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ANNALES ZOOLOGICI

Tom 35 Warszawa, 29 II 1980 Nr 10

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The influence of food density and the size of food rations on the consumption and development of aphidophagous *Syrphidae* (*Diptera*)

[With 1 figure and 6 tables]

INTRODUCTION

Investigations on the quantitative food demand of insects have been the subject of many studies carried out within the International Biological Programme. A large majority of the studies was concerned with phytophagous insects, mostly those economically important. Less attention was devoted to consumers of the second order, i.e. to predaceous and parasitic insects, important due to their relations to the group of phytophages.

The Hover Flies — *Syrphidae*, as one of the most important groups of oligophagous aphidophages, have not so far been the subject of such studies. Data on the efficiency of the influence of a predator on a population of its prey at different stages of its abundance structure may be provided by the food demand of a predator, depending on prey density, expressed in specific numerical values. In the literature (HÄGVAR 1972, BRAUNS 1953, BOMBOSCH 1964) references on the voracity of *Syrphidae* larvae are not complete because they refer to a certain stage of the larval development only. Nevertheless they point out a considerable efficiency of that group of the *Diptera* in the reduction of aphids. In this respect however flies equal the *Coccinellidae*.

The present paper is dedicated to the estimation of the food demand of the aphidophagous larvae of two *Syrphidae* species common in Poland: *Sphaerophoria scripta* (L.) and *Melanostoma mellinum* (L.). It also presents data on the influence of the quantity and density of food on the development and consumption of these *Syrphidae*. These data are a contribution to a study of the economical value of *Syrphidae* in limiting the abundance of the pea aphid,

Acyrthosiphon pisum (HARRIS) – a pest of alfalfa cultures. *Coccinellidae*, *Chrysopidae*, *Syrphidae* and *Thrombidiidae* (*Acarina*, WENGRIS 1968) are, among others, the natural enemies of aphids. Investigations on the reduction of aphid abundance by its predators are mainly concerned with *Coccinellidae* and *Chrysopidae* (BÄNSCH 1954, BLACKMAN 1967, SUNDBY 1967). The *Syrphidae* are, most often, the subject of biology and insect ecology studies (BRAUNS 1953, BÄNSCH 1954) and papers discussing the consumption of this group present estimated values (WENGRIS 1968, LAŠKA 1959) on the influence of artificial nourishment on the development of *Syrphidae* (GLUMAC, HARTOVIĆ 1972). Detailed data on aphid consumption by *Sphaerophoria scutellaris* (F.) (an oriental species) are given in the study of LAL and HAQUE (1955) where they are discussed with temperature and humidity taken into consideration. It appears from literature data that the consumption of one aphidophagous *Syrphidae* larva is from 400–2000 aphids during its development (LAŠKA 1959, LAL and HAQUE '1955, SUNDBY 1967). The differences between the numbers give rise to doubts, especially if the theory of constant amount of food taken during the development is taken into account. These data require to be checked.

METHODS AND MATERIAL

The conditions of the investigation were close to the natural ones because the rearing vessels were placed under an umbrella roof. The material for the experiments – eggs of *Sphaerophoria scripta* and *Melanostoma mellinum* – was obtained from imagines collected in a field of alfalfa, *Medicago sativa* L. Fertilized females – their selecting was based on the size of their abdomen – were placed in glass rearing vessels of the capacity of 1 litre. In those vessels there were leaved alfalfa shoots, tampons with water for ensuring constant and high humidity, and honey thinly spread on the walls, which was food for adult insects. After 5–7 days from egg-laying, the hatching of larvae began. The larvae were immediately put into Petri dishes of 9 cm diameter. Both at the egg and larval stages the most important thing was to provide the insects with proper air humidity which prevented their drying out. Single individuals were kept in rearing vessels.

The food of *Syrphidae* larvae consisted of pea aphid from alfalfa cultures which, under the experiment conditions, fed on beans (*Vicia faba* var. *minor*). For providing a food basis there were series of cages with aphids each of which contained pots with beans. Only half-grown aphid females (nymphs) were chosen for feeding the larvae because that eliminated any possibility of aphid offspring appearing in the scales.

The proper experiment was begun when the larvae were 4 days old, because since their hatching all the individuals had been given the same amount of food – 2 aphids a day. Due to a low locomotive activity of larvae in the first days of life, conclusive results on the influence of different food rations on

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Table I. *Sphaerophoria scripta* –

	5			10			
	1	2	3	1	2	3	1
	4.2	4.5	4.0	7.9	8.1	8.1	11.
x	4.2			8.2			
a	0.110			0.175			
t_p	7.5						2.3

Table II. *Melanostoma mellinum*

	5			10			
	1	2	3	1	2	3	1
	4.7	4.2	5.0	9.7	8.6	8.8	12.
x	4.7			9.0			
a	0.215			0.345			
t_p	5.4						2.5

the extent of their consumption could only be obtained for larvae with full locomotive ability.

There were carried out 48 experiments comprising the whole larval development of the studied predators in the following food variants: 5, 10, 15, 20, 30, 40, 60 aphids per day per individual with three and in the case of the last variant with six repetitions. The larvae were fed once in 24 hours and at the same time the water content humidity in the scales. The obtained data were studied both in the respect of the size of daily food rations and the sums for the whole larval development, using the means from each experimental variant.

RESULTS

The total amount of food taken by a larva throughout its development depends on the size of its daily consumption on the one hand and the length of its development on the other. When a negative correlation occurs between these two values, the accumulated consumption should be the same for the whole larval development irrespective of different food variants of an experiment. The obtained results reveal statistically important differences in the total consumption (Table I, II). In accordance with the assumptions of the

Table I. *Sphaerophoria scripta* — value (t_p) for *t*-Student of a amount of freedom $a = 4$; $t_p = 90\% - 1.53$.

	5			10			15			20			30			40			60		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	4.2	4.5	4.0	7.9	8.1	8.1	11.0	10.3	9.5	16.8	17.4	16.4	20.7	19.5	18.1	23.7	24.7	25.5	29.7	30.9	25.8
x	4.2			8.2			10.2			16.8			19.4			24.5			28.8		
a	0.110			0.175			0.570			0.260			1.490			0.785			7.110		
t_p	7.5			2.3			7.4			2.0			3.4			3.5					

Table II. *Melanostoma mellinum* — value (t_p) for *t*-Student of a amount of freedom $a = 4$; $t_p = 90\% - 2.13$.

	5			10			15			20			30			40			50		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	4.7	4.2	5.0	9.7	8.6	8.8	12.3	11.5	10.8	17.0	16.4	16.9	20.7	20.1	19.0	28.6	29.0	28.3	28.2	31.2	34.6
x	4.7			9.0			11.5			16.8			19.9			28.6			30.8		
a	0.215			0.345			0.565			0.105			0.745			0.125			5.080		
t_p	5.4			2.5			5.4			3.6			9.6			0.9					

experiment the size of a given food ration is the basic modifying factor, though the influence of other factors (abiotic and biotic) has not been completely eliminated. The abundance and density of the available food distinctly influences the length of the development of larvae — the greater amount of food the shorter the development. However, the changes in the rate of the development are not proportional to the changes in the size of the consumption and the final result given as a sum of taken food is different.

1. THE INFLUENCE OF THE SIZE OF A FOOD RATION ON THE DAILY CONSUMPTION

The daily value of consumption is a function of age and increases with the development of individuals (Tables III, IV). This dependence occurred in all the variants of the experiment. The value of the day and night consumption of one *S. scripta* larva was between 4.3 aphids for a larva on the fifth day of its development with the ration of 5 aphids a day and 43.8 with the ration of 60 aphids a day. The mean values of the consumption of one *M. mellinum* larva, depending on a studied experimental variant, were 3.0–40.6 aphids for an individual a day. The ration of 5 aphids a day was a starvation ration which caused the dying out of the larvae. Changes in the day and night consumption during the development of a larva demonstrated differences depending on the size of a given food ration. With low food rations, i.e. 5, 10, 15, 20 aphids

Table III. Mean day and night consumption of the *Sphaerophoria scripta* larvae.

Days of development	Size of a food ration (individual) development						
	5	10	15	20	30	40	60
1	4.3	7.3	8.6	13.6	12.3	16.0	19.1
2	4.6	8.3	8.6	15.3	12.0	20.3	21.0
3	4.6	9.0	9.6	18.0	13.6	25.6	25.0
4	3.3	7.3	9.6	18.6	18.6	26.0	28.1
5	4.6	8.0	12.0	19.3	22.0	24.3	43.8
6	4.6	8.6	13.3	19.0	25.6	32.3	29.1
7	5.0	9.0	14.6	18.6	28.0	27.3	
8	5.0	9.6	8.0	16.6	22.6	24.6	
9	5.0	7.6	3.6	14.3	18.3		
10	1.0	9.3					
11		7.6					

death

Table IV. Mean day and

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per individual a day there remain at a fairly constar per individual a day the d 13th days of the developm or 60 aphids per individua during the development o food ration. The above de on the amount of given f last days of the developm the approaching pupa stag of the increase of the dail occurred more often a sma situation also occurred in *M. mellinum*, where the ge

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40	60
16.0	19.1
20.3	21.0
25.0	25.0
26.0	28.1
24.3	43.8
32.3	29.1
27.3	
24.6	

Table IV. Mean day and night consumption of the *Melanostoma mellinum* larvae.

Days of development	Size of a food ration (individual) development						
	5	10	15	20	30	40	60
1	3.6	6.0	8.3	13.3	9.3	21.0	21.0
2	4.3	7.1	9.0	15.0	10.0	23.3	23.8
3	5.0	8.0	10.6	16.0	15.3	24.0	27.8
4	5.0	8.6	12.6	17.6	22.3	25.0	33.3
5	3.0	9.0	11.6	19.0	26.0	26.3	40.6
6	5.0	8.3	12.3	20.0	26.0	30.3	39.4
7	5.0	9.3	13.0	18.6	27.0	39.0	35.5
8	death	9.0	14.6	17.3	27.6	32.3	
9		9.3	13.3	15.6	15.3		
10		10.0	14.3				
11		9.6	6.0				
12		10.0					
13		10.0					

per individual a day there occurred a tendency for the daily consumption to remain at a fairly constant level, for instance, with the ration of 10 aphids per individual a day the daily consumption was identical on the 5th, 8th and 13th days of the development (Table IV). With higher food rations — 30, 40, or 60 aphids per individual a day — the daily consumption distinctly increased during the development of the larvae, the more rapidly the higher was the food ration. The above described pattern of the daily consumption depending on the amount of given food was broken in all the experiments during the last days of the development, when the consumption value decreased due to the approaching pupa stage. It seems that the departures from the principle of the increase of the daily consumption conditioned by the age of a larva occurred more often a smaller probability of a larva meeting a prey. A similar situation also occurred in the case of the second of the studied species — *M. mellinum*, where the general pattern of the phenomenon was very similar.

2. THE ACCUMULATED CONSUMPTION OF LARVAE WITH A DIFFERENTIATED FOOD RATION

A complete larval development of the two species occurred only when the food ration was higher than 5 aphids per individual a day. The pattern of the dependence between the size of the given food ration and the accumulated

consumption was similar for the two species and, therefore, the analysis of th problem refers to both.

The total amount of food taken by *S. scripta* was between 91.6 and 185. aphids per individual throughout the development and by *M. mellinum* fro 114.2 to 222.8 aphids per individual throughout the development (Tables V, VI In both cases the value of the cumulated consumption increased along wit an increasing food ration starting with 10 and up to 40 aphids per individua

Table V. *Spherophoria scripta.*

Size of a food ration (number of aphids per individual per day)	Length of larval development (days)	Quantity of available food per individual per development	Number of eaten aphids per individual per development	Utilization of food (%)
5	4+ 10	8+ 50	42.0	84.0
10	4+ 11	8+ 110	91.6	83.5
15	4+ 10	8+ 150	96.5	64.3
20	4+ 9	8+ 180	151.3	84.0
30	4+ 9	8+ 270	173.3	64.1
40	4+ 8	8+ 320	185.8	58.0
60	4+ 6	8+ 360	160.9	44.2

Table VI. *Spherophoria mellinum.*

Size of a food ration (number of aphids per individual per day)	Length of larval development (days)	Quantity of available food per individual per development	Number of eaten aphids per individual per development	Utilization of food (%)
5	4+ 7	8+ 35	30.9	88.1
10	4+ 13	8+ 130	114.2	87.5
15	4+ 11	8+ 165	125.6	76.1
20	4+ 9	8+ 180	152.4	84.6
30	4+ 9	8+ 270	177.9	65.8
40	4+ 8	8+ 320	221.2	69.1
60	4+ 7	8+ 420	222.8	53.0

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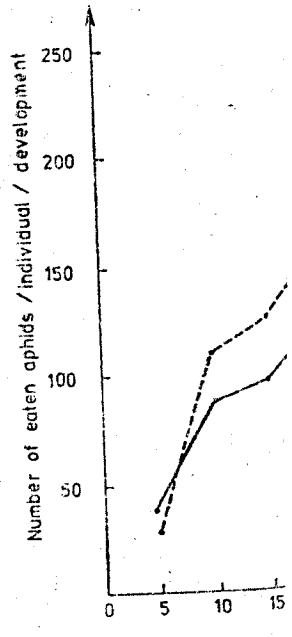

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0	84.0
6	83.5
5	64.3
3	84.0
3	64.1
8	58.0
9	44.2

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ber of en s per idual leve- ment	Utilization of food (%)
0.9	88.1
4.2	87.5
5.6	76.1
2.4	84.6
7.9	65.8
1.2	69.1
2.8	53.0

a day. With a ration of 60 aphids a day there occurred, in comparison with a ration of 40 aphids a day, a decrease in the amount of food taken by *S. scripta* larvae. In the case of *M. mellinum* the value of the summed up consumption did not change after exceeding the food ration of 40 aphids a day. However, the differentiation of the absolute values of the amount of food taken by the larvae of both species should be noted. In each variant of the food rations *Melanostoma* took more food than *Sphaerophoria* larvae (Fig. 1). The value of food ration, forming the extent of consumption, influenced the degree of utilizing the available food. This problem was in the first place connected with the density of the prey population within the area penetrated by the predator larvae. The utilization of the available food was usually higher with smaller food rations. In the case of *Sphaerophoria scripta* that value for food rations of 10–20 aphids a day was 77.6 % on the average. In the case of *M. mellinum* the respective value was 89.4 % (Table VI). It should be noted that when a ration was not big enough for the surviving of the larvae — 5 aphids a day — that food was not completely utilized either. The food which was not utilized should be considered as that part of food which was not available, in spite of the theoretical assumptions, to the larvae due to a small probability of its being found by the insects. With a higher daily food ration, which also meant a higher prey density, in spite of an increase of the absolute value of the consumption the degree of the food utilization by the predaceous larvae decreased. Thus, within the food by the *S. scripta* larvae decreased from 61.0 % to 44.2 % when the food density increased, and by *M. mellinum* from 65.8 % to 53 %. The

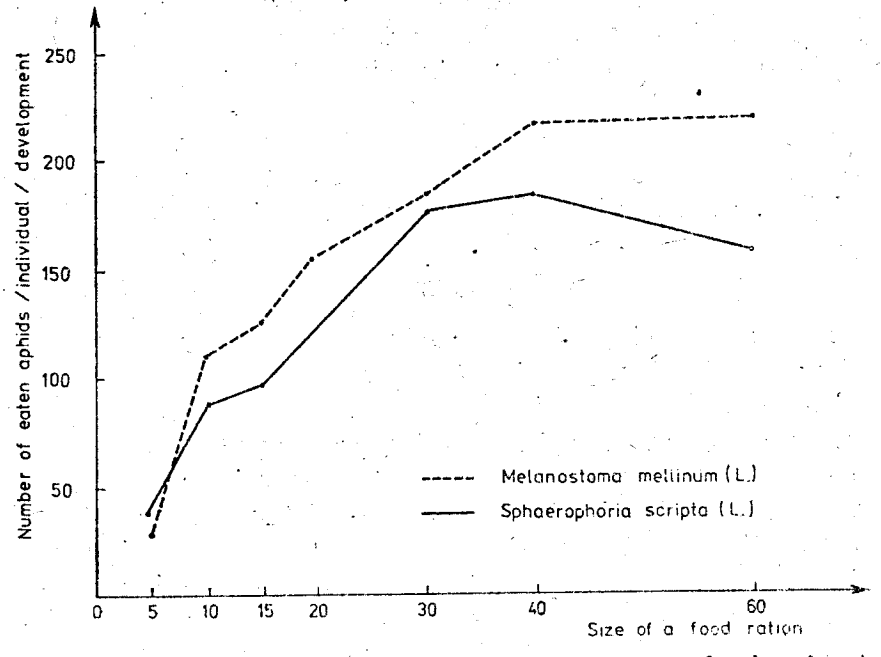

Fig. 1. Dependence of the consumption of the *Syrphidae* larvae on the size of a given food ration.

most distinct decrease in the utilization of the available food ration was 60 aphids per individual a day. These data were compared to the decrease of the consumption of *S. scripta* when the food ration was the same. The result of this was the basis for stating that the food optimum for the conditions in the experiment had occurred when the density of prey had been 40 aphids per dish. After exceeding this number, the efficiency of the larvae predacity decreased considerably. For a full justification of the optimum value of a food ration there should be taken into consideration, besides the efficiency of the food utilization and the value of the cumulated consumption, a number of other parameters.

THE INFLUENCE OF THE SIZE OF A FOOD RATION ON THE LENGTH OF THE LARVAL DEVELOPMENT

The length of the development of the *S. scripta* larvae was, depending on the size of a given ration, from 6 to 11 days and that of the *M. mellinum* larvae from 7 to 13 days. The obtained results point out to a shortening of the length of the development as the day food ration increased (Tables III, IV). A negative correlation between the daily food ration and the length of the development in the analysis of food rations of 10–60 aphids per individual a day was not valid only within the values of 20–30 aphids per individual a day. In that case the longevity of larvae did not change, irrespective of the density of the prey. With the food ration of 60 aphids a day the length of the development was shorter than with smaller food rations in spite of a decrease in the total value of *S. scripta* consumption of the *M. mellinum* larvae remaining at the same level. It seems that with a higher food density there occurred smaller energetic losses connected with its obtaining which allowed for a successful completion of the development with lower demand for food. The average length of the larval development which was 8.8 days for *S. scripta* and 9.5 days for *M. mellinum* does not demonstrate any significant difference for those conditions of the experiment which were taken into consideration (8 % of difference).

DISCUSSION

The problem of the intensity of an aphid population reduction by predators has most frequently been considered as a function of their abundance. The results of the present paper point out to significant dependences between the reduction efficiency and the density of a prey population. It appears that with a constant abundance of a predator the reduction of aphid numbers is higher with an increasing density of a prey population. In spite of considerable food surplus when the density of prey is high the total number of devoured aphids is higher. Natural regulatory mechanisms functioning in biocoenoses cause an increase in the reduction efficiency with an increase in the density of reduced organisms. It must also be pointed out that with a certain density

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of prey the predator accomplishes its development best, thus gaining a shorter length of its duration with a lower death rate and even, as the results of the experiment suggest, with a lower expenditure of energy. It seems in the light of the obtained results that it is not possible to determine the best prey density for a predator population. It might appear that a ration of 40 aphids a day, when the consumption reaches its maximum, is the density most favourable for the predator. However, an increase in the prey density ensures an equally favourable development even during a shorter period of time and in spite of the amount of taken food. It follows from the analysis of the results determining the extent of the total consumption for the larval development that a different degree of the density of a prey population has a significant influence on the formation of one of the most important parameters of the energetic budget which is the consumption value. The intensity of predation is therefore proportional to the density of a prey population and, in spite of a lower food utilization with high density, the general effect of predation, in the case of several generations of predator occurring in one season, is higher than with the "best" density. Along with an increase of the size of an available daily food ration, the value of the total consumption increases to a certain limit (density of food — 40 aphids per dish), and the length of the larval development, in the gradient taken into consideration, decreases. It is difficult to foresee how a development accomplished with a lower amount of food will be reflected later in a population of a predator, i. e. how it influences the survival rate at succesive developmental stages, general vitality, fertility, etc. These questions may be the subject of investigations within the range of the problem studied in this paper. It is possible, however, to state that the shorter the length of the development the smaller the probability of death due to predacity or parasitism.

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STRESZCZENIE

[Tytuł: Wpływ zagęszczenia pokarmu i wielkości racji pokarmowej na konsumpcję i rozwój afidofagicznych *Syrphidae* (*Diptera*)]

Badano redukcję mszycy grochowej, *Acyrthosiphon pisum* (HARR.), przez drapieżne larwy *Sphaerophoria scripta* (L.) i *Melanostoma mellinum* (L.) w warunkach hodowli doświadczalnej. Skumulowana konsumpcja larw *M. mellinum* jest wyższa niż odpowiednia wielkość konsumpcji *S. scripta*. Wykazano wpływ wielkości zagęszczenia i racji pokarmowej na długość trwania rozwoju larwalnego. Zwiększenie zagęszczenia pokarmu i wielkość racji pokarmowej skracają ten rozwój. Stopień wykorzystania dostępnego pokarmu maleje wraz ze wzrostem zagęszczenia ofiary. Dobowa racja pokarmowa o ilości 5 mszyc na dobę na osobnika jest racją głodową, powodującą śmierć zwierzęcia.

РЕЗЮМЕ

[Заглавие: Влияние обилия корма и величины рациона на потребление пищи и развитие афидофагических *Syrphidae* (*Diptera*)]

Автор исследовала редукцирование гороховой тли *Acyrthosiphon pisum* HARR. хищными личинками *Sphaerophoria scripta* (L.) и *Melanostoma mellium* (L.) в условиях экспериментального разведения. У личинок *M. mellium* общее потребление выше чем у личинок *S. scripta*. Констатировано, что обилие корма и величина рациона влияют на длительность личиночной стадии. Повышение обилия (плотности) корма и величины рациона ведет к укорочению периода личиночного развития. Степен