 1$. If we then assume a fixed number of eggs per fly as we have done before, we get in the absence of parasitoids the following dynamical model for the host

$$x_{n+1} = \gamma_1 \cdot f(x_n) \quad (5)$$

This can be extended to the case with a parasitoid as follows. We have assumed that the parasitoid does not affect the behaviour of its host. So even with parasitoids x host-eggs lead to $f(x)$ pupae. By (4), the fraction of non-parasitized pupae is given by e^{-y} . Only from these pupae hosts emerge, they replicate with a factor γ_1 as before.

Putting this altogether, we have derived the following dynamical model for the parasitoid-host interaction in the case of parasitoids with micro-type eggs:

$$x_{n+1} = \gamma_1 \cdot e^{-y_n} \cdot f(x_n) \quad (6)$$

$$y_{n+1} = \gamma_2 \cdot x_n \cdot y_n$$

$$\text{where } 0 \leq f(x) \leq x \quad \forall x \quad (6a)$$

$$f(x) = 0 \quad \forall x > 1$$

The special situation of a plague is characterized by the constant growing host-population in absence of the parasitoid (5), thus

$$\gamma_1 \cdot f(x) > x \quad \forall \quad 0 \leq x < 1 \quad (7)$$

ANALYSIS AND RESULTS

It is useful to analyse dynamical system (6) for interesting choices of $f(x)$, such as $f(x) = x$ or $f(x) = x \cdot \exp(-\lambda x)$. However, the plague-condition (7) allows us to derive some general properties for the dynamics of (6).

First of all, observe that the growth of host-densities x in (6) is smaller than in (5). More precisely, the growth of x gets smaller when the parasitoid-density gets higher.

At very high parasitoid-densities ($y > \log(\gamma_1)$), the host-densities even diminish for certain. At smaller host-densities ($x < 1/\gamma_2$), the number of parasitoids diminish. Since the only fixed point on the Y-axis, the origin, is unstable (a saddle) because of (7), the dynamics cannot be attracted towards the Y-axis.

The global picture of dynamics is given in figure 2.

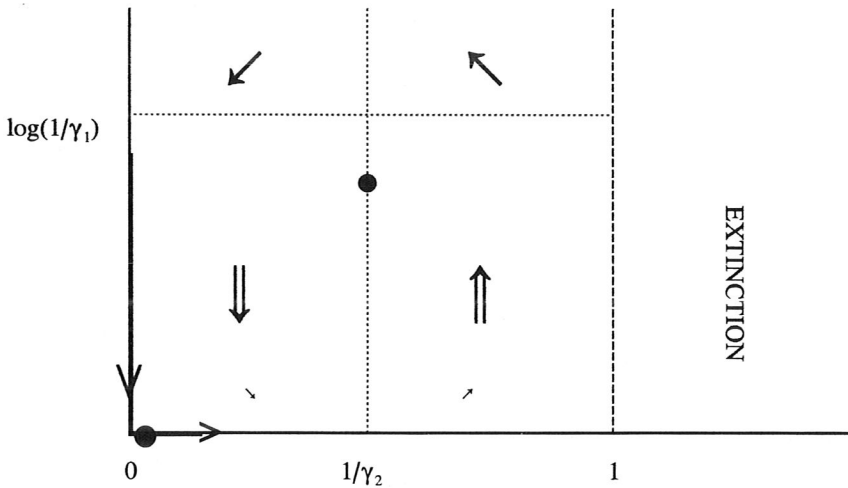


Figure 2: Global dynamics of system (6) & (7)
 Large black dot: fixed point
 Large arrow: general direction of motion
 Open arrow: general vertical direction of motion
 Small arrow: general direction of motion near invariant set

As long as $x < 1/\gamma_2$, the dynamics move towards the X-axis. Nearby the X-axis, x must grow because of (7). Therefore, eventually the host-densities must grow again and the dynamics must reach the area $x > 1/\gamma_2$. We conclude that the host-densities x cannot go to zero monotonically. The only way to extinction of the host is by entering the region $x > 1$.

Besides the origin there exists one non-trivial fixed point (x^*, y^*) . The stability of this fixed point can be analysed rigorously. It turns out that it depends on the following two parameters a and b :

$$\begin{aligned} a(\gamma_2) &= \frac{1}{\gamma_2} \cdot \frac{f'(1/\gamma_2)}{f(1/\gamma_2)} \\ b(\gamma_1, \gamma_2) &= \log [\gamma_1 \cdot \gamma_2 \cdot f(1/\gamma_2)] \end{aligned} \quad (8)$$

It follows directly from (6a) and (7) that

$$0 < b \leq \log(\gamma_1) \quad (9)$$

Parameter a tells something about the convexity of the function f . It is not difficult to show that

$$a(x) < 1 \quad \forall x \quad \Leftrightarrow \quad f''(x) < 0 \quad \forall x \quad (10)$$

One may prove that the fixed point is (hyperbolically) attractive if

$$a(\gamma_2) + b(\gamma_1, \gamma_2) < 1 \quad (11)$$

The same analysis shows the fixed point to be a spiral-point (complex eigenvalues) if

$$(a(\gamma_2) - 1)^2 < 4 \cdot b(\gamma_1, \gamma_2) \quad (12)$$

In all other cases we are dealing with a central point (real eigenvalues both inside or both outside the unit-circle). A saddle is not possible here.

In the case of a hyperbolically stable fixed point (11), there exists a set of initial conditions that gets attracted towards this fixed point. For these points, the host does not get extinct, but reaches a stable equilibrium with its parasitoid.

Similarly, in the case of a spiral-point there exists a set of initial condition, nearby the fixed point, which necessarily rotates at least once around the fixed point. For these initial conditions, extinction can only occur after one or more density-fluctuations in both host and parasitoid-densities. In the examples suggested above, part of this set of initial conditions can be constructed explicitly.

DISCUSSION

We have proven by analysis of a theoretical model that parasitoids with micro-type eggs can control a plague at best temporarily, but cannot force the plague-host to extinction. The presence of such a parasitoid prolongs the duration of the plague, in some cases (explicitly elaborated above) for at least some initial conditions quite dramatically. A stable equilibrium between host and parasitoid may even arise.

At very high densities, the parasitoid can control the host for some time. The parasitoid fails to drive the host to extinction, because it is not so effective at low densities. Adding another species of parasitoid to the system which is more effective at low densities might solve this problem. Tachinids with macro-type eggs, who search the host actively, may do this job. Therefore, a couple of two tachinids, one with micro-type eggs and the other with macro-type eggs, may be effective in controlling plagues. Even then, the plague will endure longer than in the case without any parasitoid. Therefore, the paradoxical conclusion is that usage of parasitoids in plague-controlling can be counter-productive from an economical point of view.

The last ten years at least two large plagues have occurred in The Netherlands in which a couple of tachinids as described was active. The first one has already been mentioned, namely the caterpillar *Thaumetopoea processionea* with the parasitoids *Pales processioneae* and the macro-type *Carcelia iliaca* (Ratzeburg). The second case is that of *Cerapteryx graminis* (Linnaeus) with micro-type tachinid *Gonia picea* (Robineau-Desvoidy) and macro-type *Appendicia truncata* (Zetterstedt). In both these examples even this ideal couple of tachinids did not succeed in controlling the plague. These observations support the conclusions of this theoretical study.

Finally, I note that the interaction between phytophagous hosts and parasitoids with micro-type eggs is described by (6) in general. It is also valid in non-plague situations (in cases in which (7) does not hold). The analysis of (6) without (7) is much more difficult and the results will depend more strongly on the specific host-dynamics (5).

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