

A Model for the Functional Response of Parasitoids¹

by

R. ARDITI

With 2 figures

ABSTRACT

A mathematical model is developed to describe the functional response of parasitoids that imperfectly avoid superparasitism. This new model contains older models as special cases. It is satisfactorily fitted to the measured response of a laboratory parasitoid-host system.

DEFINITIONS

Parasitoids are insects requiring a host for the development of their larvae. The free-living adult females search for hosts and oviposit in or near them. When the eggs hatch, the larvae feed on the hosts, causing at first little damage, but gradually attacking more vital parts and eventually killing the host.

Most parasitoids belong to two orders (Diptera and Hymenoptera) and they make up about 14% of the known insect species. Some of them are specific while others attack a variety of hosts species. Hosts belong to almost all insect orders, eggs, larvae, and pupae being far more frequently attacked than adults. Other species than insects can also be parasitized (spiders, snails).

Parasitoids are called solitary if one larva only can develop in a given host, gregarious if several larvae can develop in a same host. Solitary species (e.g. most Ichneumonidae) normally lay a single egg at each oviposition. Gregarious species (e.g. most Braconidae and Chalcidoidea) usually lay a batch of eggs corresponding to the host's capacity (up to several hundreds, even thousands) (BERLAND 1976).

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Superparasitism is the situation in which more individuals of a parasitoid species occur in a host than can survive. This usually happens when a same host is parasitized more than once. When superparasitism occurs, competition takes place between the developing larvae and the supernumerary ones are eliminated by various means (SALT 1961). It is therefore a selective advantage to avoid superparasitism. That many parasitoids have evolved such an ability to some extent is a well established fact, for solitary as well as for gregarious species (e.g. PODOLER & MENDEL 1977).

The number of hosts attacked per parasitoid per unit time changes with variation in host density. This relationship is called functional response (SOLOMON 1949). HOLLING (1959) distinguished three response types. The type II, which is the most common, is the only one considered here. It shows an initial increase from zero, with a gradually decreasing slope, tending to an upper horizontal asymptote (see Fig. 2).

Variation in parasitoid density also affects the number of hosts attacked, but this relationship is not studied here. The parasitoid density is assumed to be constant.

THE PROBLEM

Existing models of the functional response of parasitoids deal with two cases:

- 1) parasitoids that *do not discriminate* between healthy hosts and already parasitized hosts, i.e. parasitoids with no avoidance of superparasitism;
- 2) parasitoids that recognize (and avoid) parasitized hosts both *instantly* and *perfectly*. In such a case, the hosts can be considered as being absent from the population and the parasitoids respond like predators, which remove the prey from the population. Models for these two cases were given by ROGERS (1972).

The model developed in this work deals with the more realistic case of parasitoids that spend some time inspecting every host encountered and that may fail to reject parasitized hosts. Such a model should contain models (1) and (2) as limit cases.

The only previous attempt to build a model of this kind (ROGERS & HASSELL 1974) unfortunately suffers internal inconsistencies.

THE MODEL

Given P parasitoids and N hosts interacting for a time T , the model must evaluate the average number of hosts attacked per parasitoid per unit time, G , as a function of N and T . Let us make the following assumptions:

1. The parasitoids search randomly, with a constant searching efficiency a (probability of a given parasitoid to find a given host).
2. When finding a host, the parasitoids spend a time T_e examining whether it is healthy or already parasitized.
3. If the host is healthy, the parasitoid oviposits on it.
4. If the host is parasitized, the parasitoid has a probability p of making a "mistake" and ovipositing on it.
5. During and after each oviposition the parasitoid does not search for a time T_o (time for ovipositing *per se*, time for resting, etc.).

These assumptions are summarized on a diagram (Fig. 1). They yield the following expression for the functional response G (the mathematical proof is given in the Appendix):

$$G = \frac{N}{PT} \left(1 - \exp \left(\frac{-aPT}{1 + aT_p N} (1 - (T_h - T_p) G) \right) \right), \quad (M)$$

where $T_h = T_e + T_o$ is the time spent "handling" a healthy host and $T_p = T_e + pT_o$ is the average time spent "handling" a parasitized host.

Equation (M) is an implicit equation that must be solved by numerical iteration. Interestingly, the number of parameters needed is one less than the number that were introduced in the hypotheses. The number of hosts attacked per parasitoid per unit time is completely determined by T , N , P , a , T_h , and T_p . The last three parameters characterize the parasitoid species (in connexion with a given host species).

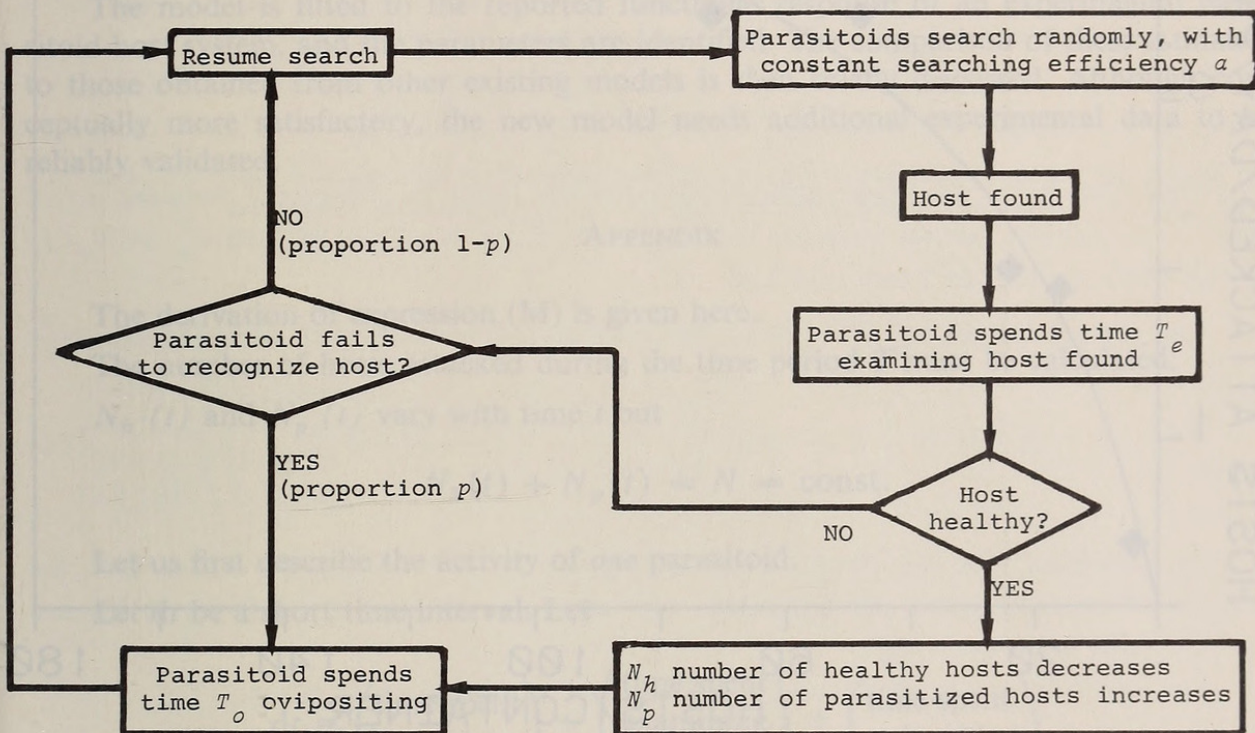


FIG. 1.

Conceptual diagram of the model for the interaction of P parasitoids and N hosts for a time T .

AN EXAMPLE

The Chalcidoid gregarious parasitoid *Nasonia vitripennis* (Walker) attacks the pupae of the house fly *Musca domestica* L. The functional response of this system in laboratory conditions was measured by EDWARDS (1961).

The new model (M) was fitted to these data, using a standard non-linear regression method (Fig. 2). With $P = 8$ parasitoids and $T = 24$ hours, the following values were obtained for the parameters: $a = 0.44 \text{ day}^{-1}$, $T_h = 0.20 \text{ day}$, and $T_p = 0.08 \text{ day}$. According to these estimates the parasitoid spends therefore 2.5 times more time handling a healthy host than a parasitized host.

Fitting alternative models to the same data yielded the following estimates:

- 1) "Random parasite" model (assumption $T_p = T_h$, see Appendix, eq. (12)): $a = 1.03 \text{ day}^{-1}$ and $T_h = 0.19 \text{ day}$.
- 2) "Random predator" model (assumption $T_p = 0$, see Appendix, eq. (13)): $a = 0.32 \text{ day}^{-1}$ and $T_h = 0.21 \text{ day}$.

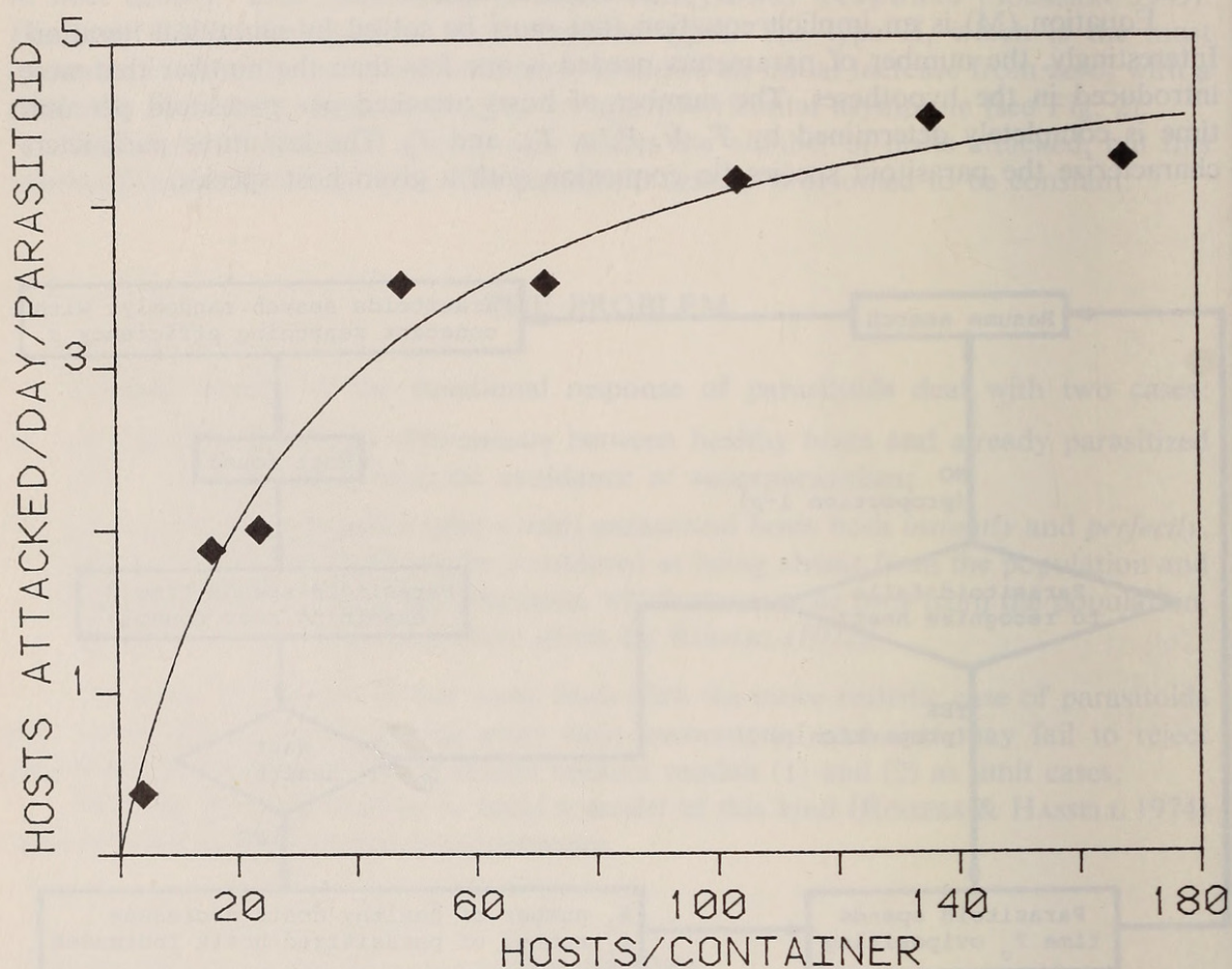


FIG. 2.

The functional response of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) attacking house fly pupae, with eight parasitoids searching simultaneously (EDWARDS 1961). The curve is the least squares fit of model (M).

The quality of the fit to the data is equally good with all three models but the estimated values of the searching efficiency a are rather different. As could be expected, the estimate of the new model is intermediate between those of the other two extreme models. It is not possible to select one model against the others with purely statistical arguments, but biological knowledge of the parasitoid's behaviour is necessary.

Such information is given by WYLIE (1965): *Nasonia* females always drill first through *Musca*'s puparium, and after piercing the enclosed pupa with the ovipositor usually (but not always) withdraw rapidly from an already parasitized pupa. Thus, there is a definite discriminatory capacity, which is neither immediate nor perfect. The

new model should then be preferred in this case. But to reliably validate this model, estimated values of the parameters (especially the searching efficiency a) should be compared to direct observational measurements, which are not available.

SUMMARY

A mathematical model is presented, which deals with the problem of insect parasitoids that *imperfectly* discriminate between healthy and parasitized hosts. The aspect examined is the functional relationship between host density and the number of hosts attacked per parasitoid per unit time.

On the basis of a few behavioural assumptions, the model is at first built conceptually and then translated into mathematical equations. The model fully characterizes a given parasitoid with three parameters: searching efficiency, time spent handling a healthy host, and time spent handling a parasitized host.

The model is fitted to the reported functional response of an experimental parasitoid-host system, and the parameters are identified. The comparison of these estimates to those obtained from other existing models is then briefly discussed. Although conceptually more satisfactory, the new model needs additional experimental data to be reliably validated.

APPENDIX

The derivation of expression (M) is given here.

The number of hosts attacked during the time period T must be calculated.

$N_h(t)$ and $N_p(t)$ vary with time t but

$$N_h(t) + N_p(t) = N = \text{const.} \quad (1)$$

Let us first describe the activity of *one* parasitoid.

Let dt be a short time interval. Let

$$dt = \left(\begin{array}{c} \text{time spent} \\ \text{searching} \end{array} \right) + \left(\begin{array}{c} \text{time spent} \\ \text{examining} \\ \text{hosts} \end{array} \right) + \left(\begin{array}{c} \text{time spent} \\ \text{ovipositing} \end{array} \right)$$

$$dt = dt_s + dt_e + dt_o \quad (2)$$

Number of encounters with healthy hosts during dt :

$$dE_h = aN_h(t) dt_s \quad (3)$$

Number of encounters with parasitized hosts during dt :

$$dE_p = aN_p(t) dt_s \quad (4)$$

We have, by definition of T_e , T_o and p :

$$dt_e = T_e(dE_h + dE_p) \quad (5)$$

$$dt_o = T_o(dE_h + pdE_p) \quad (6)$$

Inserting (3)-(6) into (2) yields

$$dt = dt_s \{ 1 + a(T_e + T_o)N_h(t) + a(T_e + pT_o)N_p(t) \} \quad (7)$$

Let us define

$$T_h = T_e + T_o \quad (8)$$

$$T_p = T_e + pT_o \quad (9)$$

The change in the number of healthy hosts during dt , due to attacks by *all* parasitoids, is

$$dN_h = -PdE_h = -aPN_h(t)dt_s$$

With (7)-(9) and (1) we obtain the following equation for the dynamics of the population of healthy hosts:

$$\frac{dN_h}{dt} = \frac{-aPN_h(t)}{1 + aT_pN + (T_h - T_p)N_h(t)} \quad (10)$$

This first order nonlinear differential equation must be integrated between $t = 0$ and $t = T$. Assume that all hosts are healthy at $t = 0$, i.e. $N_h(0) = N$. Let $N_p^T = N_p(T)$ be the total number of hosts attacked.

The integration of eq. (10) yields the following transcendental equation for N_p^T :

$$N_p^T = N \left(1 - \exp \left(\frac{-aP}{1 + aT_pN} \left(T - (T_h - T_p) \frac{N_p^T}{P} \right) \right) \right) \quad (11)$$

By definition, the functional response is given by $G = N_p^T/(PT)$, where G is the number of hosts attacked per parasitoid per unit time. Writing eq. (11) for G instead of N_p^T yields expression (M).

The existing models of ROGERS (1972) appear as special cases of eq. (11):

- 1) $T_p = T_h$, i.e. $p = 1$ (parasitoids do not recognize parasitized hosts).

$$N_p^T = N \left(1 - \exp \left(\frac{-aTP}{1 + aT_hN} \right) \right) \quad (12)$$

This is the "random parasite equation".

- 2) $T_p = 0$, i.e. $T_e = 0$ and $p = 0$ (parasitoids recognize parasitized hosts immediately and without failure).

$$N_p^T = N \left(1 - \exp \left(-a(TP - T_hN_p^T) \right) \right) \quad (13)$$

This is the "random predator equation".

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Author's address:

Université de Lausanne
Institut de zoologie et d'écologie animale
Place du Tunnel 19
CH-1005 Lausanne



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