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Estimating Predatory Efficiency of *Episyrphus balteatus* (Diptera: Syrphidae) in Cereal Fields

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ABSTRACT A model was developed to estimate the effect of predation by *Episyrphus balteatus* larvae on aphid populations in fields of winter wheat. Feeding rate of syrphid larvae was estimated from experiments in field cages using a Holling type-III function. During larval development, syrphids consumed a maximum of 396 aphids, which is only half the potential feeding rate reported from laboratory experiments. The lower consumption rate in the field may be attributed to the additional time required by the predators to find prey. Isoclines derived from the model were used to estimate the abundance of syrphid larvae necessary to prevent further pest increases.

KEY WORDS syrphids, model, consumption rate

APHIDOPHAGOUS SYRPHID LARVAE are important predators of cereal aphids (Storck-Weyhermüller 1988, Groeger 1992, Tenhumberg & Poehling 1995). In northern Germany the most abundant syrphid species is *Episyrphus balteatus* (De Geer), constituting >90% of all syrphids in the field (Tenhumberg & Poehling 1991, Tenhumberg 1992). After migration into cereal fields, syrphid females lay their eggs in response to aphid density. If syrphid larvae hatch early in the buildup of aphid populations, they are often able to prevent aphid outbreaks, especially in southern Germany (Tenhumberg & Poehling 1995).

Considerable research has been carried out on the voracity of this species in the laboratory (Table 1), because of the importance of *E. balteatus* in limiting aphid abundance. The results have been extremely variable. For example, the estimated maximum number of aphids consumed by *E. balteatus* during larval development varies between 140 and 1,322 third-instar or medium-sized aphids, depending on temperature and aphid species (Wahbi 1967, Ankersmit et al. 1986, Tenhumberg 1992). Even at the same temperature, the laboratory voracity may vary by up to 600% (17°C [Table 1]); this variation can only be partly explained by differences in aphid size or nutritional value. For example, in the experiments of Ankersmit et al. (1986), aphids were presented on leaves, whereas Tenhumberg (1992) presented aphids without leaves. The resulting different searching areas of syrphid larvae might be responsible for the variation in voracity recorded by those authors. Furthermore, mortality in the experiments of Ankersmit et al. (1986) was more than twice that observed in Wahbi's (1967) and Tenhumberg's (1992) experiments (70% versus 15-30%, respectively), indi-

cating that the syrphid larvae used by Ankersmit et al. (1986) were exposed to higher stress.

The laboratory voracities reported in Table 1 cannot be applied directly to natural conditions. The syrphids were usually reared in small arenas such as petri dishes. The voracity estimated under such conditions is determined mainly by satiation; it does not take into account the time needed to locate prey. Although aphid consumption in the field is probably lower than indicated by laboratory estimates (Luck et al. 1988), it is common to use such data to estimate the influence of syrphid larvae on the population dynamics of aphids (Chambers & Adams 1986, Hagley & Allen 1990).

In the study reported here, the effect of syrphid larvae was estimated in field cages that were approximately the same size as the foraging area of larvae in the field (unpublished data). From these data, a model was constructed to predict the potential of syrphid larvae in controlling aphid populations.

Materials and Methods

The experiments were conducted in 10-m² cages placed in fields of winter wheat during the summers of 1989-1991. These cages were divided into two parts with gauze. At the beginning of June, cereal plants (EC 49) inside the cages were infested with two aphid species, *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Walker). Four-d-old syrphid larvae were released when aphid densities were between 5 and 10 aphids per shoot. In some cases, higher densities were reached because the sampling schedule missed the beginning of exponential aphid growth. Sufficient syrphid larvae were released to establish initial predator-prey ra-

Table 1. Number of aphids consumed during larval development and mortality of *E. balteatus* larvae at different temperatures

Aphid species	Instar or size of aphids	Temp, °C	Mortality of syrphid larvae, %	No. of aphids	Source of data
<i>S. avenae</i> (F.)	Third instar	17	70	140	Ankersmit et al. (1986)
<i>M. dirhodum</i> (Walker)	Third instar	14	20	1,113	Tenhumberg (1992)
		17	15	1,041	Tenhumberg (1992)
		20	23	886	Tenhumberg (1992)
		22	27	658	Tenhumberg (1992)
<i>Aphis fabae</i> (Scopoli)	Medium size	15	30	553	Wahbi (1967)
		20	30	407	Wahbi (1967)
		25	27	1,322	Wahbi (1967)

tios between 1:40 and 1:245 (Table 2); these predator-prey ratios are frequently found in cereal fields (Tenhumberg 1992). In one cage half, no predators were released, to examine aphid development in the absence of syrphid larvae (=control). Aphid density was calculated by counting all aphids on 50 randomly selected plants per plot at three times: just before and at 3 and 6 d after the release of syrphid larvae. The syrphid consumption rate was estimated by comparing growth rates of aphid populations, r_N , in cages in the presence and absence of syrphid larvae. r_N was estimated using the following formula of Entwistle & Dixon (1987) was used:

$$r_N = \frac{\ln(D_{t_2} + 0.01) - \ln(D_{t_1} + 0.01)}{t_2 - t_1} \quad (1)$$

where D_{t_1} and D_{t_2} are the aphid densities at time t_1 and time t_2 , respectively.

Equation 1 assumes that aphid populations grow logarithmically and therefore should only be used for calculations over short periods. r_N was computed for each counting interval (3 d). Under the assumption that aphid populations in each cage half increase at the same rate, the reduction of r_N (R) caused by predators can be estimated by subtracting r_N of the control cage (Cr_N) from r_N in the cages with predators (Sr_N):

$$R = Cr_N - Sr_N. \quad (2)$$

Table 2. Experimental design used to establish different predator-prey ratios in field cages

Date of release	EC ^a	No. aphids per shoot	No. released larvae	Predator-prey ratio
24 June 1989	69	22.0 ± 6.3	1,060	1:70
27 June 1989	69	22.0 ± 7.0	460	1:170
3 July 1989	71	55.5 ± 7.7	642	1:245
11 June 1990	49	8.1 ± 3.7	300	1:110
3 July 1991	50	24.2 ± 7.5	960	1:70
8 July 1991	55	6.8 ± 2.5	280	1:70
8 July 1991	55	5.2 ± 1.9	85	1:170
10 July 1991	57	5.0 ± 2.0	120	1:120
10 July 1991	57	6.6 ± 2.7	110	1:170
12 July 1991	57	7.7 ± 2.9	330	1:40

^a Growth stage of Zadoks et al. (1974).

The correlation between R and the predator-prey ratios was tested by calculating the Pearson correlation coefficient (Sokal & Rohlf, 1981).

Results

The effect of syrphid larvae on aphid populations at different initial predator-prey ratios is shown in Fig. 1. Although syrphid larvae tended to reduce r_N more at higher predator-prey ratios (i.e., higher number of aphids per syrphid larva), these variables were not significantly correlated (Pearson correlation coefficient = 0.239, $p = 0.507$). Thus, no reliable predictions of syrphid voracity based on actual predator-prey ratios could be made.

Instead, syrphid voracity was estimated as follows. The increase of an exponentially growing aphid population per time interval, dN/dt , is given by the product of the population growth rate r_N and the number of individuals N at time t :

$$\frac{dN}{dt} = Nr_N. \quad (3)$$

Integrating equation 3 with respect to time t we obtain:

$$N = N_0 e^{r_N t}. \quad (4)$$

In equation 4, r_N denotes the growth rate of the aphid population in the absence of predators (con-

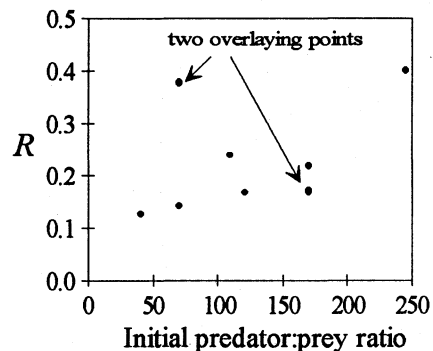


Fig. 1. Relationship between initial predator-prey ratio and the resulting reduction of the growth rate of aphids, R (for calculation of R see *Materials and Methods*).

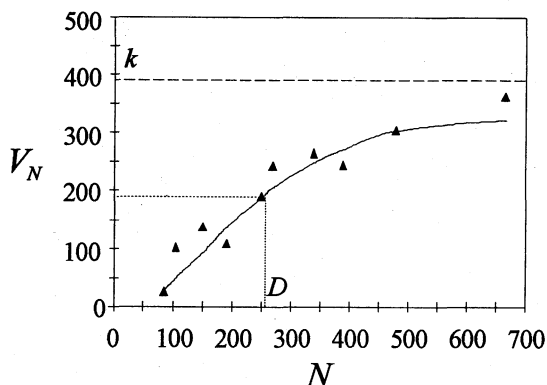


Fig. 2. Voracity (V_N) of syrphid larvae as a function of aphid abundance (N).

ontrol), N_0 the aphid numbers in the presence of predators at the beginning of the time interval t (in days), and N is the number of prey available for syrphid larvae. The difference between N and the actual aphid density at time t (N_t) divided by the number of syrphid larvae released (P) is an estimate of actual syrphid voracity (V_N):

$$V_N = \frac{N_0 e^{3r_N} - N_3}{P} \quad (5)$$

The voracity V_N was a nonlinear function of N . The distribution of cereal aphid populations is clumped, especially at low density. With increasing density, aphid populations get closer to a random distribution (Ohnesorge & Viereck 1983). Therefore, I assumed that the voracity of syrphid larvae accelerated at low aphid density and decelerated at higher densities because of a maximum rate of consumption. This is best described by the Holling type-III function (Holling 1966):

$$V_N = \frac{kN^2}{N^2 + D^2} \quad (6)$$

where the parameter D specifies the amount of prey consumed when half of the maximum feeding rate k is reached. From a nonlinear regression analysis of the estimated voracity on the number of aphids available, I obtained $k = 396$ and $D = 256$ ($r = 0.9$; $p \leq 0.001$ [Fig. 2]).

In addition the influence of syrphid voracity on the increase of aphid populations was estimated. If there is no interference between syrphid larvae, the development of the aphid population can be described as follows (Wissel 1989):

$$dN/dt = Nr_N - PV_N \quad (7)$$

The growth of the aphid population dN/dt will be zero if the net rate of increase (Nr_N) is equal to the prey consumption rate by syrphid larvae (PV_N) that is, if

$$Nr_N = PV_N \quad (8)$$

Replacing V_N of equation 8 with the Holling type-

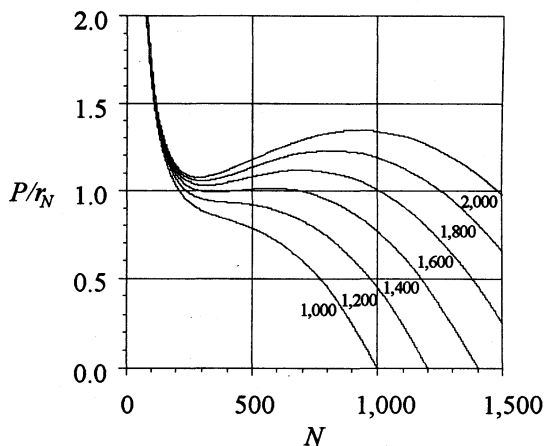


Fig. 3. N isoclines for different z values (N , P = density of aphids, predators; z = maximum density of aphid population; r_N = growth rate of aphid population).

III function and expressing the rate of increase of aphid populations (Nr_N) with the logistic Verhulst-function (Verhulst 1883) we obtain:

$$Nr \left(1 - \frac{N}{z} \right) = P \frac{kN^2}{N^2 + D^2} \quad (9)$$

The Verhulst-function takes into account that population growth declines as aphid density approaches the maximum value of z . As noted above, the values of k and D are 396 and 256. Suppose further that the value of z is between 1,000 and 2,000. Thus, zero-growth isoclines can be drawn (Fig. 3). Each isocline illustrates all quotients P/r_N for a given z value where the amount of prey consumed is equal to the net reproduction of the pest (stable system). Extreme values of P/r_N (minimum, maximum, inflexion point) only exist for $N \geq 200$. For $N < 200$, the curves join into a monotonically decreasing function. This means that, in the case of low-aphid densities, the number of predators necessary to reduce the pest density under some threshold will be independent of the maximum value of N . With regard to pest management (economic injury threshold), an aphid abundance of 5–10 individuals per shoot is tolerable (Wetzel & Schütte 1988, Basedow et al. 1989, Mann et al. 1986). In this range of low aphid numbers, z can be ignored and P can be expressed as a function of N :

$$P = \frac{r_N(N^2 + D^2)}{kN} \quad (10)$$

Thus, zero growth isoclines can be derived directly from equation 10 (Fig. 4).

Discussion

In this study, the effect of *E. balteatus* larvae on aphid populations was estimated in field cages that provided foraging conditions similar to those in the

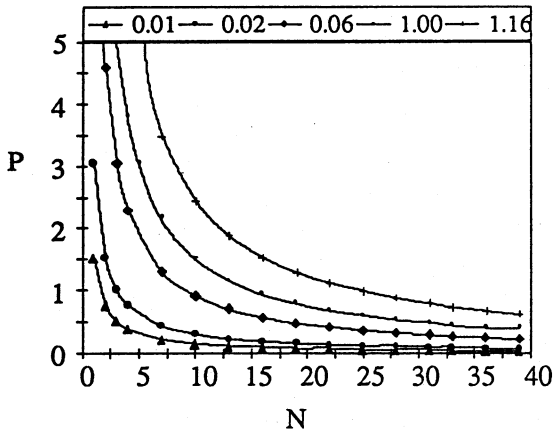


Fig. 4. N isoclines for different growth rates of aphid population r_N (N , P = density of aphids, predators).

field. Estimation was based on the Holling type-III function; thus, both satiation of the predators as well as the time for handling and for locating the prey were taken into account. In contrast to the Holling type-II function, the logistic shape of the Holling type-III function also reflects the accelerating voracity of syrphid larvae at low aphid density as a result of the clumped distribution of aphids.

The feeding rate of syrphid larvae was calculated for the first 6 d after release of 4-d-old larvae. During the first 4 d and the last 1 or 2 d of larval development, the food demand of the predators is negligible (Tenhumberg 1992). The first larvae pupated 7 d after release. Thus, their prey intake was concentrated in the observation period of 6 days. Therefore, a single predator consumed a maximum of 396 aphids during its larval development, which is only half of the mean potential voracity given in the literature. Thus, estimating predatory efficiency of syrphid larvae on the basis of their potential voracity may lead to an overestimation of their actual impact on the pest in the field.

Apart from the maximum feeding rate, the flat shape of the Holling type-III function in Fig. 2 suggests that the adaptation of the predators' consumption rate to varying food supplies holds for a relatively wide range of aphid abundance. This is important for controlling pest populations because it indicates that syrphid larvae will respond immediately to changing aphid abundance (e.g., to increasing aphid reproduction as a result of improved environmental conditions).

However, the predation efficiency of syrphid larvae is highly dependent on the growth rate of pest populations. As shown in Fig. 1, a given predator-prey ratio representing the predation pressure at a certain time is unsuitable to predict the decrease of the aphid population. To estimate syrphid impact, the ratio between the net increase of aphid populations and the number of aphids consumed per time interval has to be taken into account

(Bombosch 1963). My study utilized a general predator-prey model where the development of aphid populations was described by the Verhulst-function and syrphid voracity by the Holling type-III function. With this model the numbers of syrphid larvae necessary to prevent a further increase of aphid populations at different aphid densities and growth rates could be determined. Two rules for stability in this system could be derived from the isoclines: (1) Syrphid density required to prevent a further increase of aphid abundance rises with improved developmental conditions for the pest and the resulting increase of their growth rate; (2) The predation efficiency decreases with decreasing aphid infestation as a result of increased search time. At higher aphid abundances, the predators are able to adapt their feeding rate to the actual supply of resources. Therefore, the density of syrphid larvae needed to prevent net population growth of the pest remains at a low level.

This model has been developed assuming low-aphid abundances. It is likely that at high-pest abundances the density of predators needed to produce stability will increase. As the pest population approaches its maximum value (\bar{z}), the rate of population growth decreases and the syrphid density required to produce stability will decrease.

If a pest growth rate of 1.16, as recorded in the control cage, is taken as a basis, then the predator density required to keep the pest below 10 individuals per shoot (economic injury level) is 2.4 larvae. However, the natural abundance of syrphid larvae is normally <0.4 individuals per shoot (Adams 1984, Groeger 1992, Tenhumberg 1992). In the field, interactions with other restricting factors will lead to a lower pest growth rate. During field research conducted simultaneously in winter wheat, mean r_N values that were an order of magnitude lower than recorded in the field cages (0.03–0.015) were observed before immigration of syrphid females in areas without insecticide application (Tenhumberg 1992). Using $r_N = 0.02$, 0.3 syrphid larvae per shoot are necessary to prevent an increase of aphid populations to >10 individuals per shoot. Although syrphid larvae frequently reach the required abundance in the field, the model needs to be validated under natural conditions.

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