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MUTUAL INTERFERENCE BETWEEN PARASITES OR PREDATORS AND ITS EFFECT ON SEARCHING EFFICIENCY

By J. R. BEDDINGTON

Biology Department, York University, York YO1 5DD

INTRODUCTION

A number of experiments (Burnett 1956; Hassell & Huffaker 1969; Holling 1959; Ullyett 1949a,b, 1950) indicate that a basic assumption implicit in early population models of predator–prey and parasite–host interactions (Lotka 1925; Volterra 1926; Nicholson & Bailey 1935) is false. This assumption requires the number of hosts parasitized (or prey attacked) to be proportional to the density of hosts and the density of parasites*. It is possible to formalize this assumption in terms of searching efficiency (E) where E is defined by

$$E = \frac{N_a}{NP}. \tag{1}$$

N_a is the number of attacks per unit area and time, N is the density of hosts and P the density of predators. All the early models demand that E so defined should be constant.

The assumption has been shown to be wrong in two ways, the first indicated that efficiency declined with increasing prey density, the second that it declined with increasing predator density. Holling (1959) following Solomon (1949) explained the first phenomenon in terms of his 'functional response'. This related the density of attacks in unit time for an individual predator to the density of prey present by the equation

$$N_a = \frac{aN}{1+at_hN}. \tag{2}$$

a is the 'attack rate' and t_h the handling time i.e. the time spent attacking and consuming a prey before search is resumed. Substitution for N_a in equation (1) yields

$$E = \frac{a}{1+at_hN}. \tag{3}$$

E is thus a decreasing function of N; the form of the relationship is illustrated in Fig. 1.

The second invalidation of the assumption was considered by Watt (1959) and Hassell & Varley (1969); they noted that efficiency declined with increasing predator density and claimed that this relationship was described by the equation

$$E = QP^{-m}. \tag{4}$$

In the terminology of Hassell & Varley, Q is the 'quest constant' indicating the level of efficiency of one parasite and m the 'interference constant' a measure of the degree of

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* Throughout this paper hosts or prey and parasites or predators will be used interchangeably, largely in the context of appropriate literature pertaining to them.

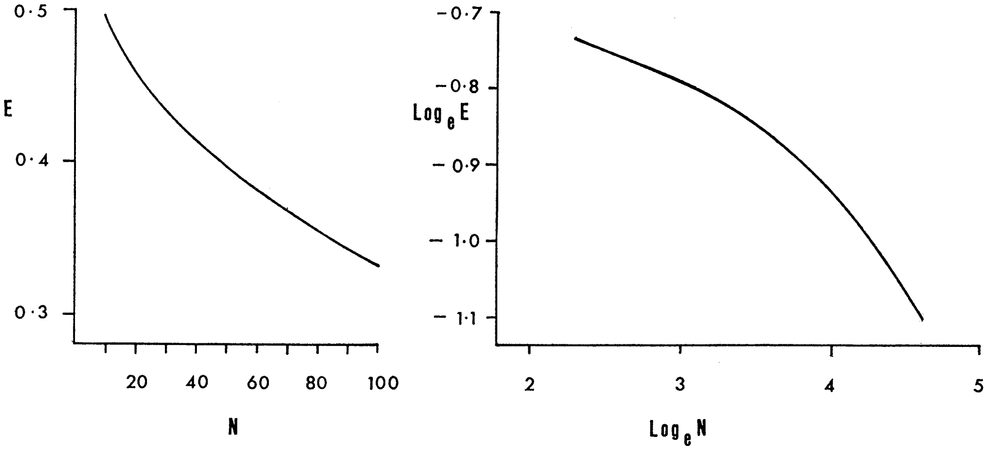

FIG. 1. The relationship between searching efficiency and prey density; (a) arithmetic scale, (b) logarithmic scale.

interference between parasites. Hassell & Varley successfully fitted this model to a variety of data on parasite efficiencies using the form

$$\log E = \log Q - m \log P. \tag{5}$$

Recently this model has been criticized on two grounds. Firstly, that it fails to describe adequately all the published data, some of which indicate a curvilinear relationship between log E and log P with increasing slope for increasing parasite density (Hassell 1971a,b; Hassell & Rogers 1972). Secondly, that on *a priori* grounds, a limit would be expected to parasite density below which interference was negligible (Royama 1971; Hassell & May 1973). It is worth emphasizing in this context that equations (4) and (5) are not explanatory models of the effect of interference and are merely an empirical approximation to the observed relationship.

Explanations of this phenomenon have been proposed by Rogers & Hassell (1974) using two models. One model (A) depends on estimating the effect of adult parasites encountering each other and then abandoning the search for hosts for a period of time. Using this idea Hassell & Rogers derived a quadratic expression in the number of searching parasites for an equilibrium between parasites commencing and ceasing searching. Using this expression they showed that the relationship between log E and log P could take a number of forms depending on the product of time wasted after an encounter and the rate of encounter between parasites, varying from a curvilinear to a linear relationship as this product increased. An important disadvantage of this model is that no method of estimating its parameters and thus testing it against observed relationships is proposed.

In a second model (B) they investigated the effect of super-parasitism in which, upon finding a parasitized host, a parasite ceased to search for some time period. They noted that in this situation the relationship between log E and log P was affected both by the time wasted and by host density. Increasing either increased the slope of the relationship from almost horizontal to a typical curvilinear one.

In a simulation aimed at corroborating these two models Rogers & Hassell produced, by judicious variation in handling time and time wasted, relationships between Host Density, Parasite Density and searching efficiency of all the types documented.

In this paper I propose an explanatory model of the interference effect, in which the relationship between searching efficiency and both Prey Density and Predator Density is shown to be of an essentially similar form. The assumptions of the model are identical to those of model (A) of Rogers & Hassell's paper, but in deriving a mathematical form for the model the ultimate relationship between searching efficiency and predator density is clarified. The mathematical form derived has the additional benefit that by its use, it is possible to estimate the parameters from observed data and thus test the underlying model.

A MATHEMATICAL MODEL FOR INTERFERENCE BETWEEN PREDATORS OR PARASITES

For the initial development of the model, assume that handling time is effectively zero and chose a unit area. The number of attacks N_a will now be given by the rate at which parasites find hosts (a) the density of hosts N, the number of parasites P' and the time spent searching T_s;

$$N_a = aNT_sP'. \tag{6}$$

The overall time (T) can be divided up into the time spent searching (T_s) and the time wasted upon encounters with other parasites (T_w), by definition therefore,

$$T = T_s + T_w. \tag{7}$$

T_w can be partitioned further so that it is given by the product of the number of encounters

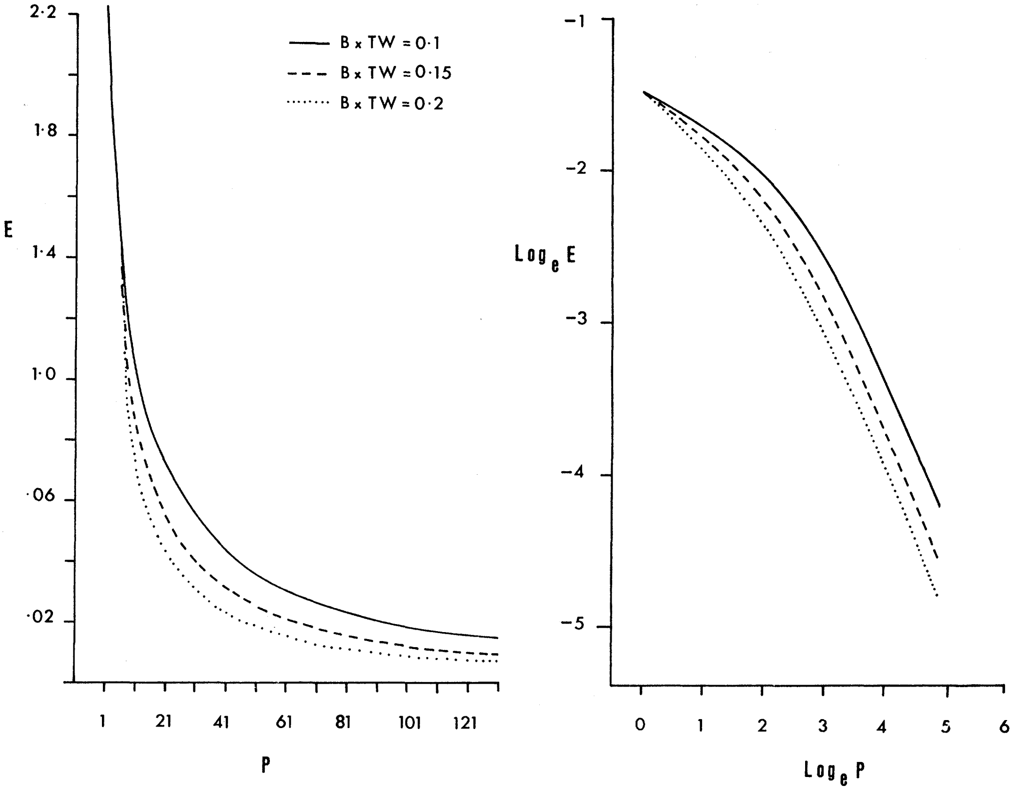

FIG. 2. The relationship between searching efficiency and predator density for varying values of the product bt$_w$; (a) arithmetic scale, (b) logarithmic scale.

between parasites (N_e) and the time wasted per encounter t_w. If the parasites move randomly, N_e can be expressed as

$$N_e = bT_sR, \tag{8}$$

where R is the density of P'-1 parasites and (b) is the rate of encounter between parasites, related both to their speed of movement and the range at which they sense each other; b can thus be greater than or smaller than a. The overall time wasted due to encounters between parasites is then given by

$$T_w = bRT_st_w; \tag{9}$$

substitution in (7) gives

$$T = T_s(1+bt_wR), \tag{10}$$

and from (6),

$$N_a = \frac{aNP'T}{1+bt_wR}. \tag{11}$$

The relationship between searching efficiency and parasite density is now given by

$$E = \frac{aT}{1+bt_wR}. \tag{12}$$

Fig. 2 indicates the relationship between E and P for various values of the constant product bt_w. It can readily be seen that the relationship between log E and log P is of the range of types to be expected, curvilinear for small values of bt_w increasing to linear for larger values.

The similarity with the effect of host density, Fig. 1 and equation (1), is apparent. The interaction between the two effects can be investigated in a similar manner. In order to do so it is necessary to distinguish between two types of time wasted, T_h, that wasted due to handling hosts, and T_p that wasted due to encountering parasites, thus

$$T_w = T_h+T_p. \tag{13}$$

T_h will be given by

$$T_h = N_at_h, \tag{14}$$

and, similarly,

$$T_p = N_et_w. \tag{15}$$

Substituting for N_a and N_e we have

$$T_h = at_hNT_s; \tag{16}$$

$$T_p = bt_wRT_s; \tag{17}$$

which gives, upon substitution in (10),

$$T_s = \frac{T}{1+at_hN+bt_wR}. \tag{18}$$

N_a is thus given by

$$N_a = \frac{aNP'T}{1+at_hN+bt_wR}, \tag{19}$$

and

$$E = \frac{a}{1+at_hN+bt_wR}. \tag{20}$$

The surface represented by equation (20) is illustrated in Fig. 3, which can be compared with a similar relationship obtained by Rogers & Hassell (1974) using computer simulation and illustrated in their Fig. 7.

Dimensional considerations

The derivation of the models in the last section has considered both time and area to be unity. In order to allow comparisons both between different species and between the effect of handling time and interference, it is necessary to consider the dimensional properties of the equations.

The parameters a and b have units L^2T^{-1} as they are the rate of searching an area. N and R are densities and have units L^{-2}. Thus the two products at_hN and bt_wR are dimensionless. It follows that P' is dimensionless and equal to the number of parasites. Expressions for the number of attacks are therefore per unit time and searching efficiency must therefore have the same units as a, namely L^2T^{-1}. In most of the parasite–host literature, searching efficiency is equated with the Nicholsonian 'area of discovery'; the time units of this measure are the average lifetime of a parasite. Cross-species comparisons between different 'areas of discovery' are thus possible simply in terms of an area covered in a lifetime. An analogous parameter b could be called the area of interference and would allow similar cross-species comparisons. Unfortunately, in any estimation procedure on the models developed, b cannot be separated from the product bt_w. However *a priori* it seems unlikely that a and b will differ much; both involve the speed of movement of a parasite, and only differ over the distance at which it senses a host or another parasite. Thus gross-comparisons of t_w between species, measured in units of a parasite lifetime, seem possible. It should perhaps be noted that for predators the appropriate time unit may not be the lifetime of the predator and inter-species comparisons would be better in terms of absolute units. Similarly it is possible to compare the two products at_h and bt_w as both are in units of L^2, the one can be considered an area unsearched, due to handling effects, and the other due to interference effects.

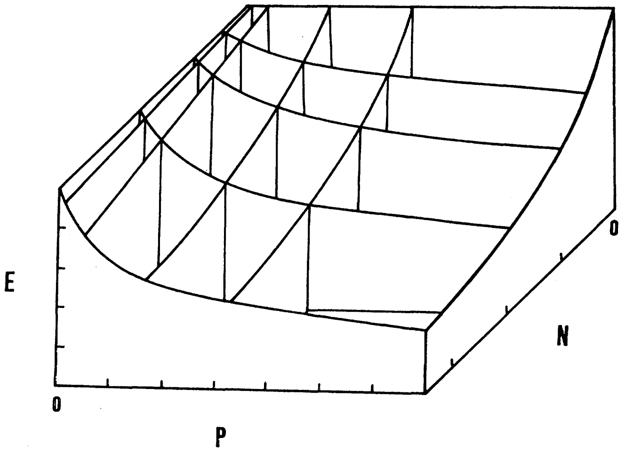

FIG. 3. The relationship between searching efficiency and prey and predator density defined by equation (20).

Area of discovery and parasite density

Hassell (1971a) and Hassell & Rogers (1972) have published observed relationships between searching efficiency considered as a Nicholsonian area of discovery and parasite density. As noted earlier these varied from an apparently linear to a curvilinear relationship. Using equation (12) it is possible to see if these observed relationships can be explained and satisfactorily fitted, affording both corroboration for the model and an opportunity to consider variation in the parameter bt_w between species. Equation (12) can be rearranged so that

$$\frac{1}{a}+\frac{bt_wR}{a}=\frac{1}{E}, \tag{21}$$

and a linear regression of the reciprocal of searching efficiency against parasite density enables the parameters to be estimated. The results of estimating the parameters of the model in this way are illustrated in Figs 4, 5 and 6 for three typical observed responses.

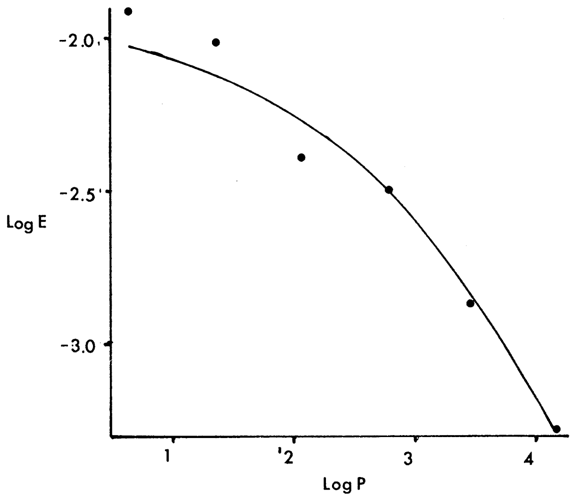

FIG. 4. Equation (21) fitted by linear regression to data from Burnett (1956) for *Encarsia formosa*, $a = 0{\cdot}1366$, $bt_w = 0{\cdot}0426$ ($P<0{\cdot}001$).

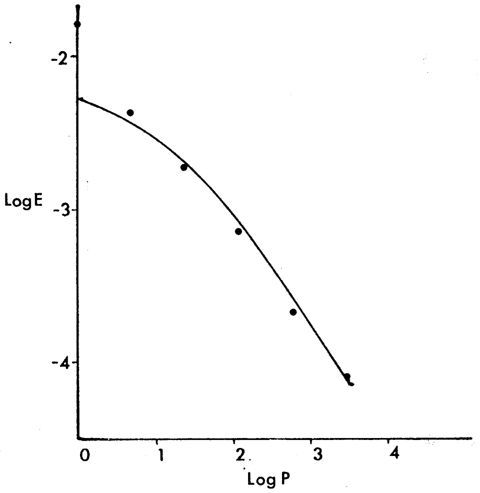

FIG. 5. Equation (21) fitted by linear regression to data from Hassell & Rogers (1972) for *Nemeritis canescens*, $a = 0{\cdot}1047$, $bt_w = 0{\cdot}1788$ ($P<0{\cdot}001$).

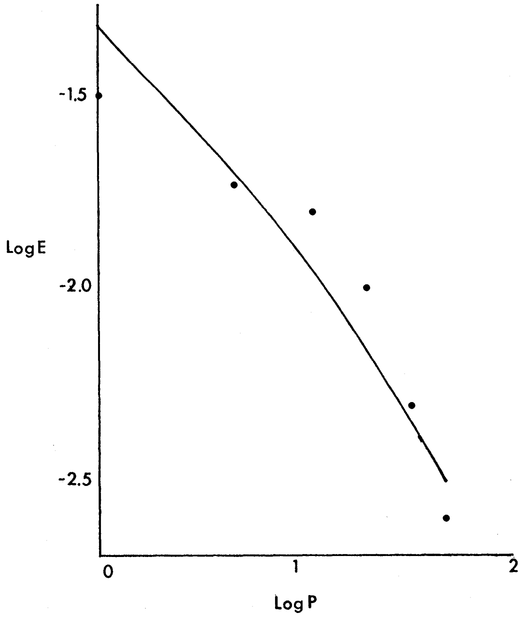

FIG. 6. Equation (21) fitted by linear regression to data from Ullyett (1949a) for *Chilonus texanus*, $a = 0{\cdot}262$, $bt_w = 0{\cdot}4447$ ($P<0{\cdot}001$).

The levels of significance associated with the fit of the model are encouraging but there is still some variation and it is likely that this is in part due to errors in the estimates of the area of discovery. Royama (1971) has considered in some detail the problems of estimating this parameter and notes that it both ignores the effect of handling time and the effect of exploitation, i.e. the decrease in available hosts or prey during the duration of the experiment. This latter is manifestly more important for a predator than a parasite and Rogers (1972) and Royama (1971) developed a model for a randomly searching predator which incorporated this effect. To analyse the effect of interference on predator efficiency using equations (12) and (20) therefore requires this extension.

Interference effects allowing for a decrease in prey density

It is possible to consider equation (19), giving the number of prey attacked in time period T, as an instaneous change in the density of prey. Conversion of the number of attacks to number per unit area then allows one to write

$$\frac{dN}{dt} = -\frac{aNP}{1+at_hN+bt_wR}, \tag{22}$$

which upon integration gives

$$(1+bt_wR)\log\left[\frac{N-N_a}{N}\right]-at_hN_a = -aPT, \tag{23}$$

or, after some adjustment,

$$N_a = N\left[1-\exp\left[\frac{a(N_at_h-PT)}{1+bt_wR}\right]\right]. \tag{24}$$

Estimating the parameters of this form of the model is unfortunately not an easy or particularly robust process. It is best performed in two stages. With predator density equal to unity, equation (23) simplifies to

$$\log\left[\frac{N-N_a}{N}\right] = at_hN_a - aT, \tag{25}$$

and, with a time interval of unity and some caution, the parameters a and t_h can be estimated (Rogers 1972; McArdle, unpublished). With these estimates define a new variable, $Z = a(N_at_h - P)$, and rearranged, this gives

$$\log\left[\frac{N-N_a}{N}\right] = Z/(1+bt_wR). \tag{26}$$

A linear regression of the logarithm of the survival rate against the derived variable Z constrained through the origin will afford an estimate of the reciprocal of $1+bt_w$ from which bt_w can be calculated. Experiments for a range of predator and prey densities will then enable the parameters to be estimated. It is manifest that this estimation technique is far from satisfactory, error variances occurring in various multiplicative and interacting ways. However, computer simulation indicates that for a carefully chosen experimental design in which N_a is not too close to N and, when sufficient replication has assured good estimates of a and t_h, equation (26) works reasonably as an estimator for bt_w.

Interference handling time and stability

Hassell & May (1973) had noted that simple parasite–host, and by implication predator–prey, models were destabilized by increased handling time and stabilized by increased interference. In the model of equation (20) these two effects occur in similar ways, both have the same dimensions and the investigation of their interaction on the stability properties of simple predator–prey and parasite host models is thus facilitated. Hassell & May analysed the equation system of the form

$$\begin{aligned} N_{t+1} &= FN_tf(N_tP_t); \\ P_{t+1} &= (1-f(N_tP_t)N_t; \end{aligned} \tag{27}$$

N_t and P_t are the density of hosts and parasites at time period t, F is the host rate of increase and $f(N_tP_t)$ a function determining the proportion of hosts that remain unparasitized. On the assumption of random search, equation (20) can be incorporated into the formalism by writing

$$f(N_tP_t) = \exp(-aP_t/(1+at_hN_t+bt_wR_t)), \tag{28}$$

and the stability analysis can proceed as outlined by Hassell & May for an arbitrary function $f(N_tP_t)$.

DISCUSSION AND CONCLUSIONS

The model suggested in this paper allows a simple physical interpretation of the effect on predator efficiency of prey and predator density. In terms of the simple Nicholsonian 'area of discovery' a predator has an innate capacity to search out an area for prey. It is never possible to cover this whole area, as a portion of the area remains unsearched due to handling time effects and a portion due to interference effects. The relative proportions of these two 'area effects' can now be estimated using the model from experimental and field data.

The incorporation of the model into standard models of predator–prey and parasite–host models becomes an easy matter.

On the basis of the stability analysis of Hassell & May (1973) one would expect that the larger the ratio of the 'area of interference' to the 'area of handling time' the more stable would be a population interaction.

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SUMMARY

(1) An explanatory model is proposed to account for the variation in searching efficiency, with predator or parasite density, noted by many authors.

(2) The model involves considering the effect of prey density to be fundamentally the same as the effect of predator density.

(3) The application of the model to observed relationships between searching efficiency, considered as an 'area of discovery' and parasite density, is successful.

(4) The observed decay in searching efficiency with both prey and predator density is given a physical interpretation. In this interpretation the intrinsic capability of a predator to search an area is shown never to be realized as one portion remains unsearched due to handling time effects and another remains unsearched due to interference effects.

(5) A method of estimating the magnitude of both these effects from laboratory and field data is described.

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