Functional Responses of the European Earwig and Two Species of Coccinellids to Densities of *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae)

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ABSTRACT   The functional response data obtained in the laboratory for the major predators of woolly aphid, *Eriosoma lanigerum*, namely *Forficula auricularia* L., *Parapriasus australasiae* (Boisduval) and *Harmonia confirmis* (Boisduval) all fitted well to the type II model of the Holling disc equation. These predators consumed larger numbers of early than later instars of *E. lanigerum* within the same time period. Adult *H. conformis* had a lower instantaneous search rate and handling time and could also consume larger numbers of *E. lanigerum* than could mature larvae. Overall, *F. auricularia* was the most efficient predator of *E. lanigerum*.

Introduction

Functional response, defined as a change in the number of prey attacked as prey density changes, is one of the basic components of predation or parasitism (Solomon 1949). The predation response of a predator to its prey is a complex series of events involving the length of time that the prey is exposed to the predator, the rate of successful attack and the handling time required for each prey by the predator (Holling 1963). These three variables when combined in the Holling disc equation can be used to describe the type of functional response that a predator exhibits for its prey (Holling 1959b).

Basically, four types of functional response have been identified. These are type I, in which prey consumption increases linearly to a plateau with increasing prey density; type II, in which prey consumption increases asymptotically to a plateau with increasing prey density; type III, a sigmoid curve rising to a plateau; and type IV, a dome-shaped response (Holling 1959a; Hassell 1978). Type II responses have been associated most often with invertebrate predators and have been described by the disc equation of Holling (1959b):

$$N_e = a' \, T_t N_t / (1 + a' \, T_h N_t),$$

where N_e is the number of prey attacked, a' is the instantaneous search rate (the rate of successful attack), T_t is the total time predators and prey are exposed to each other, N_t is the number of prey, and T_h is the time required to handle the prey. Handling time is defined as the time that the predator requires to pursue, kill, eat and digest the prey (Holling 1963). The maximum number of attacks is limited by an upper asymptote defined by the ratio T_t / T_h (Hassell 1978). As prey density increases, attack rates increase, more time is spent handling prey, and less time is available to search for prey resulting in the deceleration in the number of attacks seen in Types II-IV responses. How rapidly the curve decelerates, however, depends upon a' (Hassell 1978).

It has been shown that the functional response of predators to prey density is of fundamental importance, particularly from the biological control point of view. An explanation of this response provides an understanding of a major part of the predation process (Holling 1959a).

This paper reports on the functional responses of three important predators viz. the European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae), and the lady beetles, *Parapriasus australasiae* (Boisduval) (Coleoptera: Coccinellidae) and *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae) to various densities of woolly aphid *Eriosoma lanigerum* (Hausmann).

Materials and methods

To study the functional response of the major predators, colonies of *E. lanigerum* were established in the laboratory at constant temperature of 18°C and 14L:10D photoperiod following the method of Asante and Danthanarayana (1990). All predators used were collected from the field. They were isolated singly in petri dishes and deprived of food for 24 h to ensure that they would feed. Since the number of aphids eaten by a predator depends upon the size of the aphid (Dixon 1973), different instars of *E. lanigerum* were used in this study. Adult apterous viviparae were not included in this study because they continue to give birth.

The functional response of *F. auricularia* was studied in three separate experiments using first to third instars, first to fourth instars and third to fourth instars of *E. lanigerum* at densities of 3, 5, 8, 10, 15, 20, 30, 40, 50, 60, 80, 100, 140, 160; 4, 8, 12, 16, 20, 24, 28, 32, 36, 40, 50 60, 70, 100, 120; and 3, 5, 8, 10, 15, 20, 30, 40, 50, respectively. All *F. auricularia* used were adults, but they were not sexed.

The functional response of adult *P. australasiae* was studied using first to fourth instars and third to fourth instars of *E. lanigerum* at densities of
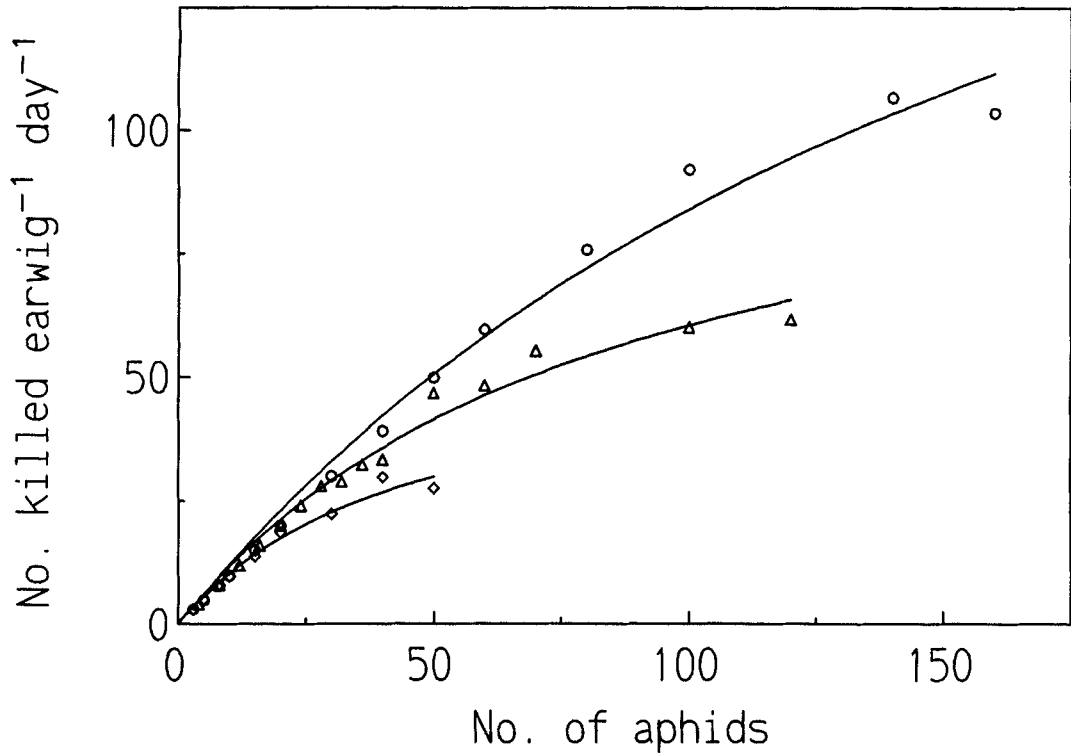
Fig. 1. Functional response of adult *F. auricularia* to different life stages of *E. lanigerum*; first-third instars (O), first-fourth instars (Δ), third and fourth instars (◇).
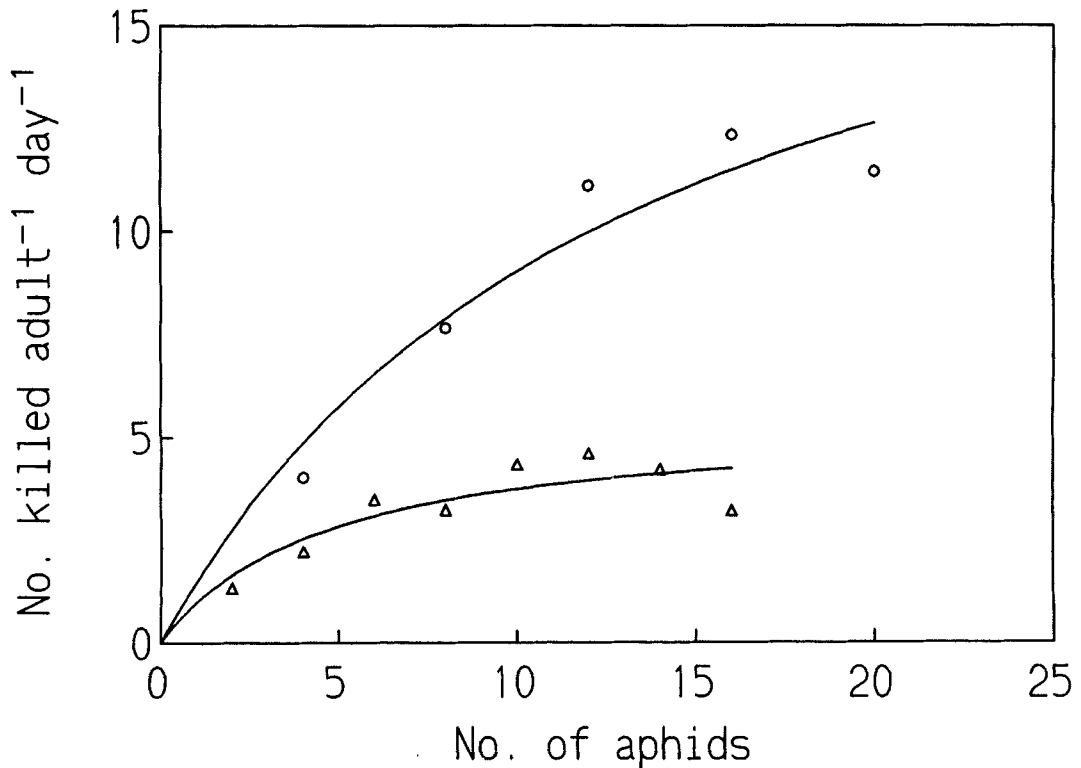

Fig. 2. Functional response of adult *P. australasiae* to the different life stages of *E. lanigerum*; first-fourth instars (O), third and fourth instars (Δ).
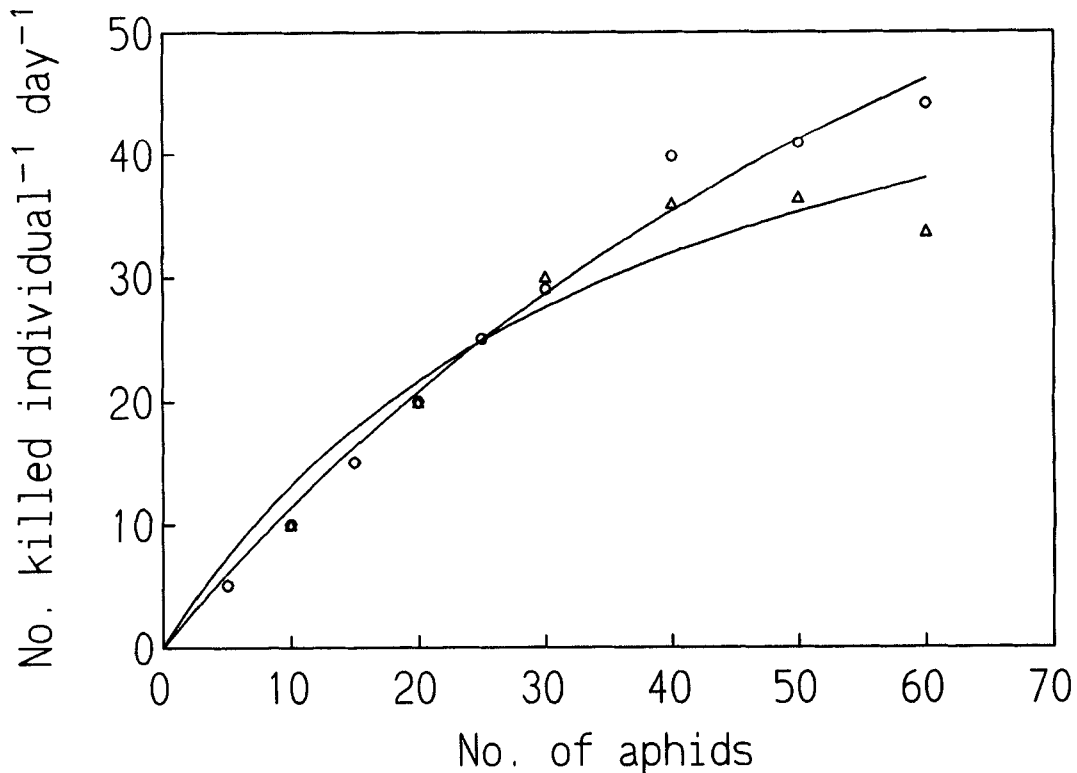
Fig. 3. Functional response of adult and mature larvae of *H. conformis* to nymphal stages of *E. lanigerum*; adult *H. conformis* on first-fourth instars of *E. lanigerum* (O), mature larvae of *H. conformis* on first-fourth instars of *E. lanigerum* (Δ).

4, 8, 12, 16, 20; and 2, 4, 6, 8, 10, 12, 14, 16, respectively. The larval functional response was not studied because large numbers of field-collected *P. australasiae* larvae were found to be parasitised.

In the case of *H. conformis*, the functional response of both adult and mature larvae were studied using first to fourth instars of *E. lanigerum*. The prey densities were 5, 10, 15, 20, 25, 30, 40, 50, 60; and 10, 20, 30, 40, 50, 60, for the adult and larvae, respectively.

For each experiment, predators were placed individually in petri dishes (9 × 1.5 cm), containing one of the above mentioned prey densities. Ten replicates of each prey density were run simultaneously. All predation trials were conducted under laboratory conditions at 16-28 °C and a relative humidity of 40-70%. After 24 h, the predation arenas were examined under the binocular microscope to record the number of prey attacked or consumed.

The number of prey attacked as a function of prey density were fitted to the Holling disc equation as a rectangular hyperbola using the absolute distance method of Marquardt (1963) to examine the type of response exhibited by these predators and to obtain estimates of T_h and a'.

Results

The functional response data for *F. auricularia*, *P. australasiae* and *H. conformis* all fitted well to the type II model of the Holling disc equation (Figs 1, 2 and 3). Estimates of T_h and a' obtained from this equation are shown in Table 1. Adult *F. auricularia* consumed large numbers of *E. lanigerum* when offered only nymphs of early instars (i.e. first, second and third instars) (Fig. 1). The number of *E. lanigerum* consumed decreased as the size of aphids offered increased (Fig. 1). Values of a' were similar for the different categories of *E. lanigerum* life stages offered. However, T_h increased as the size of aphids encountered by *F. auricularia* increased (Table 1). The ratio of T_t/T_h indicated that the maximum number of *E. lanigerum* that could be consumed by *F. auricularia* is a function of prey size (Table 1).

Similarly, adult *P. australasiae* could consume relatively larger numbers of early instars than older instars of *E. lanigerum* (Fig. 2). The value of a' decreased slightly whilst T_h increased considerably when *P. australasiae* was offered third and fourth instars of *E. lanigerum* (Table 1).

Adult *H. conformis* was found to have lower instantaneous search rate and handling time, and could also consume larger numbers of *E. lanigerum* than mature larvae (Fig. 3; Table 1).

It was found from the current investigation that at low prey densities most predators consumed all the prey offered but as prey density increased

Table 1. Estimates of the handling time (T_h), instantaneous search rate (a') and maximum number of *E. lanigerum* that could be attacked per day for *F. auricularia, P. australasiae* and *H. conformis.*

Predator stage	Prey stages	Search rate (a')	Handling time (T_h)	Upper asymptote (T_t/T_h)[1]	Maximum no. attacked/predator in 24 hours $\pm$ SE[2]
	1st-3rd instars	0.053	0.005	200	106.7 $\pm$ 10.2 (140)
F. auricularia	1st-4th instars	0.055	0.006	83.3	61.7 $\pm$ 5.9 (120)
(adult)	3rd-4th instars	0.052	0.022	45.5	29.8 $\pm$ 2.1 (40)
P. australasiae	1st-4th instars	0.066	0.075	13.3	12.3 $\pm$ 1.3 (16)
(adult)	3rd-4th instars	0.049	0.217	4.6	4.6 $\pm$ 0.5 (12)
H. conformis (adult)	1st-4th instars	0.052	0.011	90.9	44.2 $\pm$ 4.6 (60)
H. conformis (larvae)	1st-4th instars	0.070	0.027	37.0	36.5 $\pm$ 5.9 (50)

1 The maximum number of *E. lanigerum* that could be attacked per predator per day; $T_t = 1$ day.
2 Number of *E. lanigerum* provided are in parentheses.

only a few predators could consume all the available prey.

Discussion

The type II functional responses exhibited by the *E. lanigerum* predators *F. auricularia, P. australasiae* and *H. conformis* in the present study indicate that for a given number of predators, the risk to each prey individual decreases continuously as prey density increases (Hughes *et al.* 1984). Hence, these predators would fail to stabilise increasing *E. lanigerum* populations. Although the type II response of Holling is usually regarded as the form typical of invertebrate predators and parasitoids, there is increasing evidence that sigmoid type III responses are also widespread, at least amongst insects (Murdoch and Stewart-Oaten 1975; Hassell 1978). Hassell *et al.* (1977) and Hassell (1978) have shown theoretically that only type III responses stabilise a predator-prey interaction. The importance of the difference between type II and type III responses is that, given a type III response, each predator will act in a density-dependent manner, and hence stabilise the prey population over some part of the range of its density.

In agreement with the findings of Dixon (1973), these predators consumed larger numbers of early instars than older instars of *E. lanigerum*. Since *E. lanigerum* populations are generally low and comprised of a higher proportion of nymphs of the early instars during the winter and early spring (Asante and Danthanarayana 1993), the present observation suggests that when large numbers of *F. auricularia* and *H. conformis* are available in the spring, they would act as important natural control agents. On the other hand, adult *P. australasiae* appears to be an inefficient predator for *E. lanigerum*.

F. auricularia has been reported to have a varied diet consisting of both plant (Lenfant and Sauphanor 1992) and animal (Fulton 1924; Crumb *et al.* 1941) materials, with aphids comprising the greatest part of the animal food (Mueller *et al.* 1988). Previous studies have indicated that *F. auricularia* is an effective predator of *E. lanigerum*

(McLeod and Chant 1952; Mueller *et al.* 1988). Buxton and Madge (1976) have reported that older stages of *F. auricularia* are more effective on aphids. On apple, *F. auricularia* have been reported to feed on leaves, flowers and ripening fruit (Mueller *et al.* 1988). Phillips (1981) stated that *F. auricularia* are beneficial in apple orchards if their effectiveness at controlling pests outweighs the damage they cause. In the experiments reported here, *F. auricularia* consumed large numbers of *E. lanigerum* in a simplified arena in the laboratory and is potentially the most useful predator of those studied.

Acknowledgments

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