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Factors Affecting the Potential Increase Rate (e^{λ} , PIR), as Defined by Hughes, in Populations of *Sitobion avenae* (F.) (Hemiptera: Aphididae)^{1,2}

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ABSTRACT

The potential rate of increase (PIR), used in Hughes' time-specific life table analysis for aphid populations as a multiplication factor for the instar-period, was studied in populations of *Sitobion avenae* (F.) in the absence and presence of the parasite *Aphelinus abdominalis* (Dalman) under controlled conditions.

Two factors were mainly found to alter PIR values in the presence of parasites. These were the feeding preference of adult *A. abdominalis* for the first instar aphids and the prolonged instar duration of the third instar of aphids which had been parasitized by an adult parasite at the first instar. These two factors contributed to lower values of PIR and as a consequence to an underestimation of the expected (potential) population for the next instar-period.

Introduction

Sitobion avenae (F.) and *Metopolophium dirhodum* (Walk.) are the most important aphid species from the seven species of Aphididae attacking cereal crops and grasses in Europe (Vickerman and Wratten 1979, Carter et al. 1980).

Aphelinus abdominalis (Dalman) has been found parasitizing *S. avenae* in France (Michel 1969) and in England (Dean et al. 1981). It also parasitizes other aphids, i.e. *Ericaphis latifrons* (Börn) (Couchman 1977). Flanders (1953) has stated that *A. abdominalis* is an aphid-feeding species which, like many of the Aphelinidae, lacks the capacity to deposit haploid eggs i.e.

produces progeny which are all females. However, Ferriere (1965) and Graham (1976) give characters of the male.

This paper explains the causes which can lower the values of PIR, as defined by Hughes (1962, 1963), in populations of *S. avenae* where the parasite *A. abdominalis* was present. Two experiments were conducted which had the following goals: the first was carried out to see whether the developing parasite larva inside the aphid body affects the instar duration and how this possible effect could alter the relative number of aphids in the first three instars and hence the PIR by which the predicted population is estimated after Hughes. The second experiment aimed at investigating the feeding preference of the parasite since from laboratory observations it seemed that adult *A. abdominalis* prefers to feed on younger instars of *S. avenae*.

Materials and Methods

S. avenae originated from stock cultures maintained on potted barley plants in muslin cages (38×45×64

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cm) under glasshouse conditions at approximately 20° C, 60-80% relative humidity and a 16:8 hours light-dark cycle. The parasite *A. abdominalis* was cultured on *S. avenae* populations reared on barley in two separate muslin cages as above.

Experiment I

The experiment took place in an environmental cabinet (FISONS, model 600 G3 TL) at 20° C, 70 ± 3% relative humidity and 16 hours light daily. A surplus of newly emerged apterous viviparous *S. avenae* was put on barley leaf-pieces to deposit nymphs. Leaf-pieces were placed on distilled water moistened cotton wool which covered the bottom of four covered plastic containers, 10 cm in diameter. The containers were put in the cabinet. The aphids were left for 6 hours to produce 50-60 nymphs and then discarded. Subsequently, 10 adult female *A. abdominalis* were introduced into each plastic container by means of an aspirator. The parasites had been kept in small plastic containers for the previous day, during which time they had not been provided with aphids so that they would lay eggs on the first instar of *S. avenae* within a short time of their release. They were left for 4 hours to oviposit on the aphids and then removed. Subsequently, the aphids were transferred to barley leaf-pieces floated on nutrient solution in small plastic pots of 37 mm diameter and 25 mm high. The nutrient solution used was the modified Hoagland-Snyder solution of Hughes and Woolcock (1965) without streptomycin sulphate. Inspections took place every 4 hours from 08.00 to 24.00 h until the parasitized aphids became mummies and every 8 hours from mummification to adult emergence.

Experiment II

To obtain aphids of the same approximate age within each instar the following procedure was followed.

Apterous adults *S. avenae* were left to deposit

nymph for 6 hours on barley aphid-free plants grown in a pot, 11.5 cm in diameter. The pot was caged individually by a cylindrical plastic cage and placed in the environmental cabinet at 20° C. The same procedure was repeated after 2, 4 and 6 days. In this way, aphids obtained after 7 days from the beginning of the experiment belonged to the first four instars, and approximately half way through each instar since the duration of at least the first three instars of *S. avenae* is approximately 2 days at 20° C (Lykouressis 1982). The aphids from each pot were collected separately and observed under a stereomicroscope to identify their instar using the key developed by Lykouressis (1983). Subsequently 20 aphids, five aphids from each instar, were placed on a barley leaf-piece into each of 30 transparent perspex boxes (Blackman 1974). Then two adult female parasites, taken randomly from stock cultures, were introduced in each transparent perspex box by means of an aspirator. The boxes were put in the environmental cabinet. After 24 hours the number of aphids in each instar fed on by adult parasites was recorded. It was decided not to include tests on the suitability of adults for parasite feeding since they might have produced offspring within a day and this would have changed the ratio (1:1:1:1) between the first four instars.

Results

Experiment I

Mummification of parasitized aphids always occurred at the third instar. Since oviposition by *A. abdominalis* on *S. avenae* took place at the beginning of the first instar, this means that mummy formation could not have occurred before the third instar. This was also demonstrated in population dynamics experiments of *S. avenae* in the presence of parasites where no mummies were found at the second instar

TABLE 1. Instar duration of non-parasitized and parasitized *Sitobion avenae* by *Aphelinus abdominalis* in hours (Mean ± S.E.) at 20° C.

		I n s t a r				Adult pre-reproductive period
		1st	2nd	3rd	4th	
Non-parasitized aphids	Ap (30)	50.93±1.46	47.20±0.80	46.50±0.74	55.13±0.78	11.33±0.88
	Al (17)	47.94±0.92	47.05±0.79	46.82±0.65	70.41±1.17	16.00±0.76
Parasitized aphids	Ap + Al (42)	51.21±1.41	48.57±0.72	99.76±1.87	—	—

(): Number of replicates.

Ap: Apterac.

Al: Alatae.

(Lykouressis 1982).

Table 1 gives the values of instar duration in hours of parasitized and non-parasitized aphids at 20° C. The calculated mean instar duration of the first and second instar was slightly longer in the case of parasitized than non-parasitized aphids but the difference was not statistically significant. A significant difference was found in the duration of the third instar of parasitized and non-parasitized aphids ($t = 27.3$, $P < 0.001$), the mean third instar duration in parasitized aphids being twice the length of that of non-parasitized aphids. The overall time required from oviposition to mummification was found to be 194.12 ± 2.04 (Mean $\pm$ S.E.) hours, whilst the time from mummification to adult emergence of the parasite was 260.23 ± 4.28 (Mean $\pm$ S.E.) hours.

Experiment II

The numbers of *S. avenae* in each instar which were fed on by two adult parasites within 24 hours were recorded. Analysis of variance was carried out on the transformed values ($X_{trans} = \sqrt{x + 0.5}$) because of the low counts and zeros. Significant differences were found in the mean number of aphids in each instar sucked by the parasites ($F = 5.99$, $P < 0.01$ with 29 and 3 d.f.). In particular, significant differences were found in the numbers between first instar versus second and third instar (average) ($t = 2.04$, $P < 0.05$ with 87 d.f.), second and third instar (average) versus fourth instar ($t = 4.22$, $P < 0.001$ with 87 d.f.). It is obvious that the feeding preference of the parasite decreases from the first to the fourth instar in this particular situation where the instars were numerically equal. In the present experiment, an average of 1.78 aphids per day was found to be destroyed by each parasite by feeding. A similar value has been found by Cate et al. (1973) where a daily mean of 1.5 *Schizaphis graminum* (Rondani) were fed upon per female *Aphelinus asychis* (Walker).

Discussion

The prolonged instar duration in parasitized aphids seems to be the result of the disruption of aphid feeding and of disturbance in the physiology of the aphid. The first was de-

monstrated by Couchman and King (1979). They found that the egg and embryonic stages of the parasite *Diaretiella rapae* (M'Intosh) had no effect on feeding in *Brevicoryne brassicae* (L.). However, the first-instar larva lowered the food uptake which returned to a level similar to that of non-parasitized aphids when the second-instar larva of the parasite was present and dropped again when the parasite larva reached the third instar. The physiological disturbance is attributed to the fact that insect parasites affect carbohydrate metabolism, lipid metabolism and the endocrine system of their host (Vinson 1975). This has also been demonstrated by Johnson (1959, 1965) in parasitized aphids.

From the second experiment it appears most likely that the feeding preference of the parasite would be in favour of the first instar aphids in increasing populations of *S. avenae* with a stable instar distribution in which the order of numerical abundance is first > second > third instar. However, a slightly different order in the feeding preference of *A. asychis* upon *S. graminum* was found by Cate et al. (1977). They stated that the adult parasite's preference for feeding on aphids of different ages was young > old > middle.

It is obvious that the combined effects, firstly of the host feeding preference of *A. abdominalis* for the first instar aphids and secondly the prolonged third instar duration of the parasitized aphids till mummification (twice as long as that of non-parasitized aphids) considerably lowers the value of PIR for the aphids estimated by the formula $PIR = \frac{a_1 + a_2}{a_2 + a_3}$ where a_1 , a_2 and a_3 is the number of aphids in the first, second and third instar, respectively, in the sample. These apparent changes in instar distribution lead to inaccuracies in the prediction of the theoretical population after one instar-period by Hughes' method. However, third instar parasitized aphids oviposited upon by parasites in their first instar, are easily distinguished from non-parasitized aphids since the parasite's larva is quite visible beneath the host's cuticle. In this case the true number of aphids in the third instar can be estimated applying a correction factor, i.e. actual number of third instar aphids = number of third instar unparasitized aphids + (number of third instar parasitized aphids/2). On the other hand, the

number of first instar aphids, as well as second and third instars, fed on by adult parasites, is difficult to assess within an instar-period because the numbers of individuals in the different instars of an aphid population are not normally equal as they were in the preference experiment reported in this study.

To avoid errors, arising from selective pre-reproductive mortalities occurred in aphid populations, instead of using PIR for the estimate of the potential population, another method has been suggested (Lykouressis 1982). This method is based not only on the number of aphids of the first three instars in a sample but on the whole instar distribution including adults.

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KEY WORDS: Potential increase rate, *Sitobion avenae*, *Aphelinus abdominalis*, Instar-period, Aphid-feeding species, Selective pre-reproductive mortalities

**Παράγοντες που Επηρεάζουν το Δυνητικό Ρυθμό Αύξησης
(eλPIR), όπως Έχει Καθορισθεί από τον Hughes, σε
Πληθυσμούς της Αφίδας *Sitobion avenae* (F.)
(Hemiptera: Aphididae)**

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ΠΕΡΙΛΗΨΗ

Σε πληθυσμούς της αφίδας *Sitobion avenae* (F.) κάτω από ελεγχόμενες συνθήκες και με παρουσία ή απουσία του παρασίτου *Aphelinus abdominalis* (Dalman) μελετήθηκε ο Δυνητικός Ρυθμός Αύξησης (PIR). Ο ρυθμός αυτός χρησιμεύει σαν πολλαπλασιαστικός παράγοντας για τον υπολογισμό της μεταβολής του πληθυσμού σε χρονική περίοδο ίση προς τη διάρκεια του μέσου όρου των τριών πρώτων σταδίων (instar-period) μιας αφίδας.

Δύο παράγοντες που βρέθηκαν και που αφορούν, αφενός μεν την προτίμηση του ακμαίου παρασίτου ως αρπακτικού για το πρώτο νυμφικό στάδιο, αφετέρου δε την αύξηση της διάρκειας του τρίτου σταδίου των αφίδων που παρασιτίστηκαν στο πρώτο νυμφικό στάδιο, θεωρούνται υπεύθυνοι για την εύρεση μη αποδεκτών τιμών PIR κατά Hughes. Συγκεκριμένα, οι παράγοντες αυτοί οδήγησαν στον υπολογισμό μικρότερου αναμενόμενου πληθυσμού για την επομένη περίοδο (instar-period) όπως αυτή έχει αναφερθεί προηγουμένως.