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THE FUNCTIONAL RESPONSE AND PREFERENCE OF *MACROLOPHUS CALIGINOSUS* [*HETEROPTERA : MIRIDAE*] FOR TWO OF ITS PREY : *MYZUS PERSICAE* AND *TETRANYCHUS URTICAE*

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Functional response studies of females of *Macrolophus caliginosus* Wagner for 2 prey species *Myzus persicae* Sulzer and *Tetranychus urticae* Koch showed **Holling's** type II response (1959). Estimations of handling time (Th) and attack rate (a) obtained for the aphid (Th = .055 day ; a = 1.035) and for the mite (Th = .025 day ; a = .947) enabled the development of a mathematical model which describes the predation rate on the 2 prey simultaneously. This mirid shows a sharp preference for aphids over mites.

KEY-WORDS : *Heteroptera, Miridae, Macrolophus caliginosus*, predation, functional response, feeding preference, biological control, *Myzus persicae, Tetranychus urticae.*

Present development in integrated pest management programs in greenhouses have shown the necessity to increase progressively the number of potential natural enemies to control different phytophagous insects such as aphids, whiteflies, thrips and mites (e.g. on winter tomato crops or egg-plants).

Several studies have already shown that some species belonging to the *Miridae* (*Heteroptera*) could be good agents to control pests in greenhouse conditions (**Khristova** *et al.*, 1975 ; **Brzezinski**, 1982 ; **Kajita**, 1984). Among these species, *Macrolophus caliginosus* Wagner appears as a particularly good polyphagous predator which can be effectively used for crop protection (**Malausa** *et al.*, 1987).

In a previous study, we defined the main biological characteristics of this species and its responses to temperature or prey offered (**Fauvel** *et al.*, 1987). Some species such as the whiteflie *Trialeurodes vaporariorum* Westwood or the aphid *Myzus persicae* Sulzer enabled the predator to have a high rate of multiplication. Others, such as the mite *Tetranychus turkestani* Ugarov & Nikolski or the aphid *Aphis gossypii* Glover, do not.

In order to complete these first observations and to understand better the efficiency of this predator to control pests, experiments were done to analyse its functional response over different prey densities (**Holling**, 1959). Two prey species were studied separately : *Myzus persicae* and *Tetranychus urticae* Koch. Then, in order to study the preference of *M. caliginosus* between them, they were offered simultaneously, and the data obtained were compared with those predicted by functional response studies (**Coch**, 1978).

MATERIAL AND METHODS

ORIGIN OF INSECTS

All predators and prey used in these experiments came from laboratory cultures. *M. caliginosus* has been reared for many generations on tobacco plants (*Nicotiana tabacum* L.) with *Ephestia kuehniella* Zeller (*Lepidoptera : Pyralidae*) and nymphal instars of *T. vaporariorum* for food.

In order to do measurements in undisturbed conditions, predators (only females were used) were placed one week before in the same conditions as the experiment on a single head of tomato plant with the prey species to be tested.

Aphids were reared on the pea *Pisum sativum* L. under laboratory conditions. Only the 4th instar were used because, unlike adults, this instar would not reproduce during the course of the experiment. The length of aphid prey is 1.27 ± .08 mm.

Mites were reared in greenhouses on beans *Phaseolus vulgaris* L. and only adult females were used because of their bigger size (length = .51 ± .01 mm).

FUNCTIONAL RESPONSE STUDY

To facilitate the recording of the consumed prey, insects were placed on a cut plant of Prisca tomato with the stem plunged into a tube full of water. Plants were about 15 cm high with the two first leaves well developed. New leaves and cotyledons were removed. The leaf surface available for insects (both sides) was 200 cm^2. These plants were placed individually in plexiglass cages (26 × 26 × 46 cm).

Experiments were carried out in standardized conditions (22 °C ; RH 80 % ; LD 16 : 8) during a 48 h period in order to reduce the daily variation of eating intensity (**Fauvel** *et al.*, 1987). In order to equalized there appetite, the predators were starved 24 h before the beginning of the experiment.

The number of prey eaten was then recalculated for a 24 h period.

The different prey densities offered to a single *M. caliginosus* female were for *M. persicae* : 1, 2, 4, 6, 10, 20 and 30 insects per replicate ; and for *T. urticae* : 6, 14, 20, 50, 80 and 120. Five replicates were done for each prey density.

In order to fit observed data to the **Holling** disc equation, prey density must remain unchanged over the whole experiment duration. In such a way, the probability of encountering each prey remains constant. Therefore, checking was done every 4 h during the photophase, and eaten prey were replaced.

If we suppose that *M. caliginosus* shows a type II functional response, which is common among insect predators (**Holling,** 1959), the equation is :

$$Na = \frac{a.N.T}{1 + a.N.Th} \qquad (I)$$

Where N is the initial prey density, Na is the number of prey attacked during a time interval T, a and Th correspond respectively to the attack rate and to the handling time of the predator.

Different statistical procedure have been proposed to fit this model to experimental data. The most commonly used is the reciprocal transformation method (see **Williams & Juliano,** 1985 for a detailed review) which has been shown to lead to biased estimations of a and Th.

Therefore, we prefered to use a non-linear iterative procedure, a technique which has been considered to provide more precise statistical estimations of these parameters (**Juliano & Williams,** 1987). Several methods of non-linear fitting are available ; and because of the fact that data sets usually show a great heteroscedasticity in such studies, we choose to maximize a gaussian likelihood (with the Gauss-Marquart method) instead of a least-square (or weight least-square) procedure which is the most commonly used method in the literature (**Williams & Juliano,** 1985 ; **Houck & Strauss,** 1985 ; **Juliano & Williams,** 1987). All these non-linear methods are equivalent when the usual assumptions of normality and equality-of-variance for the error term are provided.

Additionally, the use of such estimation methods enables to compare the fitting of the model between 2 (or more) sets of data (here between the 2 prey species). The corresponding procedure (likelihood ratio test) works as follow : (let n1 and n2 the total number of observations for each set of data). Firstly, a different model is fitted to both sets of data simultaneously. This leads here to the simultaneous estimation of 4 parameters (2 "a" and 2 "Th"). The corresponding maximum likelihood obtained (ML1) has n1 + n2-4 d.f. Then, a single model is fitted to the pooled observations corresponding to the 2 experiments. Only 2 parameters are thus estimated and the maximum likelihood obtained (ML2) has now n1 + n2-2 d.f.

The greater the difference between the 2 sets of data, the weaker the 2nd likelihood, as compared to the first one. The statistical procedure is thus built to test this reduction of likelihood. For that purpose, it can be shown that : $-$ 2.Ln(ML2/ML1) follows a χ^2 with (n1 + n2-2)-(n1 + n2-4) = 2 d.f. (**Dacunha-Castelle & Duflo,** 1982).

This method is the generalization of the F-test method (see **Houck & Strauss,** 1985), and must be used for data with a significant heteroscedasticity.

Intermediate possibilities are also available, for example when the null hypothesis to be tested concerns only one parameter of the model. The procedure is then the same, except that, here, 3 parameters will be estimated in the 2nd step (e.g. one "a" and two "Th" for testing the equality of the 2 attack rates). In such a case, the likelihood ratio test will follow a χ^2 with only 1 d.f.

All computations were done with CS-NL, a "non-linear statistical package" on a Bull-DPS8 computer (**Bouvier** *et al.,* 1985).

Because of the fact that fitting a functional response to a set of data, leads to the estimation of only 2 parameters (a and Th), it became possible to graphically represent each fitting model by a point in the space defined by these 2 parameters. Then, using the variance-covariance matrix of the parameter, an ellipse corresponding to a given confidence interval of the estimations could be drawn for each set of estimations. This procedure is justified by the fact that estimations obtained from maximum likelihood methods are asymptotically normally distributed (**Cramer,** 1946). The graph obtained (fig. 3) which is a bi-variate generalization of those given by **Houck & Strauss** (1985) gives here a visual way to assess statistical differences between the functional response obtained on the 2 different prey.

PREFERENCE STUDY

Experiments were done under the same conditions as those described above except that the 2 prey species were offered simultaneously to the predator. The prey densities of aphids : mites were : 40 : 0, 32 : 8, 24 : 16, 16 : 24, 8 : 32, 0 : 40.

Estimates of a and Th obtained for each prey separately can be used in a mathematical model which describes the predation rate of the 2 prey presented simultaneously, under the null hypothesis that there was no preference between them (**Cock**, 1978). This model is:

$$Na_1 = \frac{a_1 . N_1 . T}{1 + a_1 . n_1 . Th_1 + a_2 . n_2 . Th_2} \qquad \text{(II)}$$

$$Na_2 = \frac{a_2 . N_2 . T}{1 + a_2 . n_2 . Th_2 + a_1 . n_1 . Th_1}$$

Where the index 1 and 2 are respectively for the aphid and the mite species.

Arranging these 2 equations leads to:

$$\frac{Na_1}{Na_1 + Na_2} = \frac{a_1 . N_1}{a_1 . N_1 + a_2 . N_2} \qquad \text{(III)}$$

a model which enables the prediction of the predation frequency of one of the 2 prey eaten. Any preference shown by the predator for one or the other species will lead to a statistical difference between experimental results and model predictions.

RESULTS

FUNCTIONAL RESPONSE FOR EACH PREY SEPARATELY

Fitting a type II functional response to the data leads to the following estimations:

For *M. persicae* (fig. 1): $Th_1 = .055 \pm .018$ days (i.e. 1 h 19 min), and $a_1 = 1.035 \pm .237$.

For *T. urticae* (fig. 2): $Th_2 = .025 \pm .007$ days (i.e. 0 h 36 min) and $a_2 = .947 \pm .225$.

Thus, the maximal theoretical number of prey that could be eaten over a 24 h period (1/Th) is 18 aphids or 40 mites.

These estimations are summarized on fig. 3 which shows that there is a strong difference between functional responses of *M. caliginosus* on the 2 types of prey. This difference is highly significant for handling time ($\chi^2 = 6.05$; d.f. = 1 ; $p < .01$), but no difference could be detected between the 2 attack rates ($\chi^2 = .003$; NS).

PREFERENCE STUDY

Fig. 4 & 5 both show results obtained and the theoretical number calculated with estimations given above under the hypothesis that there is no preference between the 2 types of prey (equation II for fig. 4 ; equation III for fig. 5). Fig. 4 strongly suggests a change in searching behaviour of the bug when the 2 prey species are present ; less prey are taken that predicted for both species. Fig. 5 shows that aphids are much more often attacked than predicted by the model (Binomial test ; $p < .001$). It seems therefore that the mirid shows a sharp preference for aphids over mites, and thus no switching effects from one prey to the other could be detected (**Hassell**, 1978).

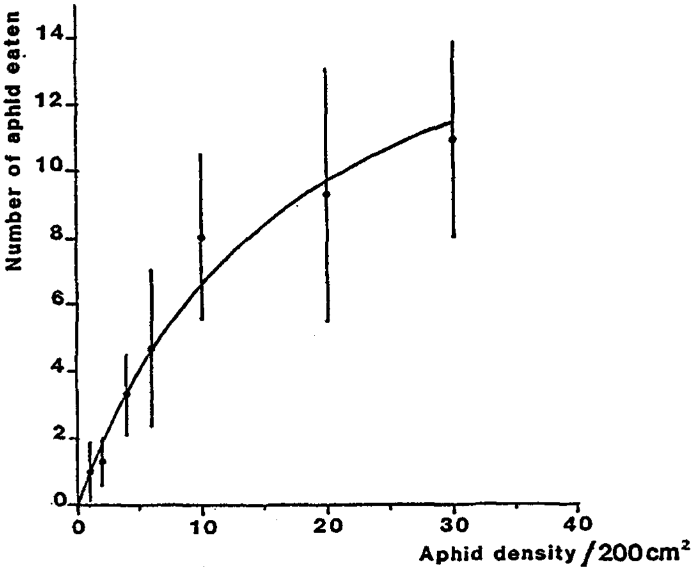

Fig. 1. Functional response of *M. caliginosus* to increasing density of *M. persicae* (4th instar). Data are recalculated for a 24 h period (means ± 95 % confidence intervals).

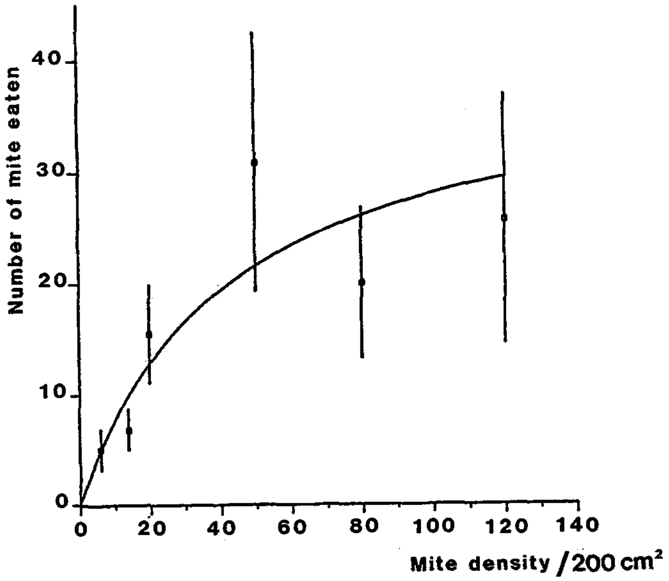

Fig. 2. Functional response of *M. caliginosus* to increasing density of *T. urticae* (adults). Data are recalculated for a 24 h period (means ± 95 % confidence intervals).

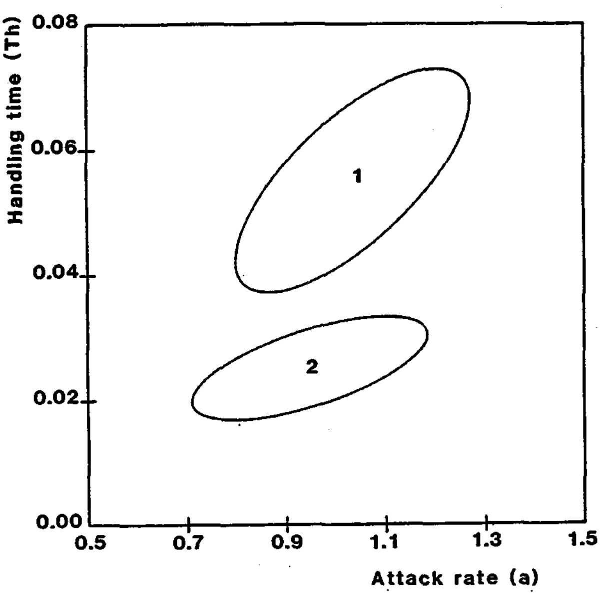

Fig. 3. Scatter plot of the two functional response shown on fig. 1 & 2, as characterized by attack rate (a) and handling time (Th). (1) *M. caliginosus* on *M. persicae*. (2) *M. caliginosus* on *T. urticae*. Ellipses correspond to 95 % confidence interval of estimations.

DISCUSSION

The type II functional response used here to describe the response of *M. caliginosus* females to variations in prey densities is very commonly observed for predatory insects under laboratory conditions (**Hassell**, 1978). Indeed, this as been shown for several Heteropteran including *Orius insidiosus* Say (**McCaffrey & Horsburgh**, 1986), *Cyrtorhinus lividipennis* Reuter (**Sivapragasam & Asma**, 1985) and *Reduviolus americoferus* L. (**Flinn** *et al.*, 1985). Few exceptions, however, have been found : a type III functional response has been shown for *Nabis kinbergii* Reuter (**Siddique & Chapman**, 1987).

With *M. caliginosus* we found a significant difference between the functional response obtained with 2 different prey species. This difference was observed mostly for Th which is, for aphid, twice as long as for mites. Such result could be explained by the fact that the biomass eaten by the predator is much more important for *M. persicae* than for *T. urticae*. Indeed, **Flinn** *et al.* (1985) have shown that the handling time is proportional to the size of the prey because the predator takes a longer time to eat larger prey. This difference leads to a change in the maximal theoretical number of prey that could be eaten per unit of time. Such information could be very useful to improve mass-rearing methods defined to produce *M. caliginosus*.

These studies do not take into account the fact that the mirid could also be phytophagous (**Fauvel** *et al.*, 1987). At low prey density, the predator, in our experiment, was restricted to the single head of a tomato plant in the cage and, therefore, it is likely that under such conditions, it will show some phytophagous behaviour. Under natural conditions, the predator could move from one infested plant to an other. This seems to be

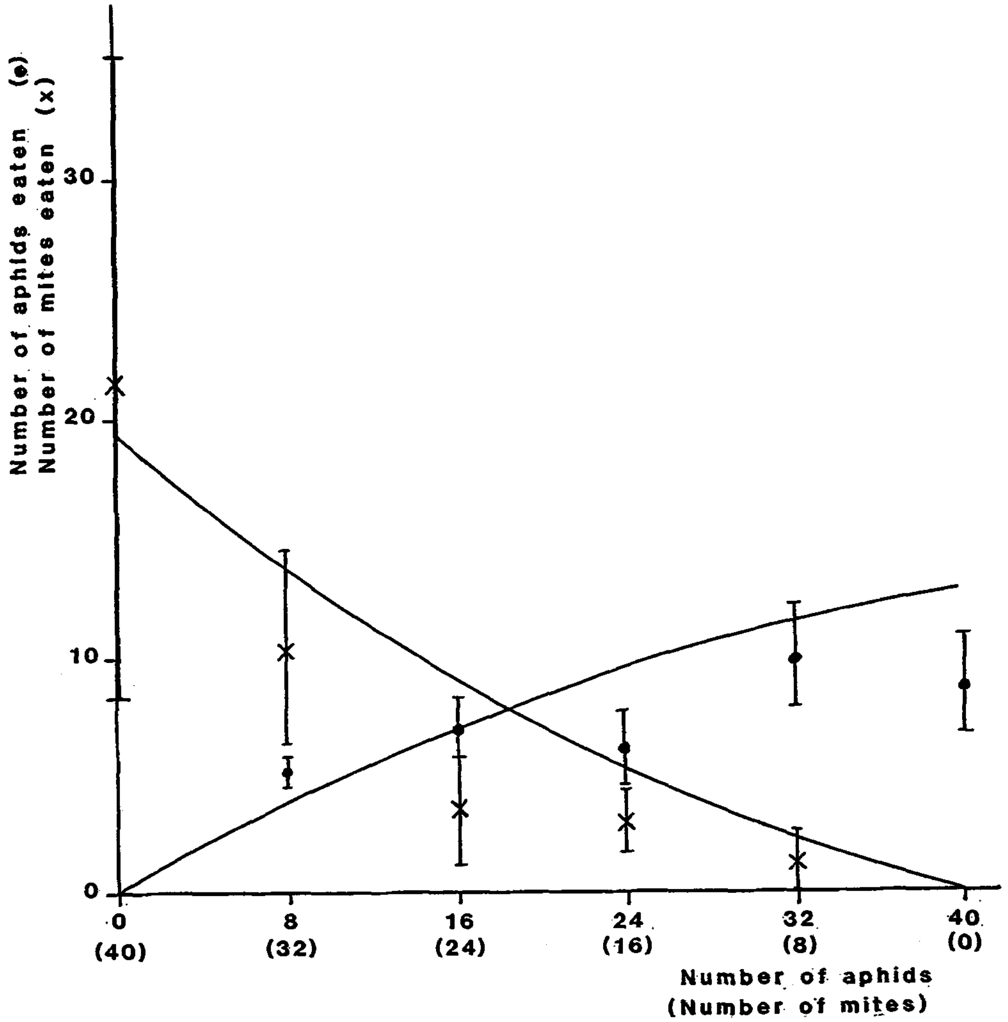

Fig. 4. Predation of *M. caliginosus* over different proportions of *M. persicae* (●) and *T. urticae* (×) out of 40 total preys. Data are recalculated for a 24 h period (means ± 95 % confidence intervals). Curves are from equation II, under the hypothesis of no preference between the 2 preys.

confirmed by the fact that, in our experiment, the mirid has often been found to walk on the cage's walls, when the prey density was low. Such a behaviour was not observed at high prey density.

The study of *M. caliginosus* preference between 2 of its natural prey gives us interesting information concerning its capacity to control these 2 pests when they live together. Obviously, such work must also be done for other prey species such as the whitefly *T. vaporariorum*, because with this prey, the multiplication rate of the predator is greater than with others (Fauvel *et al.*, 1987). However, in this last case, the withefly instars are fixed on

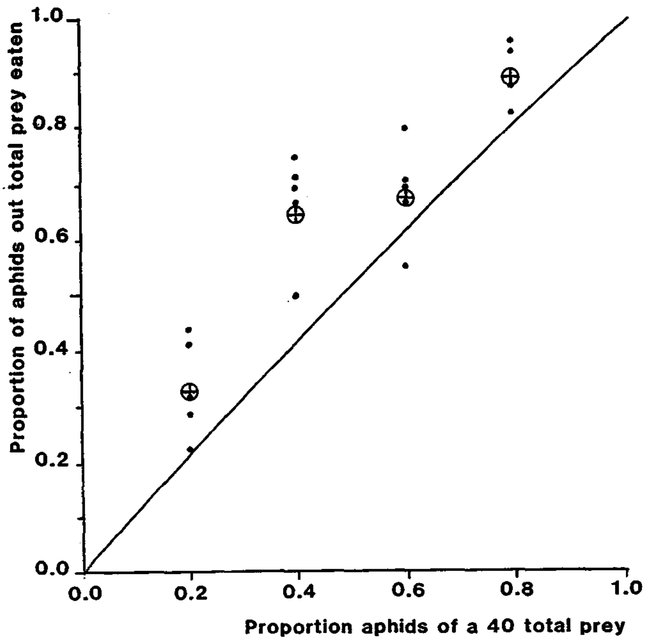

Fig. 5. Relationship between the proportion of aphids in the total number of prey offered to predators and the proportion of eaten aphids over the total number of prey eaten. Curve is from equation III. (0): experimental replicates, (+): means.

the plant. Thus, here, functional response must be studied with theoretical models for which the constraint to have a constant prey density during the whole duration of the experiment is no longer necessary (e.g. **Royama's** model, 1971).

The fact that the mirid seems to prefer aphids over mites confirms results obtained earlier by **Fauvel** *et al.* (1987) concerning the effect of these 2 types of prey on the multiplication rate of the predator. The only difference is the mite species studied.

CONCLUSION

M. caliginosus showed different functional response characteristics with *M. persicae* or *T. urticae* as prey. Moreover, this predator seems to prefer aphids over mites when they are offered simultaneously. Such results give us a better understanding of polyphagous predator-prey interactions, and enable us to better quantify the efficiency of this natural enemy to control pests in greenhouse conditions. Experiments are now carried out to know if *M. caliginosus* shows any preference for the withefly *T. vaporariorum*. Indeed, this last species is very commonly consummate in greenhouses, and is moreover one of the preys that lead to a higher rate of increase of the predator here studied.

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RÉSUMÉ

Réponse fonctionnelle et préférence de *Macrolophus caliginosus* [*Heteroptera : Miridae*] pour deux de ses proies : *Myzus persicae* et *Tetranychus urticae*

L'étude en laboratoire des réponses fonctionnelles des femelles adultes de *Macrolophus caliginosus* Wagner vis-à-vis des deux proies *Myzus persicae* Sulzer et *Tetranychus urticae* Koch montre dans les 2 cas une réponse de type II de **Holling** (1959). L'estimation du temps de manipulation (Th) et du taux d'attaque instantané (a) pour l'aphide (Th = .055 jour ; a = 1.035) et pour l'acarien (Th = .025 jour ; a = .947) permet d'établir un modèle mathématique décrivant la prédation sur les 2 proies présentes simultanément et de préciser ainsi, au regard des résultats expérimentaux, l'existence d'une préférence du miride pour le puceron *M. persicae*.

MOTS CLÉS : *Heteroptera, Miridae, Macrolophus caliginosus*, prédation, réponse fonctionnelle, préférence alimentaire, lutte biologique, *Myzus persicae, Tetranychus urticae*.

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