

SIGMOID FUNCTIONAL RESPONSES BY INVERTEBRATE PREDATORS AND PARASITOIDS

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INTRODUCTION

It is customary to classify functional responses of predators into the three categories originally suggested by Holling (1959a): type I, where there is a linear rise to a maximum in the number of prey eaten per predator as prey density increases, type II, where the response rises at a decreasing rate towards a maximum value and type III, where the response is sigmoid, again approaching an upper asymptote. Type II responses are generally associated with invertebrate predators (and here we include insect parasitoids). Type III responses are thought to be more characteristic of vertebrate predators that can learn to ‘concentrate’ on a prey as it becomes abundant (Holling 1965).

It is the type II response of invertebrate predators which has attracted the most theoretical attention, the best known description being the ‘disc equation’ of Holling (1959b):

$$N_a = \frac{a T N}{1 + a T_h N} \quad (1)$$

Here, N_a is the number of prey encountered per predator, a is the instantaneous attack rate, T is the time that predator and prey are exposed to each other, T_h is the ‘handling time’ associated with each prey eaten and N is the density of prey. Both Royama (1971) and Rogers (1972) point out that this model does not permit the depletion of available prey during the course of predation. This exploitation is easily included, however, if we assume random search for prey, in which case (following Rogers (1972)

$$N_{ha} = N [1 - \exp(-a(T - T_h N_{ha}))] \text{ for predators} \quad (2)$$

and

$$N_{ha} = N \left[1 - \exp\left(-\frac{a T}{1 + a T_h N}\right) \right] \text{ for parasitoids,} \quad (3)$$

where N_{ha} now becomes the number of prey eaten per predator (or hosts parasitized per parasitoid). The inclusion of eqns (2) and (3) in simple population models has shown that the type II functional response cannot contribute to the stability of a predator–prey interaction (Hassell & May 1973; Murdoch & Oaten 1975). It therefore follows that if the predator has a type II functional response, stability results from other components affecting predators or prey. A review of some of these has been presented by Lawton, Hassell & Beddington (1975), Murdoch & Oaten (1975), Beddington, Hassell & Lawton (1976) and Hassell, Lawton & Beddington (1976).

The importance of distinguishing between type II and type III functional responses rests on their very different contributions to stability (Holling 1959a; Murdoch & Oaten 1975). Sigmoid functional responses are density dependent up to some threshold prey density, and may contribute to stability if average prey densities fall below this. In this

paper, we argue against the notion that type II functional responses are typical of invertebrate predators, and suggest that sigmoid type III responses may be much more common than previously supposed. Given the large number of studies that have been carried out to measure invertebrate functional responses, this may seem a surprising conclusion. We will argue that the normal practice of doing experiments in relatively small, simple laboratory universes using large, preferred prey may have produced a very distorted picture of the full range of behaviour which invertebrate predators are capable of showing.

We shall present data of two kinds: new experimental results that clearly demonstrate sigmoid functional responses in a range of insect predators and parasitoids, and some previously published data showing similar responses. The biological mechanisms underlying these responses will then be discussed, drawing in particular on the results of detailed laboratory studies where the predators or parasitoids were continuously observed whilst searching for prey of different densities. Finally, we will seek to describe these responses using simple models.

EXAMPLES

Figure 1 illustrates sigmoid functional responses for three insect predators (*Plea*, *Notonecta* and *Coccinella*) and a parasitoid (*Aphidius*). They were all obtained from very simple laboratory experiments in which a single predator was permitted to search for prey at each of the prey densities shown for a fixed period of time (T in eqns (2) and (3)). The experimental details are summarized as follows.

Plea atomaria Pallas (Hemiptera)

Plastic bowls of 29 cm diameter, filled with water to a depth of 5 cm (2.5 l), were used as arenas. A piece of plastic mesh ('Netlon'), upon which the predator could rest, was placed on the water surface. Small *Aedes aegypti* (L.) larvae were used as prey, and each experiment lasted for 24 hr with 16 hr daylight, in a temperature of 18° C. Individual predators were used in experiments on five consecutive days, so that each value for the average number of prey eaten represents the mean per 24 h over this period replicated for between five to ten predators (A. Reeve, unpublished data).

Notonecta glauca L. (Hemiptera)

Plastic tanks of 22.5 × 22.5 cm floor area, filled with water to a depth of 8 cm were used as arenas. Environmental complexity was increased by sub-dividing the total arena into four compartments, with 3 cm of clear water above the divisions. 'Netlon' was again provided at the surface, on which the *Notonecta* could rest. The prey were small (3–5 mm long) *Asellus aquaticus* L., distributed evenly among the four subcompartments, and provided with a small quantity of finely ground dead leaves as food. Only adult female *Notonecta* were used and each experiment lasted three days with the prey being replaced daily. Continuous illumination and a temperature of 8° C was maintained throughout.

Coccinella septempunctata L. (Coleoptera)

Plastic Petri dishes of diameter 9 cm were used as arenas. The bottom was covered with damp filter paper on which were placed first instars of the aphid *Brevicoryne brassicae* (L.). Each experiment lasted 2 h and was carried out at the same time of day, at 20° C (M. Cock, unpublished data).

Aphidius uzbekistanicus Luzhetzki (Hymenoptera)

The cages used were transparent plastic boxes of height 21.5 cm, width 11 cm and breadth 7 cm. In each cage was placed an equal number of *Dactylis glomerata* L. leaves on which third instars of the aphid *Hylopteroides humilis* (Walk.) were allowed to settle. Each experiment lasted for 24 h (16 h light and 8 h dark) and was conducted at 15° C (Dransfield 1975).

The fitted curves shown in Fig. 1 have been drawn by eye. In no case are the responses satisfactorily described by either the 'random predator' or 'random parasite' equations (see Table 1) which, since the confidence limits are relatively small, is strong evidence that the responses are not standard type II curves. Their sigmoid (type III) nature is, however, entirely based on visual inspection.

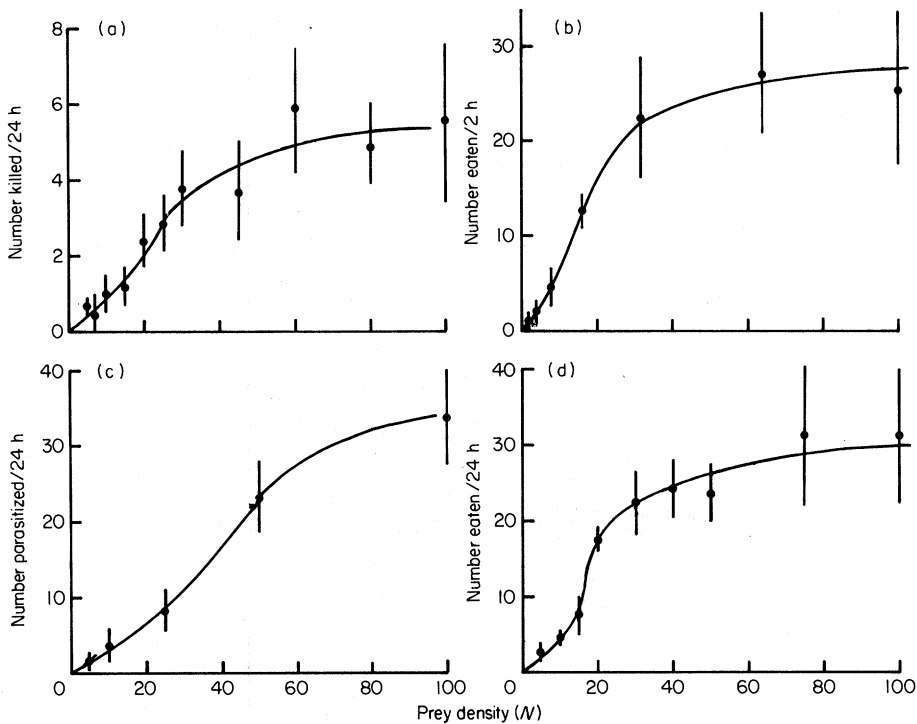


FIG. 1. Sigmoid functional responses. (a) *Notonecta glauca* on 3–5 mm *Asellus*; (b) *Coccinella septempunctata* on first instar aphids; (c) *Aphidius uzbekistanicus* on third instar *Hylopteroides*; (d) *Plea atomaria* on small *Aedes* larvae. Means and 95% confidence intervals shown; see text for experimental details.

In addition to these four examples of sigmoid responses, we can make use of two further examples that are known from the literature. These are displayed in Fig. 2. Again, the fitted curves have been drawn by eye.

The most likely explanation for these sigmoid responses is that one or more of the components of predator searching activity is itself dependent on prey density (Murdoch 1973; Murdoch & Oaten 1975). This is in contrast to eqns (2) and (3) which assume that both a and T_h remain constant at all prey densities, although in practice we know that this is often untrue even in a type II response (see in Hassell *et al.* 1976). Support for the

Table 1. Attempts to fit the data shown in Fig. 1 and Fig. 4(a) to the 'random predator' or 'random parasite' equations (see text)

Species	'Random predator' or 'random parasite' estimate of				
	a	T_h	F	d.f.	
<i>Notonecta</i>	0.103	0.023	0.29	1,9	$P > 0.25$: NS
<i>Coccinella</i>	1.219	0.016	1.43	1,6	$P > 0.25$: NS
<i>Aphidius</i>	0.422	-0.002	0.11	1,3	$P > 0.25$: NS
<i>Plea</i>	0.987	0.005	0.04	1,7	$P > 0.25$: NS
<i>Calliphora</i>	0.415	-0.0003	0.002	1,5	$P > 0.25$: NS

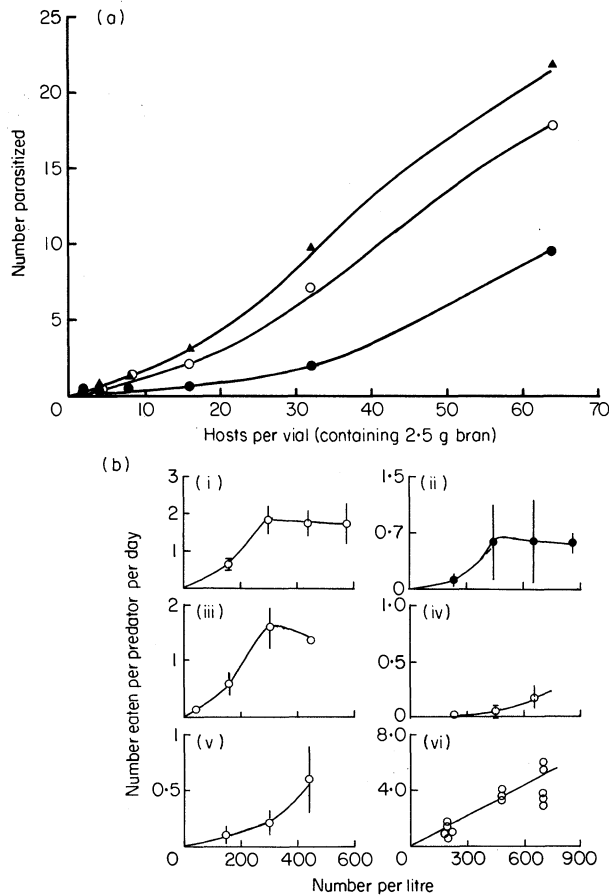


FIG. 2. Sigmoid functional responses. (a) *Nemeritis canescens* parasitizing *Cadra* larvae of (●) second, (○) third and (▲) fourth instars (Takahashi 1968). (b) Predatory copepod *Cyclops bicuspidatus thomasi* attacking (i) nauplii and (ii) copepodites of its own species; (iii) nauplii and (iv) copepodites of *Diaptomus*; (v) cladocera; (vi) rotifers (McQueen 1969).

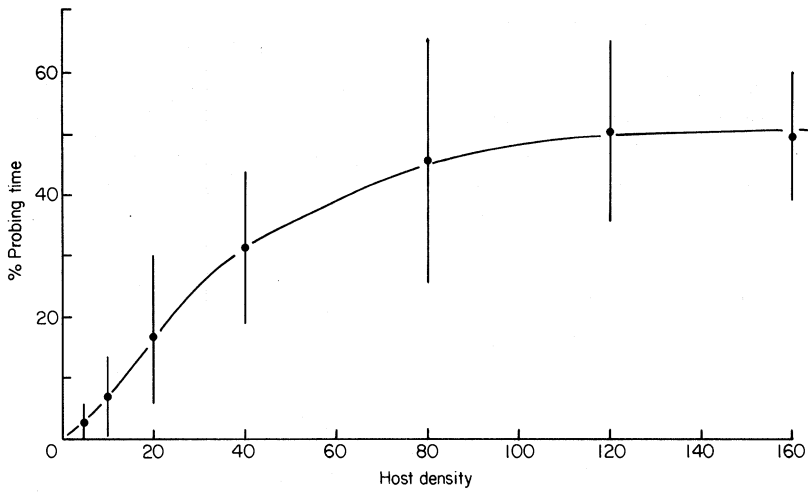


FIG. 3. Relationship between the time spent probing by *Nemeritis canescens* (as a percentage of total observation time) and the density of *Plodia interpunctella* larvae.

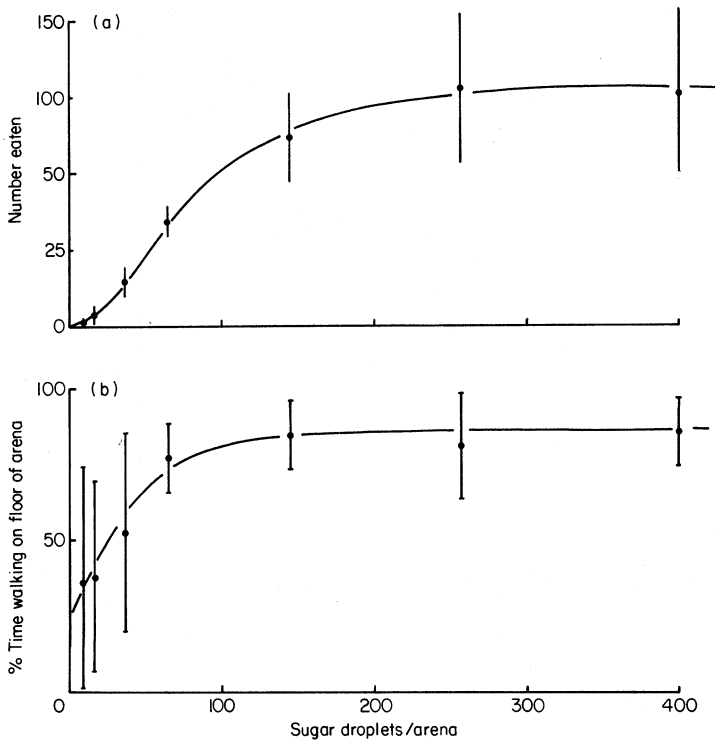


FIG. 4. (a) Sigmoid functional response of adult *Calliphora vomitoria* feeding on evenly distributed sugar droplets in a Perspex arena ($T = 30$ min). (b) Relationship between searching activity of *Calliphora vomitoria* and droplet density per arena. Activity is expressed as the percentage of total observation time spent walking on floor of arena (corrected for periods spent feeding). Means and 95% confidence limits shown.

hypothesis that predators search more actively as prey density rises is presented in Figs 3 and 4. Figure 3 shows the results of an experiment in which an individual of the ichneumonid parasitoid *Nemeritis canescens* (Grav.) was continuously observed for 30 min while exposed to one of a range of densities of fifth instar *Plodia interpunctella* Huebner larvae. The time spent actively probing the medium appears as a simple increasing function of host density: as host density is reduced, an increasing proportion

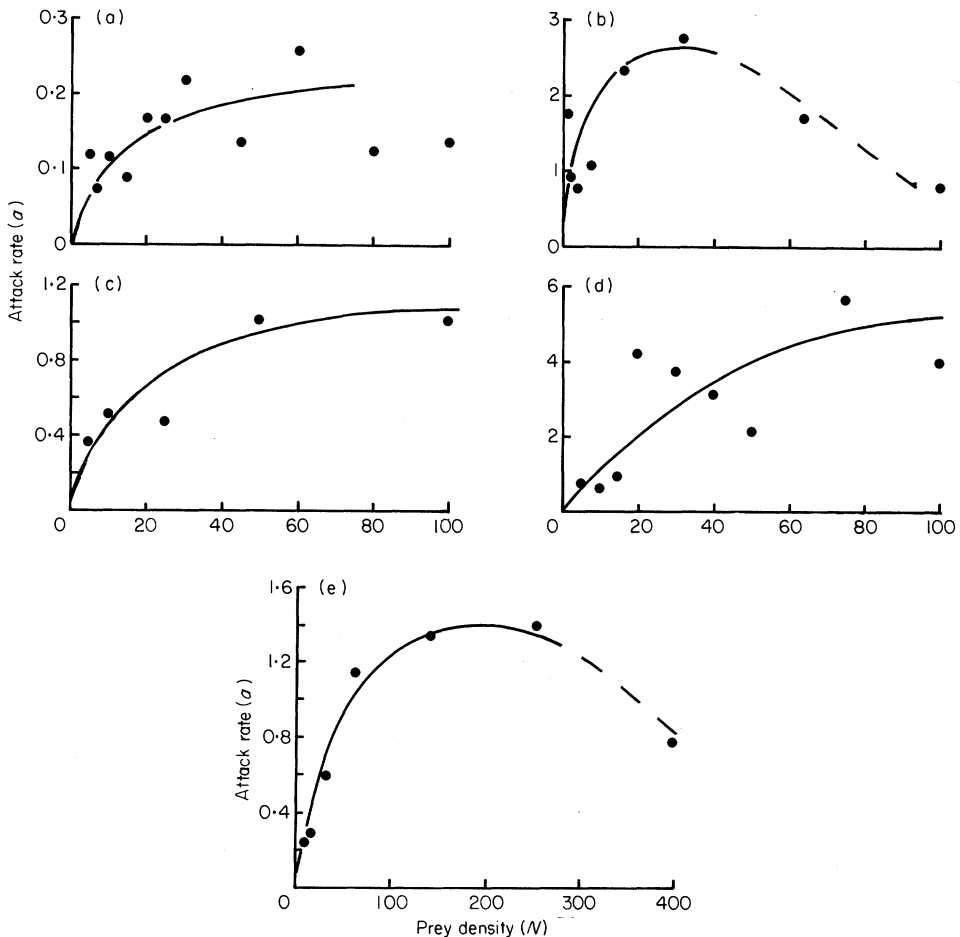


FIG. 5. Relationship between attack rate, a , and prey density (N), in five species with sigmoid functional responses. The method used to calculate a is given in the text. (a) *Notonecta*, $T_h = 0.091$; (b) *Coccinella*, $T_h = 0.025$; (c) *Aphidius*, $T_h = 0.018$; (d) *Plea*, $T_h = 0.029$; (e) *Calliphora*, $T_h = 0.0095$. Attack rates are defined per experimental universe, with $T = 1$.

of the time available is spent in non-hunting activities, such as walking and resting on the sides of the cage. This behaviour provides an explanation for the functional responses of *Nemeritis* shown in Fig. 2(a). A similar result was obtained from experiments using adult blowflies (*Calliphora vomitoria* L.) as 'predators' and sugar droplets as 'prey' in a simple perspex arena of 0.2 m^2 (see Murdie & Hassell (1973) for details). The sigmoid functional response obtained from these experiments is shown in Fig. 4(a), and from

Fig. 4(b) it is clear that this again is the result of searching activity, which in this case is time spent walking on the floor of the arena, increasing with prey density.

In both these examples the predators hunt more actively as prey density rises, specifically by spending proportionally more time searching for prey. Other, related, behaviours are also possible. In the *Calliphora* experiment, for example, the speed of movement of the fly walking in the arena also appears to depend upon the frequency of encountering droplets, while for *Nemeritis*, there may be a more rapid rate of probing of the host's medium at higher host densities. Neither of these particular behavioural details were quantified accurately.

In most cases, functional responses have been obtained without any attendant detailed behavioural observations. However, provided that some estimate of handling time,

Table 2. Two examples of the method used to estimate T_h for sigmoid functional responses; the 'random predator equation' was fitted to the data after eliminating successive data points, commencing with the lowest prey density; above the sigmoid portion of the curve, reasonable estimates of T_h (indicated by *) were possible

Predator	Data			Fit to 'random predator'	Data points eliminated				
	Points	N	N_{ha}		None	1	1-2	1-3	1-4
<i>Plea</i>	1	5	2.6						
	2	10	4.5	a	0.99	1.09	1.63	3.67	2.79
	3	15	7.9						
	4	20	17.5	T_h	0.005	0.008	0.018	0.029*	0.027
	5	30	22.2						
	6	40	24.2	F	0.04	0.16	1.04	17.44*	6.35
	7	50	23.8	d.f.	1,7	1,6	1,5	1,4	1,3
	8	75	31.2	P	NS	NS	NS	0.02 > P > 0.01	0.1 > P > 0.05
	9	100	31.2						
<i>Calliphora</i>	1	9	1.9						
	2	16	3.9	a	0.42	0.51	0.75	1.17	1.59
	3	36	14.6						
	4	64	34.3	T_h	-0.0003	0.003	0.007	0.0095*	0.011
	5	144	61.7						
	6	256	77.9	F	0.002	0.195	2.37	14.78	3.07
	7	400	76.6	d.f.	1,5	1,4	1,3	1,2	1,1
				P	NS	NS	NS	0.1 > P > 0.05	NS

T_h , is at hand, it becomes possible to calculate the way in which the attack rate a would be related to prey density, assuming the total time T to be a constant. Figure 5 shows the relationship between the estimated values for a and prey density for the examples shown in Fig. 1 and for *Calliphora* shown in Fig. 4(a). In each case, eqn (2) (or in the case of *Aphidius*, eqn (3)) has been used and solved for a , knowing N , N_{ha} , T_h and T . The value of T was taken to be the duration of the experiment, and T_h estimated from the data above the inflexion of the sigmoid response by using eqn (3) and following the method of Rogers (1972) for all except *Aphidius*, where the number of data points above the inflexion was insufficient and T_h was obtained from the functional response in Fig. 8. Examples of this procedure for obtaining T_h are illustrated in Table 2, using the data for *Calliphora* and *Plea*. The general similarity between the relationships of a to N in Fig. 5,

and those between the proportion of time spent searching for prey and N in Figs 3 and 4(b) is obvious.

A check on the validity of this result is provided by the data shown in Fig. 6, where the relationship between a and prey density has been calculated using an identical procedure, but in this case the original functional responses are 'normal' type II curves. Under these circumstances, a shows no tendency to increase with increasing prey density;

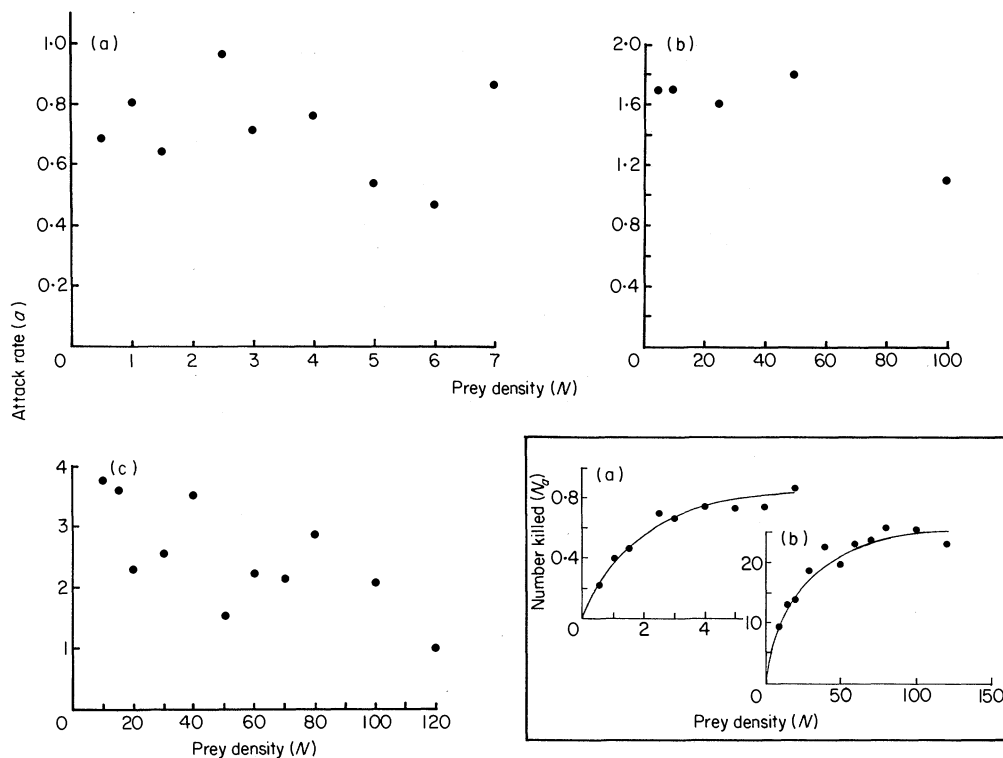


FIG. 6. Relationship between attack rate, a and prey density (N), in three species with standard type II functional responses. The method used to calculate a is given in the text. (a) First instar spiders (*Linyphia triangularis* Clerck) feeding on *Drosophila* (Turnbull 1962), $T_h = 0.98$; (b) *Aphidius uzbekistanicus* attacking *Metapolophium*, $T_h = 0.018$; (c) final instar *Ischnura elegans* (van der Lind.) larvae attacking *Daphnia* (Thompson 1975), $T_h = 0.034$. The inset shows the original functional responses for (a) *Linyphia* and (c) *Ischnura*.

The original functional response for *Aphidius* is shown in Fig. 8.

if anything the reverse is true, particularly at high prey densities. A similar tendency for a to decrease at high prey densities is suggested by two of the responses shown in Fig. 5. If this decrease in a is real, it occurs at prey densities well above the sigmoid region of the response, and hence will not be considered further here. The fundamental difference, therefore, between the two types of response rests on the tendency for a to increase over an initial range of low prey densities in a type III response, but to remain constant at low prey densities in a type II response.

MODELS

If we ignore any decreases in a at high prey densities, the data shown in Fig. 5 suggest that where the original functional response is sigmoid, the attack rate itself increases with prey density in a similar way to a type II functional response, i.e.

$$a = bN/(1 + cN) \quad (4)$$

where b and c are constants.

Substituting eqn (4) in eqn (1), and cancelling gives

$$N_a = \frac{bN^2T}{1 + cN + bT_h N^2}. \quad (5)$$

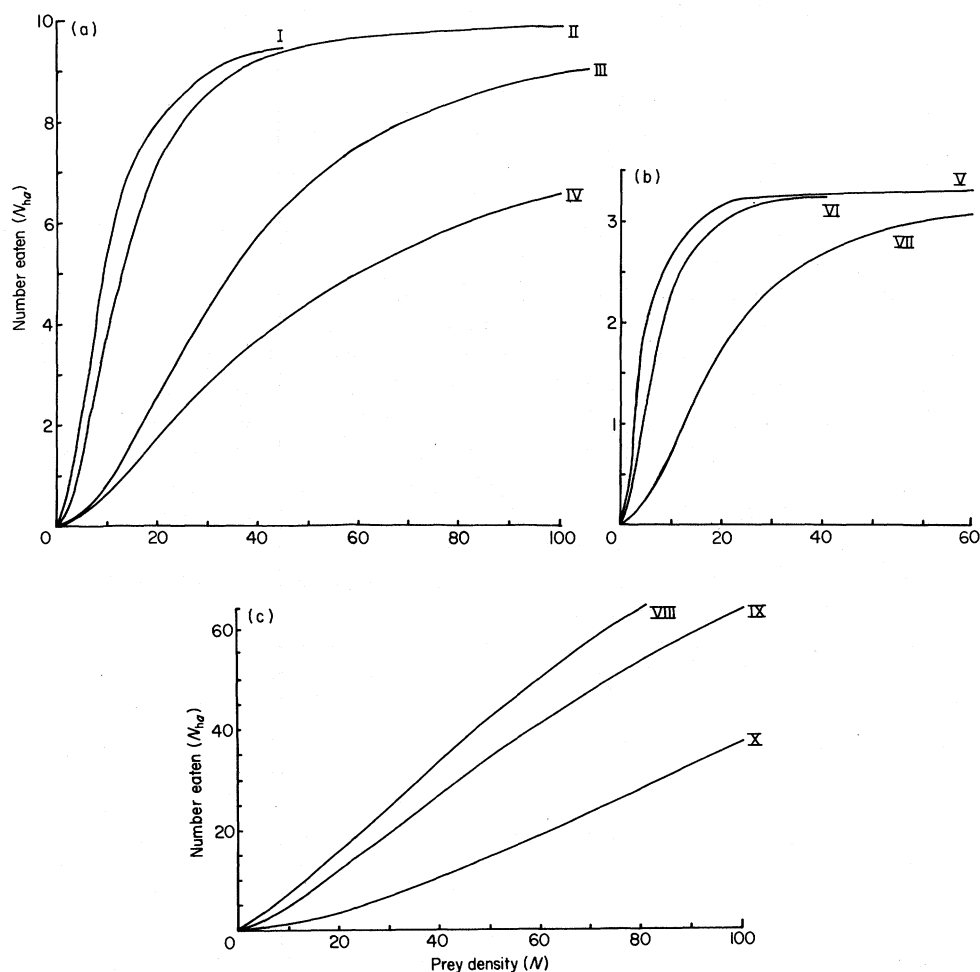


FIG. 7. Simulated functional responses using eqn (6). Parameters are (a) $T_h = 0.1$ with (I) $b = 0.3$ and $c = 0.04$, (II) $b = 0.1$ and $c = 0.001$, (III) $b = 0.01$ and $c = 0.001$, (IV) $b = 0.01$ and $c = 0.04$; (b) $T_h = 0.3$ with (V) $b = 0.3$ and $c = 0.02$, (VI) $b = 0.1$ and $c = 0.001$, (VII) $b = 0.01$ and $c = 0.001$; (c) $T_h = 0.01$ with (VIII) $b = 0.3$ and $c = 0.04$, (IX) $b = 0.1$ and $c = 0.02$, (X) $b = 0.01$ and $c = 0.001$.

In the situation where prey are exploited, eqn (5) can then be considered as an instantaneous death rate and integrated over the duration of an experiment, T , to give a predator functional response model comparable to that in eqn (2)

$$N_{ha} = N(N - N_{ha}) \left[c \log \left(\frac{N - N_{ha}}{N} \right) - bT_h N_{ha} + bT \right]. \quad (6)$$

We have used eqn (6) to simulate a series of functional responses. The results are shown in Fig. 7. Approximate values for b and c were obtained by fitting a 'disc equation' (eqn (4)) to the data shown in Fig. 5. Equation (6) was then solved iteratively using a standard Newton-Raphson technique, for appropriate values of b , c , and T_h .

It is clear from Fig. 7 that eqn (6) yields realistic, sigmoid responses that are similar to the range of real responses shown in Figs 1, 2 and 4(a). This does not, of course, imply that eqn (6) is necessarily 'correct', but merely serves to illustrate that the observed changes in a are capable of generating sigmoid functional responses.

DISCUSSION

The examples in Figs 1–4 suggest that sigmoid functional responses are not atypical of invertebrate predators and parasitoids. They are likely whenever there is a threshold prey density below which the efficiency of searching by the predator declines. This density will vary from species to species. Where prey are cryptic, relatively small or not the preferred species, the threshold is likely to be at rather higher densities than those where prey are conspicuous and easy to find. We would expect, therefore, that sigmoid functional responses could be obtained for almost all species of predator provided that the rate of encounters with prey can be reduced to sufficiently low levels. In support of this hypothesis, we find that three of the species showing type III sigmoid functional responses (*Notonecta*, Fig. 1(a); *Coccinella*, Fig. 1(b) and *Aphidius*, Fig. 1(c)) have been shown to give type II responses, well described by eqns (2) or (3), when the rate at which they encounter prey has been increased, as shown in Fig. 8. This has been achieved by only slightly varying the experimental conditions; by providing either a preferred host *Metapolophium dirhodum* (Walk.) for *Aphidius*, or larger prey of the same species for both *Notonecta* and *Coccinella*. (In the latter case, the resulting functional response is still not exactly of type II, although adequately described by the random predator eqn (2).) We predict that sigmoid responses might well be recovered for the predator–prey combinations shown in Fig. 8 by greatly increasing the size of the experimental universes, and so once more reducing the rate of encounter between predator and prey.

Observations with an entirely different group of invertebrates, namely zooplankton, tend to support these conclusions. McQueen (1969) obtained a series of functional responses for the predator *Cyclops bicuspidatus thomasi* Forbes (Fig. 2). It is significant that whilst five of these responses are clearly or probably sigmoid, the sixth is not. This was obtained using the rotifer *Keratella* as prey, which McQueen (1969, p. 1610) states 'might be the preferred prey species' although subsequent field work failed to confirm this prediction. A more robust example is provided by Frost's (1975) work on the filter-feeder *Calanus pacificus*. This species feeds at a significantly depressed rate when the concentration of algae falls below a critical level. The similarity between the way in which the clearance rate depends on algal density in *Calanus* (Fig. 9), and attack rate, a , depends on prey density in predatory insects (Fig. 5) is obvious. Frost also provides evidence suggesting that the size of the algae determines the density of food at which

Calanus clearance rates start to decline. This threshold occurs at progressively lower food concentrations as the size of the food particles increases, so that copepods may cease filtering, or decrease their filtering effort, at relatively high densities of small food particles. The parallel with the insect predators is striking.

In passing, it is of interest to note that a very similar mechanism has been proposed to explain sigmoid functional responses in the protozoan, *Stentor* (D. J. Rapport, in Murdoch & Oaten 1975). Murdoch & Oaten suggest that the cilia that cause the feeding

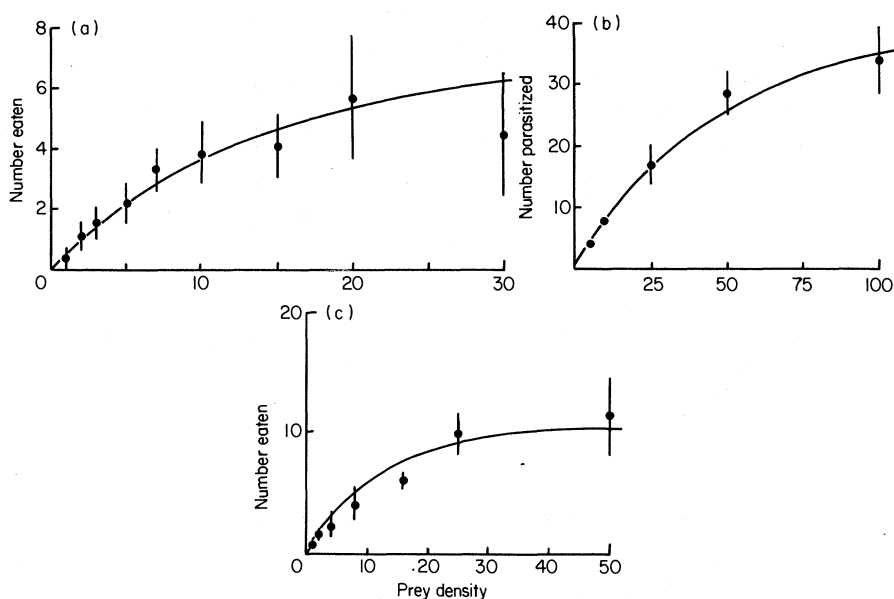


FIG. 8. Type II functional responses obtained with 'preferred' or large prey, for two predators and one parasitoid which have been shown to yield sigmoid responses with other prey. (a) *Notonecta* attacking 7-9 mm *Asellus*, $a = 0.74$, $T_h = 0.11$. (b) *Aphidius* parasitizing *Metapolophium*, $a = 2.13$, $T_h = 0.018$. (c) *Coccinella* attacking fifth instar cabbage aphids, $a = 1.97$, $T_h = 0.087$. In each case, the responses are satisfactorily described by either the 'random predator' or 'random parasite' equations ((a) $F_{1,7} = 7.28$, $0.05 > P > 0.025$; (b) $F_{1,3} = 107.8$, $0.005 > P > 0.001$; (c) $F_{1,5} = 7.33$, $0.05 > P > 0.025$).

current may beat faster as the concentration of the prey's metabolites increase, and it is this increasing filtering rate that generates a type III response.

The only behavioural observations made in the present study show the time spent searching (by *Calliphora* and *Nemeritis*) to increase over a narrow range of low prey densities. There are a number of ways that these observations can be interpreted in terms of the 'disc equation' (1). For convenience, we have assumed that handling time, T_h , remains constant and that it is only the attack rate, a , which changes (i.e. a reduction in the time spent searching reduces the rate of encounter between the predator and its prey recorded over the whole of the experimental period). An alternative view would be to hold a constant and allow T_h to vary (since any change in time spent searching with changes in prey density must influence T_h in eqns (1-3)). In practice, both are likely to

vary with prey density. Distinguishing between these alternatives, or some combination of the two, would require very detailed behavioural observations, and would be an overdissection of an essentially simple model.

The effects of a sigmoid functional response on the stability of phytoplankton-zooplankton population dynamics have been discussed by Steele (1974), and in a more general context by Murdoch & Oaten (1975) who stress the obvious density dependent properties of the response up to a critical prey density, above which satiation and/or handling time become destabilising. It is evident that, in the absence of any other stabilizing influences acting on the prey (a very special, and rather unrealistic assumption), a stable equilibrium may only be possible if the equilibrium prey density N^* lies within the density dependent part of the predator's functional response, which in turn is dependent on all factors affecting the natality and mortality of the prey. For true predators, rather than parasitoids, there are also important factors affecting the predator's rate of increase that bear on the significance of a sigmoid response. In particular, Lawton *et al.* (1975) and Beddington *et al.* (1976) discuss the importance of threshold prey densities for predator growth, survival and reproduction. If these thresholds lie above that for the

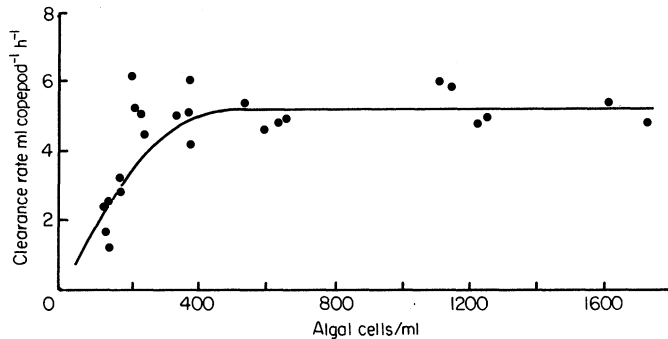


FIG. 9. Clearance rate (millilitres water filtered per copepod per hour) by adult female *Calanus* feeding at various cell densities of *Thalassiosira* (Frost 1975).

density dependent part of the functional response, any effect of the latter will be completely obscured.

Questions of population stability apart, the existence of a type III functional responses in various predatory and parasitic insects is interesting on two further counts. First, at least for true predators, the fact that searching effort decreases at low prey densities has interesting implications for optimum foraging theory. A reduction in searching effort in an environment which yields a very low return may obviously be an advantage, particularly when it is not always possible to leave that environment (as in many aquatic insect larvae). By reducing searching effort, a predator may hope to reduce costs until conditions once more improve. The prey density threshold below which searching effort is reduced should then be larger the higher the 'search costs' of the predator and the smaller the 'rewards' for each prey captured. This latter prediction, at least, is born out by the data. Equivalent arguments apply to parasitoids, although costs and gains are less easily defined. They may involve, for example, the costs that arise from exposure of the parasitoid to its own natural enemies, which must be balanced against the gains that accrue from the number of hosts successfully parasitized.

The other point of interest is that it should have taken so long to realize that type III responses may not, after all, be confined to vertebrate rather than invertebrate predators. This almost certainly stems from the fact that invertebrate functional responses are normally measured in small, simple universes, using medium to large prey that are a 'preferred' food of the predator. Results are easier to obtain like this. By making apparently trivial alterations in experimental design, so that we employ somewhat larger and sometimes slightly more complex universes, and relatively smaller or less suitable prey, we can obtain very different results, with different ecological implications.

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SUMMARY

(1) It is generally assumed that sigmoid functional responses are more characteristic of vertebrate than invertebrate predators or parasitoids. There are, however, several examples in the literature of invertebrates showing sigmoid responses, and to these we add some further examples.

(2) Behavioural observations on the parasitoid *Nemeritis canescens* and on *Calliphora vomitoria* searching for sugar droplets as 'prey', show that the time spent searching by an individual increases with prey density towards an upper asymptote.

(3) All the examples of sigmoid functional responses shown can be analysed by assuming that it is the instantaneous attack rate, a , that is increasing with prey density. A model including this relationship is used to generate a variety of sigmoid responses.

(4) The significance of these responses is discussed in terms of their contribution to the stability of predator-prey interactions and their possible selective advantage to the predator.

REFERENCES

- Beddington, J. R., Hassell, M. P. & Lawton, J. H. (1976). The components of arthropod predation. II. The predator rate of increase. *J. Anim. Ecol.* **45**, 165–85.
- Dransfield, R. (1975). *The ecology of grassland and cereal aphids*. Unpublished Ph.D. thesis, University of London.
- Frost, B. W. (1975). A threshold feeding behaviour in *Calanus pacificus*. *Limnol. Oceanogr.* **20**, 263–6.
- Hassell, M. P., Lawton, J. H. & Beddington, J. R. (1976). The components of arthropod predation. I. The prey death rate. *J. Anim. Ecol.* **45**, 135–64.
- Hassell, M. P. & May, R. M. (1973). Stability in insect host-parasite models. *J. Anim. Ecol.* **42**, 693–726.
- Holling, C. S. (1959a). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Ent.* **91**, 293–320.
- Holling, C. S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Ent.* **91**, 385–98.
- Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. entomol. Soc. Can.* **45**, 1–60.
- Lawton, J. H., Hassell, M. P. & Beddington, J. R. (1975). Prey death rates and rate of increase of arthropod predator populations. *Nature, Lond.* **255**, 60–2.
- McQueen, D. J. (1969). Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. *J. Fish. Res. Bd Can.* **26**, 1605–18.
- Murdie, G. & Hassell, M. P. (1973). Food distribution, searching success and predator-prey models. *The Mathematical Theory of the Dynamics of Biological Populations* (Ed. by R. W. Hiorns), pp. 87–101. Academic Press, London.

- Murdoch, W. W. (1973). The functional response of predators. *J. appl. Ecol.* **10**, 335–41.
- Murdoch, W. W. & Oaten, A. (1975). Predation and population stability. *Adv. Ecol. Res.* **9**, 1–125.
- Rogers, D. J. (1972). Random search and insect population models. *J. Anim. Ecol.* **41**, 369–83.
- Royama, T. (1971). A comparative study of models for predation and parasitism. *Researches Popul. Ecol. Kyoto Univ. Suppl.* **1**, 1–91.
- Steele, J. H. (1974). *The Structure of Marine Ecosystems*. Harvard University Press, Cambridge, Mass.
- Takahashi, F. (1968). Functional response to host density in a parasitic wasp, with reference to population regulation. *Researches Popul. Ecol. Kyoto Univ.* **10**, 54–68.
- Turnbull, A. L. (1962). Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae: Linyphiidae). *Can. Ent.* **94**, 1233–49.

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