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Underestimation of mutual interference of predators

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Summary. The usual method of estimating the mutual interference constant, *m*, assumes a linear (type I) functional response of predators. In the cases where the response is not linear, the application of the method introduces a bias in the estimation of the searching efficiencies. It is shown that, as a consequence, the value of *m* is underestimated. A new method is proposed, which allows for a type II functional response due to a handling time. A comparative analysis of 15 data sets from the literature shows that the proposed method gives values of *m* that are consistently higher than those estimated by the traditional method. The new method calculates the parameters with nonlinear regression and provides standard errors for the estimates. Therefore, the reliability of the searching efficiencies, the handling time and the constant *m* can be quantified. Very few of the interference constants are significantly different from $m=1$. This special value implies that the functional response is a function of the ratio of prey and predator densities. These empirical findings support the suggestion of Arditi and Ginzburg (1989) that the functional response might often be ratio-dependent, especially in complex and heterogeneous situations.

Key words: Predation – Mutual interference – Functional response – Searching efficiency

Mutual interference denotes the adverse influence of predator density *P* on the 'instantaneous' success of individual predators. Specifically, the searching efficiency a, defined as the proportion of prey encountered per predator per unit of searching time, is a decreasing function of *P*. If the relationship between log *a* and log *P* is rectilinear, the intensity of interference can be quantified by the slope *m*, defined in the empirical model of Hassell and Varley (1969):

$$a=a(P)=\alpha P^{-m}. \qquad (1)$$

This effect has been observed in numerous arthropod systems, in the laboratory as well as in field conditions, for true predators as well as for parasitoids, and reported values of *m* vary between 0.2 and 1.2 (e.g. Hassell 1978, chap. 5).

A behavioural model of predator interference was developed by Beddington (1975). However, direct behavioural interference is not the only reason for the searching efficiency to decline with *P*. In heterogeneous systems, 'pseudo-interference' (Free et al. 1977) can occur. This is particularly the case under field conditions, when attack rates are estimated over large temporal and spatial scales. Model (1) is a conveniently simple description of the cumulated effects that lead *a* to decline with *P*.

The first task in the estimation of mutual interference is to obtain values of *a* for several values of *P*. In published studies reporting estimations of *m*, the efficiency *a* was calculated as

$$a=\frac{1}{PT}\ln\left(\frac{N}{N-N_a}\right), \qquad (2)$$

where *T* is the duration of the interaction period, *N* is the number of prey present at the start, and N_a is the number attacked. Typical experiments repeat interaction sessions with identical values of *N* and *T* and different values of *P*. The parameter *m* is then estimated by fitting the logarithmic form of (1) through the efficiencies calculated with (2).

This procedure rests on the assumption that *a* varies with *P* only, i.e. that it does not depend on the specific choice of the values of *N* and *T*. With this condition, (2) is equivalent to the Nicholson-Bailey expression:

$$N_a=N[1-\exp(-aPT)], \qquad (3)$$

which is valid if *T* is entirely devoted to searching, i.e. if the predators' functional response is of type I.

However, if the predators obey a type II functional response, for example because of a handling time t_h, the attack equation (3) must be replaced by the expression (Royama 1971; Rogers 1972)

$$N_a=N[1-\exp(-aPT+at_h N_a)]. \qquad (4)$$

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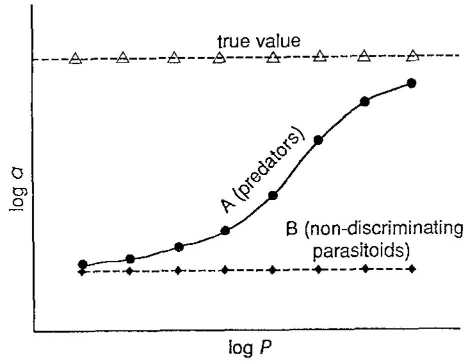

Fig. 1. The use of the Nicholson-Bailey expression to estimate the searching efficiency a gives biased values if the handling time is not zero. Here, the true value of a does not vary with P (no interference)

For a given value of P (and T), the observation of the number attacked N_a for a single value of N can no longer give an estimate of a since (4) also contains the unknown parameter t_h. Ideally, a complete functional response curve should be obtained for each value of P. For each of these curves, nonlinear regression techniques can then provide estimates of a and t_h.

If the searching efficiency is calculated with (2) in spite of the fact that predators have a nonzero handling time, a bias is introduced. This bias is illustrated in Fig. 1. A type II predator was simulated by using (4) to calculate exploitation of the prey, N_a, for several values of P, with known values of a, t_h and T. Using these values of N_a, the expression (2) was then applied as an estimator of a. Even though the correct value of a was the same for all values of P (no interference), Fig. 1 (curve A) shows that the estimate of a using (2) increases with P. Calculating m by fitting a straight line through these points would give a negative value (positive slope) instead of $m=0$; the longer the handling time, the steeper this slope. If interference is present, the correct slope should be negative. Since the bias adds a positive contribution, values of m resting on the use of (2) will be underestimated.

In the case of parasitoids, an appropriate attack equation was given by Arditi (1983):

$$N_a = N\left[1-\exp\left(\frac{-aPT+a(t_h-t_p)\,N_a}{1+at_p\,N}\right)\right], \tag{5}$$

where t_h and t_p are handling times on encounters with healthy and parasitized hosts, respectively. In the special case where $t_p=0$, this equation reduces to (4): parasitoids that instantaneously recognize and abandon parasitized hosts behave like predators. In the case where $t_p=t_h$, parasitoids do not discriminate between healthy and parasitized hosts and (5) reduces to the expression (Rogers 1972):

$$N_a = N\left[1-\exp\left(\frac{-aPT}{1+at_h N}\right)\right]. \tag{6}$$

Figure 1 (curve B) shows the values of a given by the estimator (2) when N_a follows in fact (6). The absolute magnitude of a is estimated incorrectly but the bias does not vary with P. Therefore, the slope m is not biased as in the case of predators. In the case of imperfectly discriminating parasitoids, the bias has intermediate severity.

We can conclude that most published values of m are likely to be underestimates, except in the case where the handling time is negligible and in the case of parasitoids that are strictly non-discriminating. In the rest of this paper, we compare values of the interference constant m resting on the use of the customary equation (2), to values obtained with another method using (4) where the parameter t_h is estimated along with the searching efficiency a.

Data and methods

As explained above, the studies of responses to prey density alone or to predator density alone cannot be used to apply model (4). Measurements of the number of prey attacked are needed for various values of prey *and* predator densities. We found in the literature 15 data sets that satisfied this condition (these are numbered in the legend of Fig. 3). In addition to predators, studies on parasitoids were included if the species were reported to discriminate between healthy and parasitized hosts, in which case perfect discrimination was assumed.

For each data set, m is estimated with two methods. In both methods, $-m$ is the slope of the log-log regression of searching efficiency a against predator density P. They differ in the way that a is estimated for each value of P. They are illustrated with the data of Katz (1985) that were read off his graphs (Table 1).

The first method uses (2). Since, for any given P, there are several values of N for which N_a is available, each one could provide a different value of a. To obtain an overall value of a for each P, we followed the procedure used by Jones and Hassell (1988) in this type of situation: (2) is applied to the total number of prey offered N^{tot} (240 in Katz's data) and the total number attacked N_a^{tot}. Table 1 (columns 4–6) gives the values of a obtained with

Table 1. Application of the two methods to the field observations of Katz (1985) on predation of barnacles (*Balanus balanoides*) by marine snails (*Urosalphinx cinerea*). The unit of time is the interaction time $T=24.7$ h. In method I, a is calculated as $(-1/P)\ln(1-N_a^{\text{tot}}/N^{\text{tot}})$. In method II, a is obtained from a nonlinear regression of eqn. (4) through all available data points

P	N	N_a	Method I			Method II
			N^{tot}	N_a^{tot}	a	$a \pm \text{SE}$
1	16	2.14	240	15.14	0.065	0.167 ± 0.078
	32	4.14				
	64	4.29				
	128	4.57				
2	16	1.29	240	26.86	0.059	0.099 ± 0.032
	32	8.29				
	64	8.14				
	128	9.14				
3	16	1.71	240	29.57	0.044	0.059 ± 0.017
	32	6.43				
	64	7.86				
	128	13.57				
4	16	2.29	240	36.29	0.041	0.053 ± 0.013
	32	7.29				
	64	8.71				
	128	18.00				

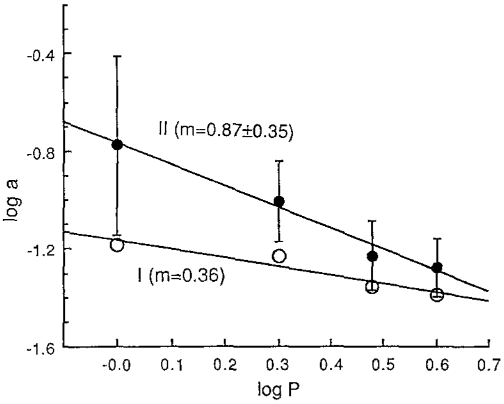

Fig. 2. Application of both methods to evaluate the searching efficiencies *a* and the mutual interference constant *m* in the data of Katz (1985). In method II, the *a*'s and *m* are given with one standard error

this method and Fig. 2 (curve I) shows the decline of *a* with *P* giving the interference constant $m = 0.36$.

The second method rests on the use (4). For each value of *P*, a nonlinear regression must be performed on the functional response (N_a as a function of *N*) to obtain the parameters *a* and t_h. However, since there is no reason to expect that the handling time varies with predator density *P*, the parameter t_h is forced to be unique. In other words, *p* functional response curves are fitted simultaneously, *p* being the number of different values of *P*. This is done with the procedure NLIN of the SAS statistical package. (The programme is available from the authors upon request.) Table 1 (last column) gives the values obtained on Katz's data. NLIN also gives the asymptotic standard error of each estimated parameter. The interference constant *m* is then obtained by a weighted linear regression of $y = \log a$ against $x = \log P$, using the reciprocal of the variance of *y* as the weight *w*. Finally, the standard error of *m* is given by $\mathrm{SE}^{-2}(m) = \Sigma w_i (x_i - \bar{x})^2$. The statistic $t = |m - \mu| / \mathrm{SE}(m)$ tests whether *m* is different from μ. Katz's data show an interference constant $m = 0.87$ with a standard error of 0.35 (Fig. 2, curve II). It is not statistically different from 1.

Table 2. Interference constants *m* obtained with both methods. The data sets are as numbered in the legend of Fig. 3. t_h is the handling time estimated with method II. df is the residual number of degrees of freedom (number of observations minus total number of adjusted parameters). The last column gives the cases where *m* is significantly different from 1

Data set	Method I *m*	Method II			
		$m \pm$ SE	$t_h \pm$ SE	df	$m \neq 1$
1	0.21	1.05 ± 0.36	6.8 ± 0.72 s	9	
2	0.49	0.83 ± 0.09	4.6 ± 0.64 day	11	
3	0.45	0.54 ± 0.16	2.1 ± 0.69 h	9	< 0.02
4	0.31	0.73 ± 0.17	5.3 ± 1.1 h	8	
5	0.28	0.66 ± 0.17	4.1 ± 2.0 h	13	
6	−0.05	0.50 ± 0.09	0.49 ± 0.045 h	9	< 0.01
7	0.41	0.92 ± 0.16	1.2 ± 0.22 h	14	
8	0.36	0.87 ± 0.35	1.9 ± 1.3 h	11	
9	0.55	0.89 ± 0.07	1.1 ± 0.16 h	65	
10	0.50	1.14 ± 0.15	3.4 ± 2.0 h	12	
11	0.11	0.33 ± 0.14	0.69 ± 0.073 h	8	< 0.02
12	0.58	0.64 ± 0.15	0.10 ± 0.07 min	4	
13	0.58	0.62 ± 0.21	0.078 ± 0.15 min	4	
14	0.58	0.66 ± 0.15	0.17 ± 0.20 min	4	
15	0.39	0.70 ± 0.22	0.00 ± 4.4 h	119	

Table 3. Separate applications of the usual method (method I) at several values of the prey density *N*. The estimates of *m* vary greatly. They should have been identical if method I were correct. (Data of Katz 1985)

N	*P*	N_a	*a*	*m*
16	1	2.14	0.14	0.98
	2	1.29	0.042	
	3	1.71	0.038	
	4	2.29	0.039	
32	1	4.14	0.14	0.60
	2	8.29	0.15	
	3	6.43	0.075	
	4	7.29	0.065	
64	1	4.29	0.069	0.48
	2	8.14	0.068	
	3	7.86	0.044	
	4	8.71	0.037	
128	1	4.57	0.036	0.03
	2	9.14	0.037	
	3	13.57	0.037	
	4	18.00	0.038	

Results and discussion

Table 2 compares the values of *m* obtained with the two methods. As predicted, the new method gives values that are consistently higher than the usual method based on the type I functional response.

Another analysis confirms the inadequacy of the conventional method. If (3) described exploitation correctly, the estimation of the searching efficiency *a* should be insensitive to the choice of *N*, since *a* is supposed to vary with *P* only. Table 3 shows that this is not the case: rearranging Katz's data to group them by *N*, the values of *a* and *m* vary greatly between different values of *N*.

A benefit of the new method is that nonlinear least squares regression takes advantage of all available data to calculate standard errors for the estimated parameters. Figure 3 shows that, in some cases, the errors of the searching efficiencies can be quite large, making the estimation of *m* rather uncertain. The usual method reduces the data first; it does not provide error bars for the *a*'s and cannot quantify the precision of the estimate of *m*. The errors of *a* are particularly large when the proportion of prey consumed is very low or very high. Good estimates of *a* are obtained when this proportion is between 0.2 and 0.8. This can be achieved by adjusting the interaction time *T*. In the experiments analyzed here, *T* was set identically for all data points. This is unnecessary: the new method can handle data sets with different values of *T* for each predation session. As for the handling time, its estimate will only be good if the plateau of the functional response is attained. This explains why t_h is poorly estimated in cases 13 and 15 (Table 2). When devising experiments, the necessity of minimizing the estimation errors can serve as a guide in the choice of suitable values of *T*, *P* and *N*.

In a few cases (9, 10, 15), the relationship between $\log a$ and $\log P$ looks curvilinear. This is clear in case

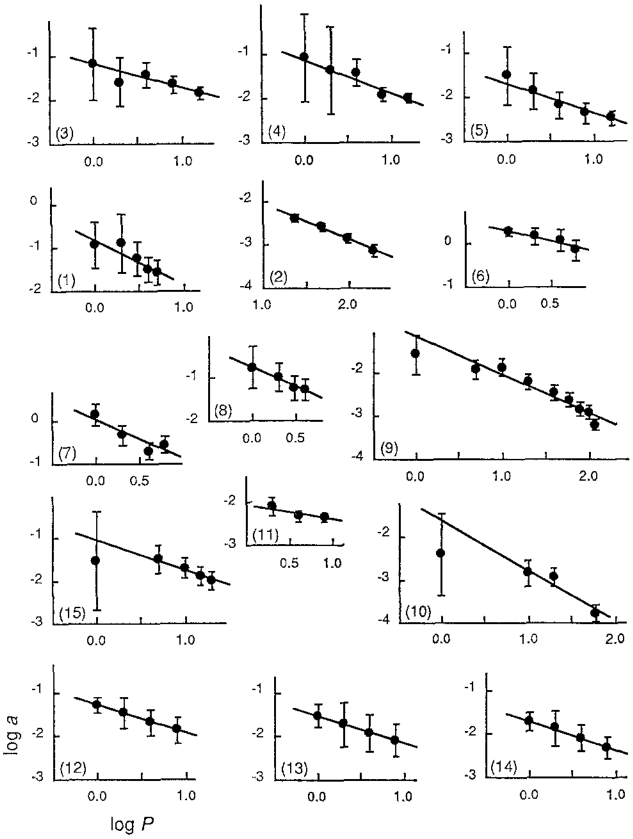

Fig. 3. Application of the new method to 15 data sets found in the literature. Points are given with one standard error. All plots are to the same scale. Cases (1)–(8) refer to predators and prey, and cases (9)–(15) to parasitoids and hosts. (1) *Carassius auratus* and *Daphnia pulex* (Chant and Turnbull 1966); (2) *Tribolium castaneum* adults and *Tribolium castaneum* larvae (Mertz and Davies 1968); (3)–(5) *Hyperoche medusarum* and *Clupea harangus* (Westernhagen and Rosenthal 1976); (6) *Amblyseius degenerans* and *Tetranychus pacificus* (Eveleigh and Chant 1982); (7) *Phytoseiulus persimilis* and *Tetranychus pacificus* (Eveleigh and Chant 1982); (8) *Urosalphinx cinerea* and *Balanus balanoides* (Katz 1985); (9)–(10) *Trichogramma evanescens* and *Sitotroga* (Edwards 1961); (11) *Trichogramma pretiosum* and *Phthorimaea operculella* eggs (Kfir 1983); (12)–(14) *Trioxys indicus* and *Aphis craccivora* (Kumar and Tripathi 1985); (15) *Trybliographa rapae* and *Delia radicum* (Jones and Hassell 1988)

9. In cases 10 and 15, the error bars of the a's at low density are so large that the rectilinear fit cannot be rejected: these points have very little weight in the regression.

All values of m are significantly different from zero. When using (1) to describe P-dependence in the searching efficiency a, Holling's 'disc' model for the functional response becomes dependent on both prey and predator densities:

$$g(N,P)=\frac{aNP^{-m}}{1+\alpha t_h NP^{-m}}. \qquad (7)$$

Table 2 shows also that only three values of m obtained with the new method are significantly different from 1. For simplifying purposes, it may therefore be acceptable to assume that $m=1$ in many of the systems analyzed here. With this assumption, the functional response (7) becomes simply a function of the ratio of prey and predator densities. This provides empirical support to the arguments of Getz (1984) and of Arditi and Ginzburg (1989) who have suggested that ratio-dependent functional responses may be common, especially in natural systems with complex heterogeneities.

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