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RÉSUMÉ

*Étude de la biologie d'*Aphidius rhopalosiphi *(Hymenoptera: Aphidiidae), parasitoide de pucerons des céréales*

Nous avons examiné quelques aspects des relations entre le parasitoïde *Aphidius rhopalosiphi* et son hôte *Sitobion avenae*. La fécondité potentielle à l'émergence (144 œufs) était inférieure à la fécondité "réalisée": nombre de pucerons momifiés (212). La plupart des œufs étaient pondus dans la première semaine de la vie imaginale (fig. 1). Le super-parasitisme s'est produit dans les conditions expérimentales, mais la distribution des larves (fig. 2) s'écartait souvent de la distribution au hasard, ce qui indiquait une certaine discrimination parmi les hôtes.

La longévité moyenne était de 13,1 jours et le maximum de 23 jours. Le taux sexuel (fig. 3) pour l'ensemble de la descendance était 1/1, mais changeait dans le temps. Après le premier jour de ponte, plus de femelles que de mâles étaient obtenues; mais après 6 jours, il n'y avait presque plus que des mâles.

Le taux de rencontre des aphides et des parasitoïdes augmentait avec la taille (fig. 4a). Le temps de prospection de l'hôte était en moyenne de 2 secondes, mais dans certains cas il atteignait 10 secondes ou plus. La proportion de rencontres efficaces était plus faible au 4ème stade (fig. 4b). Il n'y avait pas de différence significative dans le nombre de larves de parasitoïdes obtenues par rencontre pendant les stades 1 à 3 des pucerons, mais elle était significativement inférieure au 4ème stade par rapport au second. Les taux globaux de succès (taux de rencontre et nombre de larves formées par rencontre) étaient plus élevés aux 2ème et 3ème stades des pucerons. La réponse fonctionnelle était sigmoïde (fig. 5).

REFERENCES

Carter, N., McLean, I. F. G., Watt, A. D. & Dixon, A. F. G. (1980). Cereal aphids — a case study and review. *Applied biology,* 5: 271—348.

Dransfield, R. D. (1979). Aspects of host-parasitoid interactions of two aphid parasitoids, *Aphidius urticae* (Haliday) and *Aphidius uzbekistanicus* (Luzhetski) (Hymenoptera: Aphidiidae). *Ecol. Ent.* 4: 307—316.

Edwards, C. A., Sunderland, K. D. & George, K. S. (1979). Studies on polyphagous predators of cereal aphids. *J. appl. Ecol.* 16: 811—823.

't Hart, J., de Jonge, J., Collé, C., Dicke, M., van Lenteren, J. C. & Ramakers, P. M. J. (1978). Host selection, host discrimination and functional response of *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae), a parasite of the green peach aphid, *Myzus persicae* (Sulz.). *Med. Fac. Landbouww. Rijksuniv. Gent* 43: 441—453.

Hassell, M. P., Lawton, J. H. & Beddington, J. R. (1977). Sigmoid functional response by invertebrate predators and parasitoids. *J. anim. Ecol.* 46: 249—262.

Holling, C. S. (1959). The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Can. Ent.* 91: 293—320.

Jones, M. G. (1972). Cereal aphids: their parasites and predators caught in cages over oat and winter wheat crops. *Ann. appl. Biol.* 72: 13—25.

Lenteren, J. C. van. (1976). The development of host discrimination and the prevention of superparasitism in the parasite *Pseudeucoila bochei* (Hymenoptera: Cynipidae). *Neth. J. Zool.* 26: 1—83.

Lenteren, J. C. van & Bakker, K. (1976). Functional responses in invertebrates. *Neth. J. Zool.* 26: 562—572.

MacKauer, M. & van den Bosch, R. (1973). General applicability of evaluation results. *J. appl. Ecol.* 10: 330—335.

McLean, I. F. G. (1980). Ecology of the Natural Enemies of Cereal Aphids. Unpubl. Ph. D. Thesis, University of East Anglia, Norwich, England.

Rabbinge, R., Ankersmit, G. W. & Pak, G. A. (1979). Epidemiology and simulation of population development of *Sitobion avenae* in winter wheat. *Neth. J. Pl. Path.* 85: 197—220.

Rautapää, J. (1972). The importance of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in controlling cereal aphids, and effect of aphids on the yield and quality of barley. *Ann. Agric. Fenn.* 11: 424—436.

—— (1975). Control of *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) with *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae) in cages and effect of late aphid infestation on barley yield. *Ann. Agric. Fenn.* 14: 231—239.

Starý, P. (1962). Hymenopterous parasites of the pea aphid *Acyrthosiphon onobrychis* (Boyes) in Czechoslovakia. I. Bionomics and ecology of *Aphidius ervi* (Haliday). *Folia Zoologica, Brno,* 11: 265—278.

—— (1972). *Aphidius uzbekistanicus* (Luzhetzki) Hymenoptera: Aphidiidae), a parasite of graminicolous pest aphids. *Ann. Zool. Bot.* 85: 1—7.

Wiackowski, S. K. (1962). Studies on the biology and ecology of *Aphidius smithi* Sharma & Subba Rao (Hymenoptera: Braconidae), a parasite of the pea aphid *Acyrthosiphon pisum* (Harr.) Homoptera: Aphididae). *Bull. Ent. Pologne* 32: 253—310.

BIOLOGY OF *APHIDIUS RHOPALOSIPHI*, A PARASITOID OF CEREAL APHIDS

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Aphidius rhopalosiphi produced 212 offspring on average but in one case 509 deposited eggs were found. Superparasitization occurred but the frequency distribution of parasitoid larvae in aphids differed significantly from random, indicating a certain degree of host discrimination. Average life span of adults was 13.1 days and sex ratio was 1 : 1. It changed in time among successively produced offspring.

Handling time was about 2 sec and was somewhat longer in the fourth instar than in the second. Second and third aphid instars were preferred for oviposition. Functional response was sigmoid and at an aphid density of 100 aphids per cage percentage parasitization decreased.

KEY WORDS: Hymenoptera — Aphidiidae — Aphidius rhopalosiphi — Sitobion avenae — Functional response.

Several aphid species attack cereals in Western Europe but *Sitobion avenae* F. and *Metopolophium dirhodum* Wlk. are the dominant ones (Rabbinge *et al.,* 1979; Carter *et al.,* 1980). Both species are attacked by a large number of predator and parasitoid species but relatively little is known of their bionomics. It has been suggested, however, that these enemies exert a significant delaying effect on aphid population development (Edwards *et al.,* 1979; Jones, 1972; Rautapää, 1972, 1975). The lack of information concerning natural enemies has also caused problems in developing simulation models to predict aphid population build-up with a view to forecasting outbreaks.

An intensive laboratory study was undertaken on one parasitoid species, *Aphidius rhopalosiphi* De Stephanie-Perez, with *S. avenae* as the host, to provide information to assess its importance in aphid population and for use in simulation models.

Although the species composition of parasitoids changes from year to year, *A. rhopalosiphi* is usually one of the commonest species (McLean, 1980) in Western Europe. The study looked at several aspects of the adult female parasitoids biology; fecundity, longevity, host selection and functional response.

MATERIALS AND METHODS

Standardization of adult parasitoids. The biology of a parasitoid depends on many factors — age, body size, initial number of eggs in the ovaries, etc. — so all the experiments were carried out with standardized parasitoids. They were cultured in the following way: groups of two to three adult aphids (green colour form) (from a greenhouse mass culture, kept at approx. 18°, 70% r.h. and 18 hr light) were placed in small plastic cages (3 × 3 × 10 cm), each enclosing one winter wheat seedling leaf (cv. Arminda), for 2—3 days in a constant temperature room (used in all the experiments to follow — kept at 18°, 75% r.h. and 18 hr light). After this period the adult aphids were removed and one female and one or two male parasitoids (also from a greenhouse culture kept under the same conditions as the aphid culture) were introduced into a cage for 24 hr. After 10—12 days, any mummies (parasitized aphids) which had been produced were put, separately, into either glass tubes (1.5 cm diameter and 5.0 cm high) or small gelatine capsules, together with a piece of leaf. These mummies were checked daily until the parasitoids emerged. Thus parasitoids of known age and history were produced in sufficient numbers for the experiments.

Fecundity, longevity and sex ratio. Forty 2—3

day old aphids (first to second instar) were placed on a seedling (fifth leaf stage, each leaf measuring about 0.5 cm wide by 10.0 cm long) in a cylindrical plastic cage (11 cm diameter and 62 cm high, with six circular gauze windows, 8 cm diameter) and then left for at least one day.

Then one mated female parasitoid was introduced into the cage. After 24 hr the parasitoid was transferred to a fresh seedling in another cage, also with 40 aphids. This process was repeated daily until the parasitoid died. The parasitoids were fed with honey on glass slides placed in the cages every day. In total 17 specimens (six newly emerged, three 1 day old, four 2 days old and four 3 days old females) were used in these tests. At least 10 of the 40 aphids were dissected 5 days after parasitization to determine the degree of superparasitization. Realized fecundity was determined by adding to the number of mummies found per parasitoid, the numbers of dissected aphids with at least one larva of the parasitoid. All the hosts from one replicate were dissected to find the total number of eggs laid by that parasitoid. Longevity and sex ratio (of the adults emerging from the mummies) could also be determined.

To obtain an estimate of the potential fecundity, 18 standardized parasitoids were dissected soon after emergence and before egg laying to count the initial number of eggs present in the ovaries.

Host selection and handling time. Prior to the experiment on host selection and handling time the parasitoids went through a procedure to gain experience in handling aphids. On the day of emergence ♀ parasitoids were mated with ♂♂ and then left for 2—3 hr with a mixture of aphid instars in a small glass tube. The ♀ parasitoids were then left overnight with no aphids but were fed with honey and water (Van Lenteren, 1976). As these parasitoids had been deprived of hosts they quickly started searching for aphids when they were introduced into the experimental arena.

The parasitoids were given a choice between 2—3 day old (second instar) and 7—8 day old (fourth instar) aphids or 1—2 day old (first instar) and 5—6 day old (third instar) aphids. Ten aphids from each instar were weighed before each experiment. Four nymphs of each instar to be tested were placed onto eight seedling leaves stuck to the bottom of a glass Petri

dish (18.6 cm in diameter). This was placed 25 cm over a light-box in a blacked-out cubicle. This design encouraged the parasitoids to search on the bottom of the dish as they are attracted to light. Once the eight aphids had settled the parasitoid was introduced and the moment it started searching was noted. Every encounter, a clearly visible contact of the parasitoid's antennae with an aphid, was timed, classified by instar and noted, together with information on whether the parasitoid appeared to oviposit or not. If an aphid was attacked it was replaced with a similar aphid, thus keeping the aphid density and instar composition constant. When ten aphids of the least favoured instar had been attacked the observations were stopped, the time noted and the parasitoid removed and weighed. The aphids were reared for 5—6 days and then dissected to determine the proportion parasitized.

Functional response. The functional response of the parasitoid was investigated using host densities of 5, 10, 20, 40 and 100 (2—3 day old aphids, first to second instar), seedling plants and plastic cylindrical cages similar to those used in the fecundity experiment. The aphids were carefully transferred to the leaves of the plant and allowed to settle. One day after, one mated female parasitoid (2—5 days old) was introduced and left with its hosts for 24 hr and then removed. The aphids were then reared on the plant until mummification. After 12 days any mummies which had been produced were counted. The numbers of replicates for densities 5, 10, 20, 40 and 100 were 50, 40, 20, 57 and 10 respectively.

RESULTS

Fecundity, longevity and sex ratio. The potential fecundity (number of eggs in the ovaries found by dissecting 18 parasitoids) was 144.3 ± 17.8 (mean ± s.e.) which is significantly less than the realized fecundity of 212.4 ± 69 found in 14 parasitoids (Table I) (t = 3.99, P < 0.001, d.f. = 30). Eggs were therefore still being matured during adult life.

Egg laying was most intensive during the first week or so of adult life but then declined rapidly such that it had all but stopped by the end of the second week (Fig. 1). The results of the parasitoid experiment, where all the aphids were dissected, indicate that 1.5 times the number of eggs were laid than the number of mummies suggested, which means a realized

aphid density (five) the average number of mummies produced was 1.7 (33% parasitization). Up to and including the aphid density of 20 the percentage parasitization declined while the number of mummies produced increased, although this result is not significant. The highest percentage parasitism of 64% was recorded at aphid density 40. At the highest aphid density (100) the average number of mummies produced was 46.7 but this represents a reduction in the percentage parasitization probably due to egg limitation (see fecundity experiment), or perhaps because disturbance from the parasitoid caused many of the aphids to drop from the plant which resulted in a low parasitization rate.

DISCUSSION

A. rhopalosiphi showed the typical characteristics of the genus: high fecundity (a realized fecundity of 212), moderate longevity (maximum longevity at 18° of 23 days), and a short handling time (about 2 sec). Other species which have been studied include *A. ervi* (Starý, 1962), *A. matricariae* ('t Hart *et al.*, 1978), *A. smithi* (Wiackowski, 1962; Mackauer & van den Bosch, 1973), and *A. uzbekistanicus* (Starý, 1972; Dransfield, 1979). Although there is some doubt it appears that they locate their hosts with their antennae and then oviposit very quickly. The ability to discriminate between parasitized and unparasitized hosts is present ('t Hart *et al.*, 1978), although Starý (1962) states superparasitism does take place but this might be due to the experimental set-up. *Aphidius* spp., in general, attack the younger instars, especially second and third instar. 't Hart *et al.* (1978), although finding no clear preference with *A. matricariae*, concluded that it would be preferable (for biological control) for *Aphidius* to parasitize small larvae because (1) the percentage of eggs resulting in adult parasitoids is higher if oviposition takes place in small larvae rather than in large larvae; (2) it takes less time to parasitize small than large larvae although this is likely to be unimportant as the time taken to parasitize large aphids is still short; (3) kicking of the aphids, especially the 4th instar larvae and adult aphids frightens the parasitoids.

The first reason is important to the survival of the parasitoid species while the third one is important for the control of the aphid population. It is not clear, however, from their description whether the lower percentage of

adult parasitoids emerging from larger aphids is a result of lower larval parasitoid survival or from a lower egg laying rate. In the present study the latter was more likely unless the mortality was occurring during the egg or early larval stage. Dransfield (1979) demonstrated that *A. uzbekistanicus* has a type 2 functional response when confined in a small cage (1656 cm³) for 24 hr. Van Lenteren & Bakker (1976) have shown that this experimental procedure invariably leads to a type 2 response because the parasitoid is prevented from leaving the cage. This results in repeated searches of the host location and eventually in the parasitization of nearly all the hosts. In the present study a larger cage (5890 cm³) was used and this probably resulted in fewer visits to the seedlings and hence the type 3 response was not obscured. Hassell *et al.* (1977) imply that invertebrate predators and parasitoids have type 3 responses caused by changes in the instantaneous attack rate 'a'. As prey or host density increases then 'a' increases and when this is incorporated in mathematical models sigmoid responses are generated. Verification of this relationship is however very difficult.

The biological characteristics of *A. rhopalosiphi* make it potentially an important regulating factor in cereal aphid population dynamics. Unfortunately, parasitoids are themselves parasitized by several hyperparasitoid species and these can be very numerous (Carter *et al.*, 1980; Rabbinge *et al.*, 1979). Indeed, Jones (1972) has argued that the aphid-parasitoid-hyperparasitoid interaction causes cyclic outbreaks of cereal aphids about once every 4 years. Although this interaction may be important it is unlikely to be the only factor influencing aphid outbreaks as during the late 1970's outbreaks occurred in 1975, 1976, 1977 and 1979 (Rabbinge *et al.*, 1979; Carter *et al.*, 1980).

handling times being about 2 sec. Apparently this short handling time is not a limiting factor in parasitizing. In most cases handling time is very short and the exceptional cases with longer handling times have a considerable effect on the average of 2 sec, which is nevertheless very short. Paired sample t-test and Wilcoxon signed-rank test show no significant difference between handling times of the parasitoid with first and third instar aphids (t = 0.04, n = 14, N.S.; T = 48.5, N.S.) but a significant difference between handling times with second and fourth instar aphids (t = 2.97, p = 0.01, n = 15; T = 11.5, P < 0.01, n = 14). It also encountered stronger defence mechanisms, especially kicking with the back legs, with the later instars, while the parasitoid had problems locating first instar aphids.

Aphid weight affected the proportion of successful encounters, which were high for the first three instars but dropped for the fourth (Fig. 4b). The difference between the number of resulting parasitoid larvae/encounter with aphid instars one and three is not significant (t = 0.78, d.f. = 6, N.S.; T = 10, N.S.) but with instars two and four it is (t = 3.35, d.f. = 8, p = 0.01; T = 3.5, P < 0.05). When the encounter rate and the number of resulting larvae/encounter were combined, an overall success rate was determined. For first instar aphids this was 0.08 ± 0.02, second instar 0.12 ± 0.02, third instar 0.15 ± 0.04 and for fourth instar 0.07 ± 0.02 resulting larvae/min, which suggests that A. rhopalosiphi "preferred" to lay eggs in second and third instar aphids but there is no significant difference between either pair of results. It is probable also that an unknown number of eggs or young larvae of the parasitoid did not survive to be recorded. Hence what was being measured was a combination of the egg laying success and survival of the young parasitoids.

Functional response. The shape of the parasitoid's functional response curve is the sigmoid type 3 (Holling, 1959) (Fig. 5). At the lowest
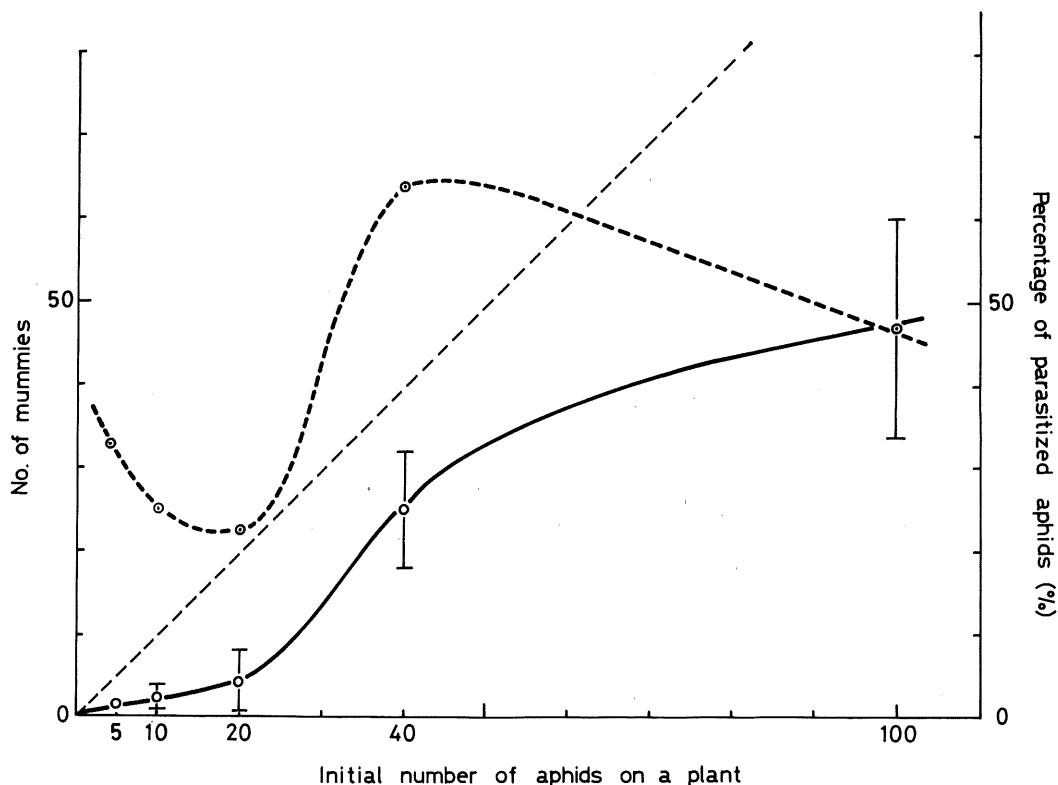

Fig. 5. The functional response of A. rhopalosiphi (solid line) and percentage of parasitized aphids (broken line) to changes in host density.

TABLE I

Realized fecundity of A. rhopalosiphi when offered 40 aphids per day

N (parasitoid)	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
1	29	26	37	31	33	27	13	21	23	7	8	14	14	2	0	D									289
2	3	32	32	20	30	29	12	11	23	7	7	15	19	1	1	0	4	3–D							218
3	17	14	16	28	22	28	24	23	22	3	7	22	13	10	13	0	0								265
4	11	16	23	29	27	24	13	13	9	D															176
5	27	27	18	1	0	5	25	1	0	5	2	2	0	0	0	D									91
6	27	5	9	0	D*																				41**
7	—	20	33	38	40	36	14	11	23	9	16	15	5	4	0	4	3	D							264
8	—	24	30	21	37	32	22	0	D	7	D	D													166
9	—	7	6	4	7	12	34	14	17	7	8	29	8	8	3	D	0	0	D						108
10	—	—	28	9	18	7	D	27	27	22	20	25	20	11	0	4	D	0					23		62**
11	—	—	2	5	24	35	34	27	27	22	8	D	15	8	0	0	0	0							184
12	—	—	25	34	30	33	33	12	33	8	20	29	8	11	3	4	0	D							264
13	—	—	35	38	40	34	23	23	24	20	22	25	15	11	0	D	D	6	D						333***
14	—	—	(101)	(59)	(56)	(51)	(58)	(31)	(39)	(31)	(25)	(27)	(19)	(12)	(0)										(509)
15	—	—	—	25	34	18	28	10	24	15	5	D	6	D											159
16	—	—	—	21	16	1	25	26	29	18	21	19	29	10	11	1	0	0							182
17	—	—	—	23	35	29	27	30	14	29	20	16	0												274
	—	—	—	0	0	D																			0**

Days after emergence

* 102 eggs remained in ovary. — ** Data omitted to calculate average realized fecundity. — *** All aphids dissected. Numerals in parentheses mean totals of parasitoid larvae found in the 40 aphids. — — No aphids offered, only honey and water. — —— Same aphids offered to parasitoid repeatedly. —
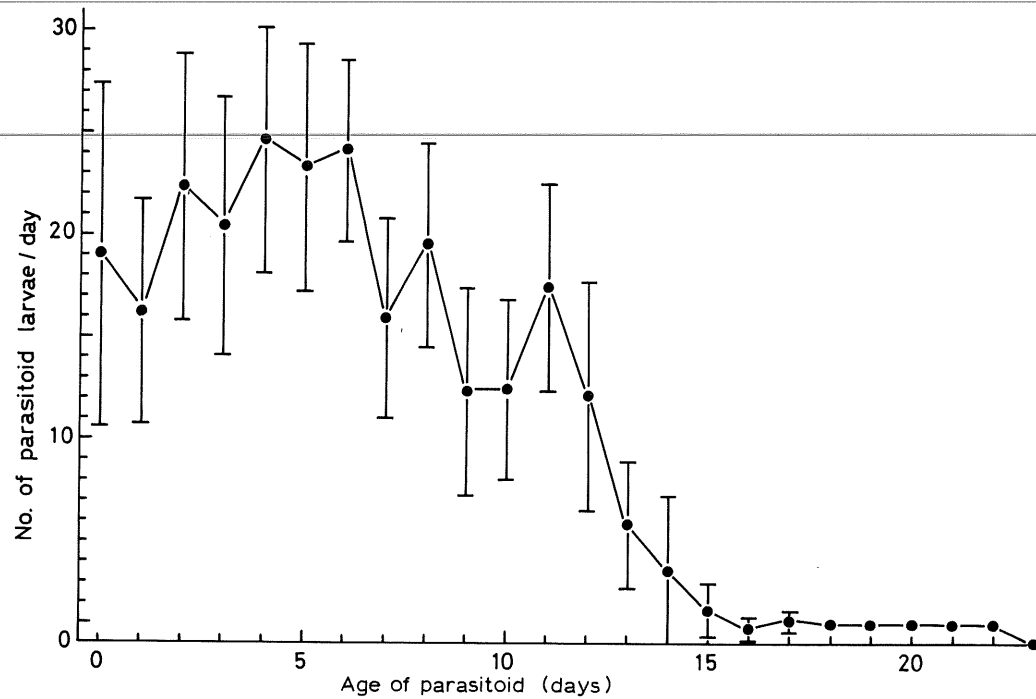D Death of the parasitoid.

Fig. 1. Daily realized reproduction of *A. rhopalosiphi* with 40 aphid nymphs as hosts ($\alpha = 0.05$ Con. Int.).
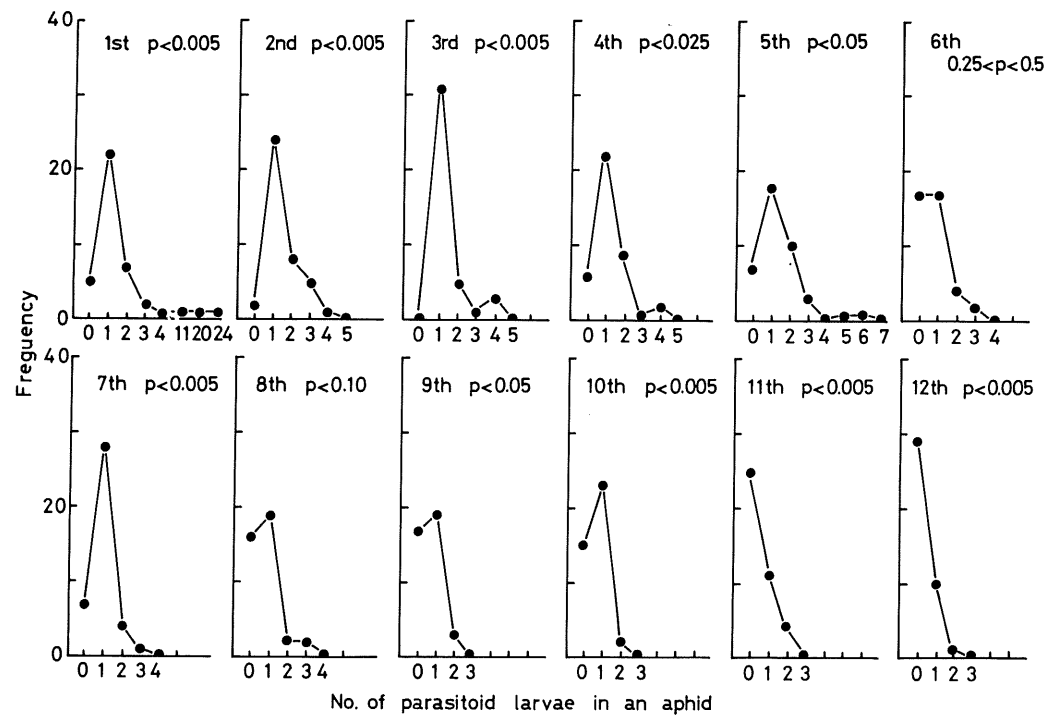

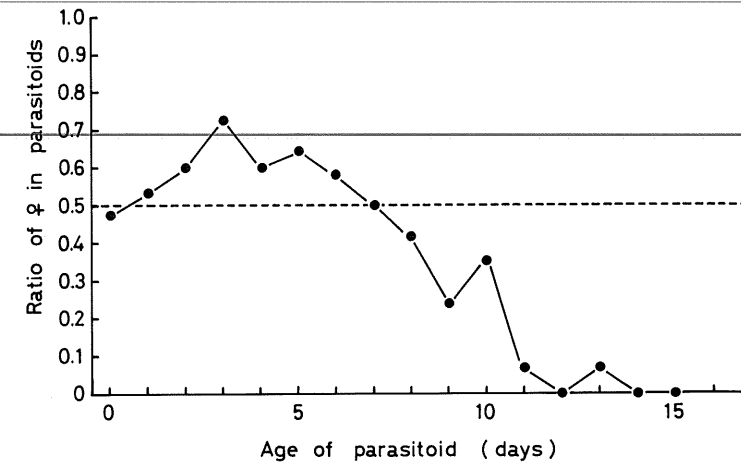Fig. 2. Frequency distribution of larvae of *A. rhopalosiphi* in aphids.

Fig. 3. Sex ratio of emerging *A. rhopalosiphi* as a factor of age of parent female.

fecundity of about 318 and not 212. Hence superparasitism occurred in this species under these experimental conditions. However, the frequency distribution of parasitoid larvae in aphids (Fig. 2) shows a significant difference (χ^2-test) from a random distribution on the 1st, 2nd, 3rd, 4th, 5th, 7th, 9th and 10th day. This is due to the observed high frequency of aphids with one parasitoid larva. These results show that the parasitoid had a partial tendency to avoid superparasitism.

The maximum longevity was 23 days while the average was 13.1 ± 1.3. Thus the average life span corresponded to the period of reproduction — i.e. the post-reproductive period was very short. The sex ratio shows a consistent trend among all the parasitoids tested (Fig. 3). For the first day the ratio was almost 1 : 1 but after this the proportion of ♀♀ was higher up to 6 days after emergence, after which the proportion of ♂♂ increased to 0.9 or more. The sex ratio of total offspring was 1 : 1.

Host selection and handling time. The encounter rate of aphids and parasitoids depended on the size (or age) of the aphid (Fig. 4a) — the larger the aphid the more frequently it was encountered — but not on the size of the parasitoid. The parasitoid took 1.6 ± 0.2 sec to handle second instar aphids but 2 sec or more to handle the other three nymphal instars (2.1 ± 0.3, 2.0 ± 0.2 and 2.3 ± 0.2 sec respectively). The distribution of handling times is skewed to the left because most encounters lasted for 1 sec or less but on several occasions longer handling times occurred (10 sec or

greater) as the parasitoid had problems in attacking the aphid. This resulted in the mean
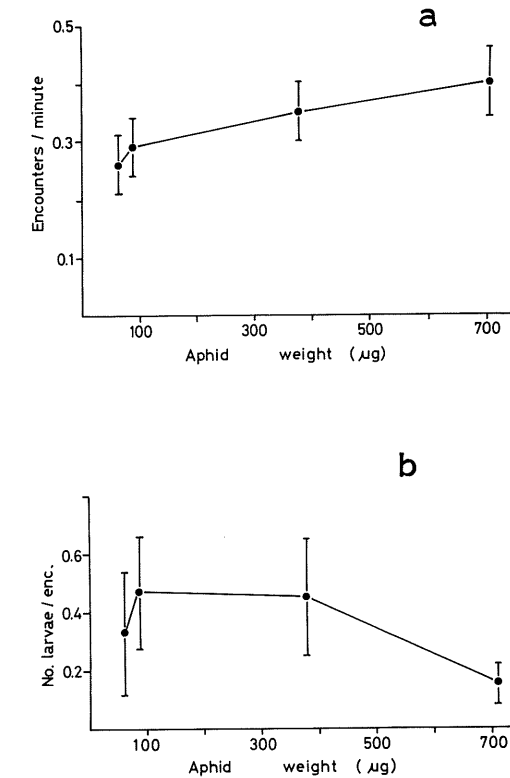

Fig. 4. (a) The effect of aphid weight on the encounter rate of *A. rhopalosiphi*. (b) The effect of aphid weight on the proportion of successful encounters of *A. rhopalosiphi* ($\alpha = 0.05$ Con. Int.).