PARALYSIS BY THE HYMENOPTERAN PARASITE, *APHELINUS ASYCHIS*, AS A MORTALITY FACTOR OF TWO APHID SPECIES.

by

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Paralysis by the hymenopteran parasite, Aphelinus asychis as a mortality factor of two aphid species

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August 13th, 1979

(date)

ABSTRACT

Paralysis by the hymenopteran parasite, Aphelinus asychis, as a mortality factor of two aphid species.

The aphid parasite Aphelinus asychis (Walker) (Hymenoptera: Aphelinidae), when reared on the pea aphid, Acyrthosiphon pisum (Harris) or the potato aphid, Macrosiphum euphorbiae (Thomas) (Homoptera: Aphididae), contributes to host mortality in three different ways: by internal parasitism as a larva and by paralyzing and feeding on hosts as an adult female. The relative importance of any one cause of host mortality varies with the physiological condition of the parasite and the weight/size of the host, or both. After female Aphelinus had been deprived of hosts for 24 h they preferentially laid eggs into pea aphids weighing 0.06 mg or less by dry weight (or potato aphids weighing 0.07 mg or less), larval parasitism being the chief cause of host mortality. Paralysis was the chief cause of mortality of older (and larger) aphids.

For deprivation times ranging between 1 h and 37 h, host mortality due to paralysis increased with increase in deprivation time whereas mortality due to larval parasitism decreased. For deprivation times of up to 13 h, paralysis accounted for about 6% and 9% mortality of first-and second-instar pea aphids, respectively. For deprivation times between 13 h and 25 h, mortality increased to 85% in first-instars and to 70% in second-instars of pea aphid; aphid mortality remained unchanged for deprivation times longer than 25 h, averaging 75% and 65%

respectively, in first- and second-instar pea aphids. It is suggested that first-instar pea aphids, being smaller, are more susceptible to paralysis than second-instars. Differences in physiological stress, it is suggested, are the reason for the nonlinear relationship between host mortality due to paralysis and the length of time the Aphelinus female was deprived of hosts.

First-instar potato aphids suffered an average mortality of 70% or more from paralysis; the percentage mortality was not correlated with deprivation times. In second-instar potato aphids the pattern of paralysis-related mortality was comparable with that of second-instar pea aphids. At deprivation times between 1 h and 20 h, mortality averaged 26%; it increased linearly from 26% to 88% for deprivation times between 20 h and 37 h.

Aphelinus asychis attacked and laid eggs into a higher proportion of pea aphids than potato aphids; the proportion of parasite larvae successfully completing their development was higher for pea than for potato aphids as hosts. Neither the host species, nor the host size/weight, nor the length of the deprivation time appeared to influence the sex ratio of the emerging parasite generation; the ratio was approximately 3 females to 1 male for all conditions tested.

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CHAPTER I. INTRODUCTION

(A). General

Species of the genus Aphelinus Dalman (Hymenoptera: Aphelinidae) are protelean parasites of aphids (Homoptera: Aphididae). The aphelinid larva develops as a solitary endoparasite inside the aphid host, which it consumes and kills. The females of Aphelinus and of related genera behave like predators, feeding on host fluids that exude from wounds made with the ovipositor. Parasite feeding* generally contributes to or causes host death, either immediately or within a short period. The biology of the aphelinid parasites of aphids and the relative impact of parasitism and host feeding on aphid population growth was reviewed by Hagen and van den Bosch (1968).

The predatory behaviour of aphelinid females has been described widely in the literature. Rockwood (1917) noted that Aphelinus lapisligni Howard fed on its host, Nearctaphis bakeri Cowen. Hartley (1922) described the feeding of A. semiflavus Howard on the green peach aphid, Myzus persicae Sulzer, and Schlinger and Hall (1959) described that of A. asychis (Walker) (= semiflavus sensu auctt.) on the spotted alfalfa aphid, Therioaphis maculata Buckton. Upon emergence, A. asychis females feed first on their hosts before they lay eggs (Michel 1967). A detailed quantitative account of feeding by A. asychis on the greenbug, Schizaphis graminum Rondani, was given by Cate et al. (1974).

*The term feeding or host feeding will be used only to describe the feeding of adult Aphelinus females and not of their larvae, on host aphids.

The Aphelinus female may paralyze an aphid before feeding on it. Griswold (1926, 1929) reported that the geranium aphid, Acyrthosiphon malvae Mosley (= Macrosiphum cornelli Patch) is paralyzed when fed upon by A. jucundus Gahan and that many aphids never recover. A. semiflavus paralyzed its hosts before feeding or oviposition (Hartley 1922; McLeod 1937), but Wilbert (1964) and Boyle and Barrows (1978) observed paralysis by A. asychis only in aphids selected for feeding and not in aphids selected for oviposition. Wilbert suggested that the parasite injected a toxin when using the ovipositor for wounding the host prior to feeding but not when actually laying an egg. Hamilton (1973) found no differences in the manner A. flavus Thompson used the ovipositor for feeding or for oviposition; the sycamore maple aphid, Drepanosiphum plantoides Schrank, was paralyzed in both instances. Though the aphid recovered from paralysis after oviposition, it did not recover after parasite feeding; aphid death was the result of the paralysis and not of mutilation caused by the probing of the parasite's ovipositor, as had been suggested by Flanders (1953).

Host paralysis and host feeding are not restricted to the Aphelinidae but occur also in other families of the parasitic Hymenoptera. The ichneumonid Mastrus carpocapsae Cushman paralyzed, but did not feed on, the larvae of the codling moth Laspeyresia pomonella Linnaeus; and paralyzed larvae were not always accepted for oviposition (Lloyd 1956). Lloyd suggested that paralysis rather than oviposition serves as a deterrent against subsequent parasite attack and superparasitism

by causing the codling moth larvae to move abnormally. In some parasites, the host must be paralyzed to enable successful oviposition. For example, Beard (1952) reported that Bracon hebetor Say (= Habrobracon juglandis Ashmead) paralyzed its host, Galleria larvae, by injecting a venom before laying eggs on or near the host. Gerling and Rotary (1973) working with the some parasite but a different host, found that the parasite fed on the host readily and repeatedly prior to oviposition, but paralyzed the host only for oviposition. Asaphes lucens Provancher, a hyperparasite of aphids, injected a venom into the host prior to feeding and oviposition (Keller and Sullivan 1976). The chalcid Solenotus begini Ashmead injected a venom into its hosts, dipterous leaf-miners. A single egg is laid into the mine after the host is immobilized, thus ensuring the availability of the food source for the parasite larva (Doutt 1957). Stenobracon deesae Cameron, a parasite of lepidopterous borers of graminaceous crops in India, also paralyzed its host prior to oviposition; the parasite larvae did not feed on nonparalyzed hosts (Narayanan and Chaudhuri 1954).

Very little research has been done on the chemical nature and pharmacological properties of the paralyzing venoms of the Hymenoptera. Beard (1952, 1963) suggested that the venoms of predaceous wasps are neurotoxic. In their detailed study of the paralyzing venoms of B. hebetor and Philanthus triangulum Fabricius, Piek and Spanjer (1978) found that the venoms inhibit the excitatory neuromuscular transmission of waxmoth larvae; the site of the venom action is believed to be presynaptic, a

fact that could explain why paralyzed larvae continue twitching.

No corresponding work has been done on the venoms that may be injected by the Aphelinus female prior to or during oviposition and feeding. Although the presence of an acid gland as part of the reproductive system of Aphelinus (Copeland 1976) suggests that the female is capable of producing a venom, the evidence is circumstantial and based solely on symptoms observed in aphids following Aphelinus attack. After attack by A. asychis, the abdominal region of the greenbug S. graminum becomes swollen and the hind legs of the aphid wave in an uncoordinated manner (Esmaili and Wilde 1972; Boyle and Barrows 1978). A colour change from green to brown, observed in S. graminum during parasite feeding, has also been attributed to a paralyzing agent (Cate et al. 1973; Esmaili and Wilde 1972; Boyle and Barrows 1978).

(B). Objectives.

Aphid death is hastened by parasite feeding, but the ultimate cause of death, as suggested by Cate et al. (1977), is either some foreign substance or a venom injected with the ovipositor or the mechanical damage or trauma resulting from ovipositor action. The injection of venom into aphid hosts, by A. asychis, and the subsequent non-recovery from paralysis could be an important host mortality agent with respect to the biological control of aphids.

The pea aphid, Acyrthosiphon pisum (Harris), the potato aphid, Macrosiphum euphorbiae (Thomas), and the aphelinid parasite, Aphelinus asychis (Walker) were selected as a model

system for studying aphid paralysis. The study had the following objectives:

(1) to determine, in a quantitative manner, whether host paralysis is in fact a third modality of aphid death, in addition to adult feeding and larval parasitism;

(2) to identify variables affecting aphid mortality from paralysis, and

(3) to relate aphid susceptibility to paralysis to host preference by the parasite.

CHAPTER II. MATERIALS AND METHODS

(A). Laboratory cultures.

1. The Hosts.

Synchronous (± 2 h) colonies of the pea aphid, Acyrthosiphon pisum (Harris) were produced by transferring two hundred apterous, viviparous adults, of reproductive age, from a stock culture to potted broad bean, Vicia faba Linnaeus c.v. "Exhibition longpod". The plants were 15-to-17-days old. After four hours, the adults were removed and their progeny, on the broad bean, were maintained in an environmental chamber at 21 ± 2°C, 50-60% r.h. and an 8/16 (dark/light) light regime.

Four hundred apterous, viviparous adults of the potato aphid, Macrosiphum euphorbiae (Thomas), of reproductive age, were transferred from a stock culture and set up and maintained in much the same manner as for A. pisum, to produce synchronous (± 2 h) colonies. The potato aphid usually did not reproduce for six hours after transfer; therefore a six-hour "settling period" was allowed after transfer, followed by a four-hour reproductive period.

2. The Parasites.

A nucleus colony of A. asychis was obtained from R. D. Eikenbary (Oklahoma State University), and a laboratory colony was established on A. pisum. The colony was maintained at 19 ± 1°C, 50-60% r.h. and continuous light. Many parasites have activity cycles with respect to oviposition and emergence, which are keyed to the photoperiod. To avoid photoperiodic effects on

parasite behaviour arythmic colonies were produced by maintaining both the aphids and their parasites under continuous light (Corbet 1966; Mackauer and Henkelman 1975). Female A. asychis reared on A. pisum, were transferred to M. euphorbiae; this colony was reared under similar conditions as the one on the pea aphid. For experiments involving either host, only female parasites 7 ± 2 days-old were used to ensure that they were not in a post-emergence feeding cycle (Michel 1967; Esmaili and Wilde 1972; Hamilton 1973). Prior to any experiment the parasites were removed from the laboratory culture and placed in a mini-cage (Mackauer and Bisdee 1965) containing one bean shoot infested with first- and second-instars of the appropriate host species, for 24 hours. The majority of parasites would then be at a low hunger level prior to any experiment.

(B). Experimental Methods.

The materials and methods for each experiment apply to both the pea aphid and potato aphid. In section B.1. the experiments involved first-instar (24 ± 2 h) or second-instar (48 ± 2 h) hosts of both species. For all experiments, aphid dry weight was determined by drying a sample of 10 to 20 aphids, used during each experiment, at 93° C in a Precision scientific oven for three days. The dried aphids were individually weighed on a Cahn (Model G-2) electrobalance. The mean and standard error of each sample was calculated. Each experiment was run twice; the runs are distinguished as run 1 and run 2.

1. Increase in parasite deprivation time.

The purpose of this experiment was to determine the effect of increase in parasite deprivation time on aphid mortality, measured 24 h after parasite attack, the proportion of aphids attacked, and the proportion of mummy formation. Increases in deprivation time should increase the hunger level of the parasite. This may cause the parasite to switch its manner of attacking hosts from that of oviposition to that of paralysis; the paralyzed aphids being used as a food source. Of additional interest was the effect of deprivation time on the sex ratio of male and female offspring produced by the parasites. The increase in the parasite's hunger level may lead to oosorption of the parasite's eggs as a means of conserving energy and nutrients (Flanders 1935, 1942).

Female parasites (20-50) were removed from the laboratory colony and placed, for 24 hours, in a mini-cage containing a bean shoot infested with young aphids. The parasites were maintained in an environmental chamber at 19 ± 1 °C, 50-70% r.h. and continuous light. The parasites were then transferred to a second mini-cage containing a bean shoot without aphids. These parasites were deprived of hosts for periods of time ranging from 0 h to 36 h.

A new group of parasites from the stock colony was used for each deprivation time interval. All parasites were discarded after each experiment. Parasites were placed singly into #00 gelatin capsules containing one aphid each; the aphid age was either 24 h or 48 h. Each capsule was placed on corrugated

cardboard to minimize the disturbance of the parasite while it oviposited. The capsules were carefully monitored using a luxo-magnifier to ensure that aphids were attacked only once. Parasites were not allowed to turn and feed on the host. After the parasite removed its ovipositor from the host, the aphid was immediately transferred to a small petri dish. Each parasite, at each deprivation time, was allowed to attack 4 to 6 aphids.

Each experiment consisted of four data-collection intervals (DCI) of one-half-hour each, per deprivation time interval. Depending on the host species, 20 to 50 aphids were exposed to parasites per DCI. The attacked aphids were placed on broad bean shoots and maintained at 21 ± 2 ° C, 50-60% r.h. and an 8h/16h (dark/light) light regime. Aphid mortality was recorded at 24 h after attack. All developing parasitoids were allowed to complete development and then were sexed.

2. Increase in aphid weight.

This experiment was conducted to determine (1) if host size would affect the proportion and type of aphid mortality inflicted on hosts by parasites deprived of hosts for 24 hours, and (2) if host size would affect the sex ratio of the F_1 parasites. Various authors have noted that A. asychis prefer to attack first-instar or second-instar aphid nymphs either for successful oviposition or host feeding, depending on the species being studied (Cate et al. 1977; Hagen and van den Bosch 1968; Raney et al. 1971).

Reproductive, apterous aphids were set up and maintained as prevously described in section (A).1 to produce progeny of the

same age class. Age interval one consisted of aphids 24 ± 2 h old. Age intervals two to seven used aphids of age incremented by 12 h. For each of four one-half-hour DCI, per age interval, 30 to 40 female parasites of 9 ± 2 days post-emergence, were removed from the laboratory culture, placed in mini-cages which contained a broad bean stem infested with young aphids and maintained at 19 ± 1 ° C, 50-70% r.h. and continuous light, for 24 h. These parasites were then transferred to a second mini-cage containing only a broad bean shoot. This cage was returned to the environmental chamber for 24 h. Each parasite then came in contact with the host species as described in section (B).1.

3. Host developmental study.

Aphids near or at ecdysis may be more susceptible to parasite attack. The aphid cuticle at this time is very soft and does not give much support. The host may find it difficult to ward off attack by the parasite. In addition, if any egg is laid in a host during moulting, the act of moulting may affect the mobilization of the defence mechanisms of the host. This may lead to a greater level of aphid mortality than would be expected on the basis of the increase in parasite deprivation time and the increase in host weight experiments. The experiment tried to determine the approximate duration of the first- and second-instar period of the pea aphid and the potato aphid.

Two reproductive, apterous aphids were placed on each of 12 individually caged, broad bean shoots. The method described in section (A).1 produced aphids of age zero (± 2 h). These nymphs

were maintained at 21 ± 2 ° C, 50-60% r.h. and continuous light. At six hour intervals each cage was checked for the number of aphids alive and the number of aphids moulting. Any aphids found off a shoot were returned to the leaf, using a fine camel hair brush. At each check time the temperature was recorded from a Digi-sense Thermister Thermometer (Model 8520) connected to two thermocouples inside the environmental chamber. One thermocouple was placed above the cages; the other was placed below the cages. The mean time to ecdysis for each instar and the standard error of the mean was calculated.

4. Alternate host study.

Parasites reared on A. pisum were deprived of this host for 24 hours and then allowed to attack second-instar M. euphorbiae. Similarly, parasites reared on M. euphorbiae were deprived of this host for 24 hours and then allowed to attack second-instar A. pisum. These experiments were run concurrently and were used as a means of assessing host preference of A. asychis.

Thirty female parasites 6 ± 2 days old were removed from the laboratory colony and placed in mini-cages for 24 hours. Each cage contained a bean shoot infested with the permanent host. Second-instar (48 ± 2 h) aphids of the alternate host were then exposed to these parasites following the method described in section (B).1. The attacked aphids were maintained as in section (B).1.

(C). Data analysis

In each experiment data was collected on the following variates:

(1) The proportion of aphids attacked (p) is that fraction of the total number of aphids exposed (N) to parasites that were in fact attacked.

(2) The proportion of aphids dead 24 h after attack (p_1) is that fraction of the proportion of aphids attacked by the parasite which died within 24 h after attack.

(3) The proportion of mummies formed (p_2) is that fraction of the proportion of aphids attacked in which a parasite egg was laid and in which larval development was completed, as was demonstrated by the formation of a mummy.

(4) The proportion of aphids not parasitized (q) is that fraction of the total number of aphids exposed to parasites which were not attacked, or, if apparently attacked, which did not die within 24 h or which did not develop into a mummy.

Thus, $p = p_1 + p_2$ and $p + q = 1$

(5) The sex ratio of emerging parasites of the F_1 generation.

The analysis included one- and two-way analysis of variance, Student-Newman-Keuls test, regression analysis, a heterogeneity-chi square test (Sokal and Rohlf 1969) and probit analysis (Finney 1971).

CHAPTER III. APHELINUS ASYCHIS ON PEA APHID.

(A). Response of the parasite after being starved for 24 hours, to six age-groups of pea aphids.

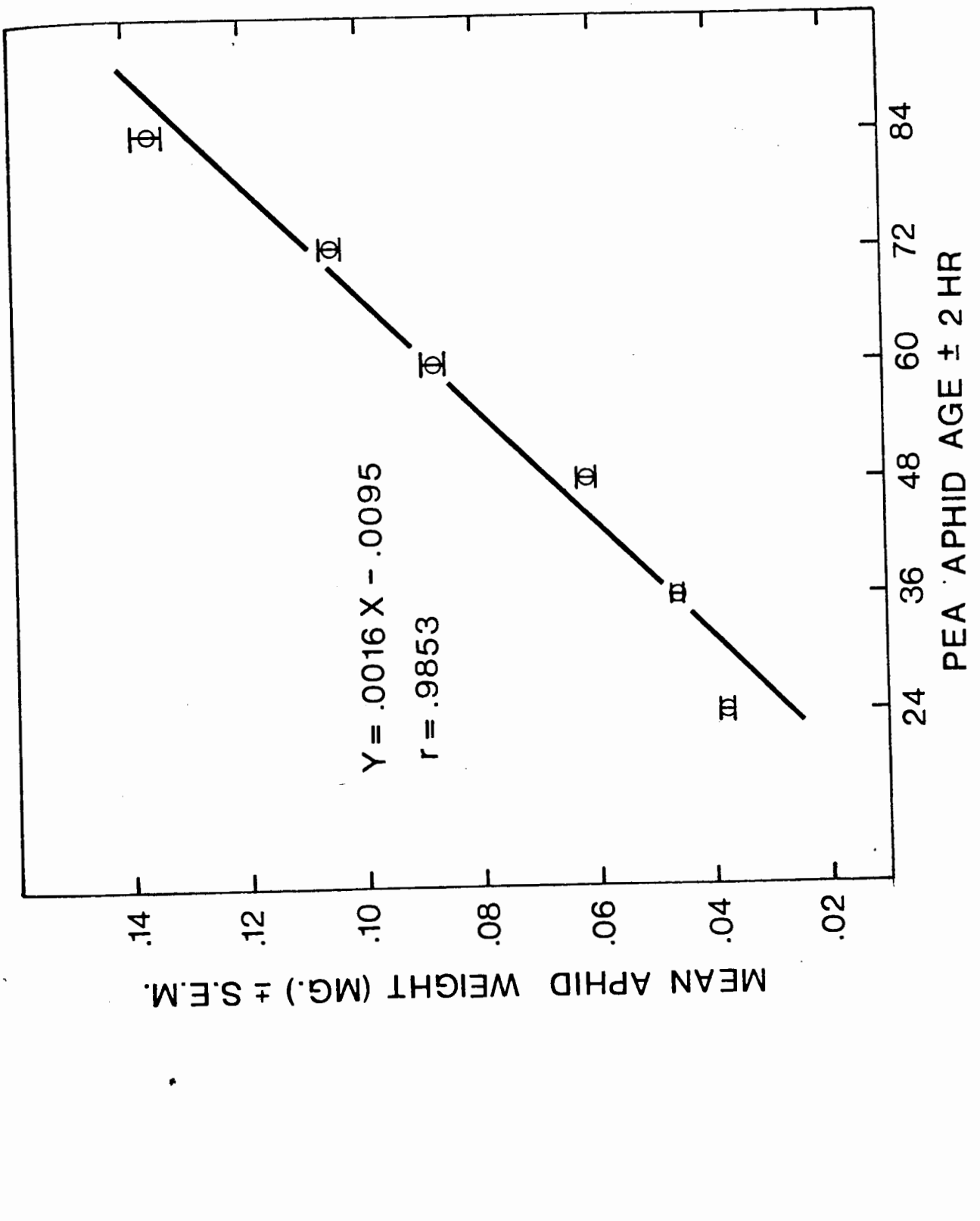
1. Relationship between aphid age and weight.

With an increase in aphid age from 24 h to 84 h there is a linear increase in aphid dry weight (Table I.). Though deviations from linearity were significant these accounted only for 2-3% of the total variability. Both runs exhibited significant, positive correlations ($r_1 = 0.9858$, $t_1 = 11.249$, $P_1 = 0.0004$; $r_2 = 0.9835$, $t_2 = 10.886$, $P_2 = 0.0004$) between the increase of host weight with the increase in host age. Figure 1 shows the data of run 1 and the equation of the line.

2. Influence of data-collection intervals and host weight on the parasites' behaviour.

The data collected during the four one-half-hour data collection intervals (DCI) for the proportion of aphids dead within 24 hours, were found to be comparable to one another; no added variance coming from the DCI. Similarly, the proportion of aphids attacked, the proportion of mummies formed, and the proportion of aphids not parasitized, had no added variance attributed to the DCI (Tables II. & III.). The aforementioned variables, with the exception of the proportion of aphids not parasitized in run 1, were significantly affected by the increase in aphid weight. Subsequent analysis on each dependent variable, were made on the mean of the data obtained within the four DCI, for each aphid weight.

Figure 1. Mean dry weight, per aphid age of apterous *A. pisum* (Harris).


MEAN APHID WEIGHT (MG.) ± S.E.M.
.14
.12
.10
.08
.06
.04
.02
Y = .0016 X - .0095
r = .9853
24
36
48
60
72
84
PEA APHID AGE ± 2 HR

In run 1 (Fig. 2) the proportion of aphids attacked remained relatively constant, the mean being 0.633 (S.E.= 0.021), as host weight increased from 0.038 mg to 0.061 mg. It then increased to 0.765 (S.E.= 0.033) at a heavier host weight of 0.105 mg. The proportion of aphids attacked decreased to 0.428 (S.E.=0.049) when the host weight was 0.133 mg. In addition, of those aphids attacked, the proportion of aphids not parasitized remained relatively constant, the mean being 0.216 (S.E.= 0.026), for aphid weights two (0.045 mg) to four (0.088 mg).

Female A. asychis appear to favour host paralysis as a means of causing aphid mortality with the increase in host weight. The mean proportion of aphid mortality within 24 h (Fig. 3) decreased from 0.846 (S.E.= 0.083) to 0.187 (S.E.= 0.024) for weights one and two, respectively. Thereafter it increased from 0.53 to 0.66, with additional increases in host weight. The proportion of mummies formed decreased from 0.593 at weight two to 0.076 at weight four; thereafter, with further increases in host weight, the proportion of mummies formed remained relatively constant ($\bar{x}$= 0.078, S.E.= 0.014).

In run 2 the parasites' response to increase in host weight was similar to run 1. The proportion of aphids attacked was quite constant, the mean being 0.854 (S.E.= 0.017) from weight one (0.0396 mg) to weight six (0.109 mg). The mean proportion of aphid mortality within 24 h decreased from 0.146 to 0.067 from weight one to weight three (0.0544 mg); thereafter it increased to a mean of 0.434 (S.E.= 0.025) with host weight four (0.0806 mg) to weight six. The mean proportion of aphids not parasitized

increased from 0.295 to 0.427 from weight one to three. Thereafter it remained relatively constant ($\bar{x}$= 0.464, S.E.= 0.023) with further increases in host weight. There was a trend towards a decrease in proportion of mummies formed as host weight increased; the maximum proportion of mummies formed being 0.602 at a host weight of 0.0484 mg.

In run 1 the proportion of female parasites in the F1 generation, emerging from different host weights, ranged from 0.68 to 1.00; in run 2 this ranged from 0.77 to 1.00. A heterogeneity-χ^2 showed that the data of both of the runs were homogeneous (χ^2_1= 6.43, P_1>0.1, df= 5: χ^2_2 = 2.81, P_2= 0.5, df=5) and that the deviations from the assumed 1:1 sex ratio are in the same direction. The overall mean proportion of females emerging was 0.908 (S.E.= 0.052) in run 1; in run 2 this proportion was 0.88 (S.E.= 0.043).

(B). Increase in parasite deprivation time. Host = first-instar pea aphid (24 ± 2 h).

1. Host weight for each deprivation time interval.

The mean aphid weight differed at each of the deprivation times (Table IV). The variation was not linear as the deviation from linearity was significant; this accounting for 13.3% of the total variability in run 1 and 17.2% of that in run 2. The data are therefore either curvilinear or heterogeneous about the line.

Since my primary interest was in the mean aphid mortality within 24 H, for each deprivation time interval, this dependent variable was plotted against the mean aphid weight per deprivation

Figure 2. Response of female A. asychis (Walker) to different weights of A. pisum (Harris). Parasite deprived from host for 24 hours.

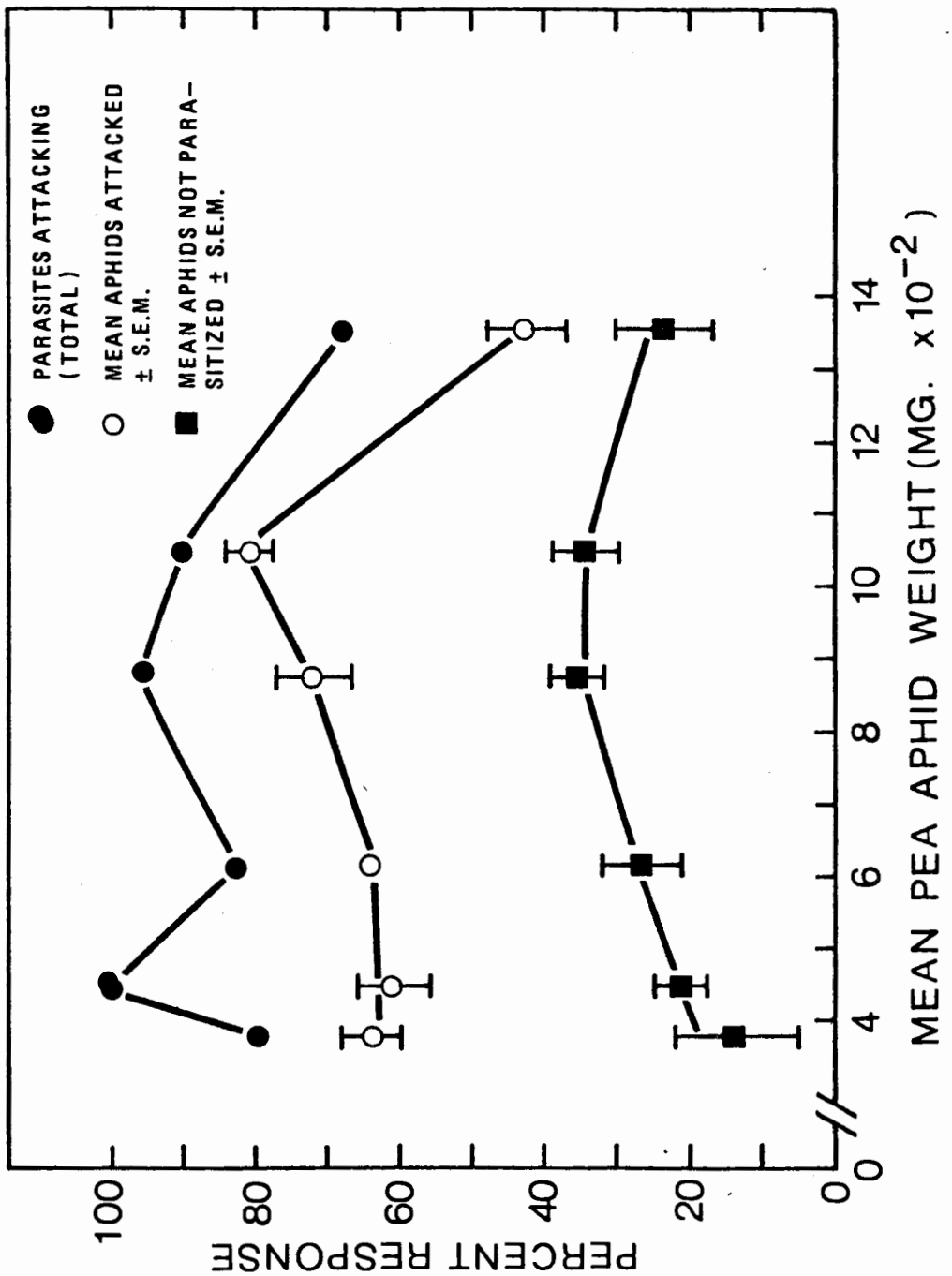
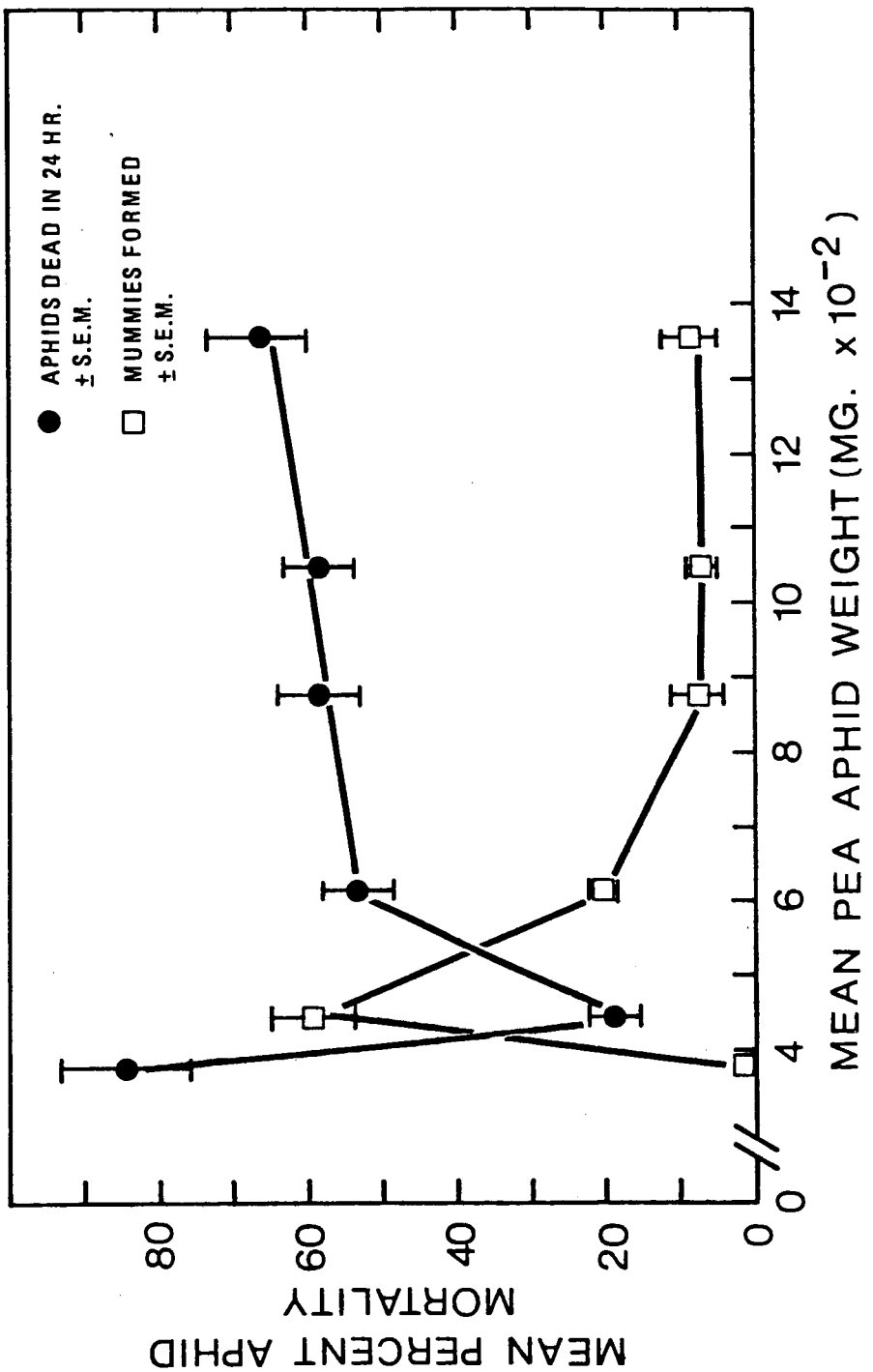

PARASITES ATTACKING (TOTAL)
MEAN APHIDS ATTACKED ± S.E.M.
MEAN APHIDS NOT PARASITIZED ± S.E.M.
PERCENT RESPONSE
100
80
60
40
20
0
0
4
6
8
10
12
14
MEAN PEA APHID WEIGHT (MG. x10^{-2})

Figure 3. Mean percent A. pisum (Harris) mortality, with increase in host weight, due to attack by female A. asychis (Walker). Parasite deprived from host 24 hours prior to attack.


APHIDS DEAD IN 24 HR. ± S.E.M.
MUMMIES FORMED ± S.E.M.
MEAN PERCENT APHID MORTALITY
0
20
40
60
80
0
4
6
8
10
12
14
MEAN PEA APHID WEIGHT (MG. x 10⁻²)

time interval (Fig. 4). As can be seen, aphid weight was not correlated systematically with aphid mortality.

2. Influence of the data-collection and deprivation time intervals.

In both runs all dependent variables were significantly affected by the deprivation time as it was increased from 1 h to 37 h; no added variance could be attributed to the data-collection intervals (Tables V & VI). In run 1 the proportion of aphids attacked ranged from 0.637 to 0.822, the mean being 0.737 (S.E.= 0.0105). In run 2 (Fig. 6) this mean was 0.706 (S.E.=0.02). Both runs have weak correlations (r_1= 0.355, P_1= 0.217; r_2=-0.188, P_2= 0.328) and the slope of the lines are near zero.

Some differences exist between the proportion of aphids dead within 24 h with the increase in deprivation time. The data, after probit-$\log_{10}$ transformation, had a linear relationship between four of the deprivation time intervals. In run 1, the mean proportion of aphids dead within 24 h increased linearly from 3.588 probits (0.079) to 5.799 probits (0.788) between deprivation times 16 h to 31 h. Below 16 h aphid mortality within 24 h was quite variable. In run 2 (Fig. 5) it increased linearly from 3.04 probits (0.025) to 6.01 probits (0.844) between deprivation times of 13 h to 25 h. The mean proportion of aphids dead within 24 h ranged from 3.199 probits (0.03) to 3.72 probits (0.10) ($\bar{x}$= 0.053, S.E.= 0.013) at deprivation times below 13 h. Whereas, it was high, the mean being 5.57 probits (0.716) (S.E.= 0.026) at deprivation times equal to or exceeding 25 h.

Figure 4. Mean percent mortality within 24 h of first-instar A. pisum (Harris) at each host weight, per deprivation time for female A. asychis (Walker).

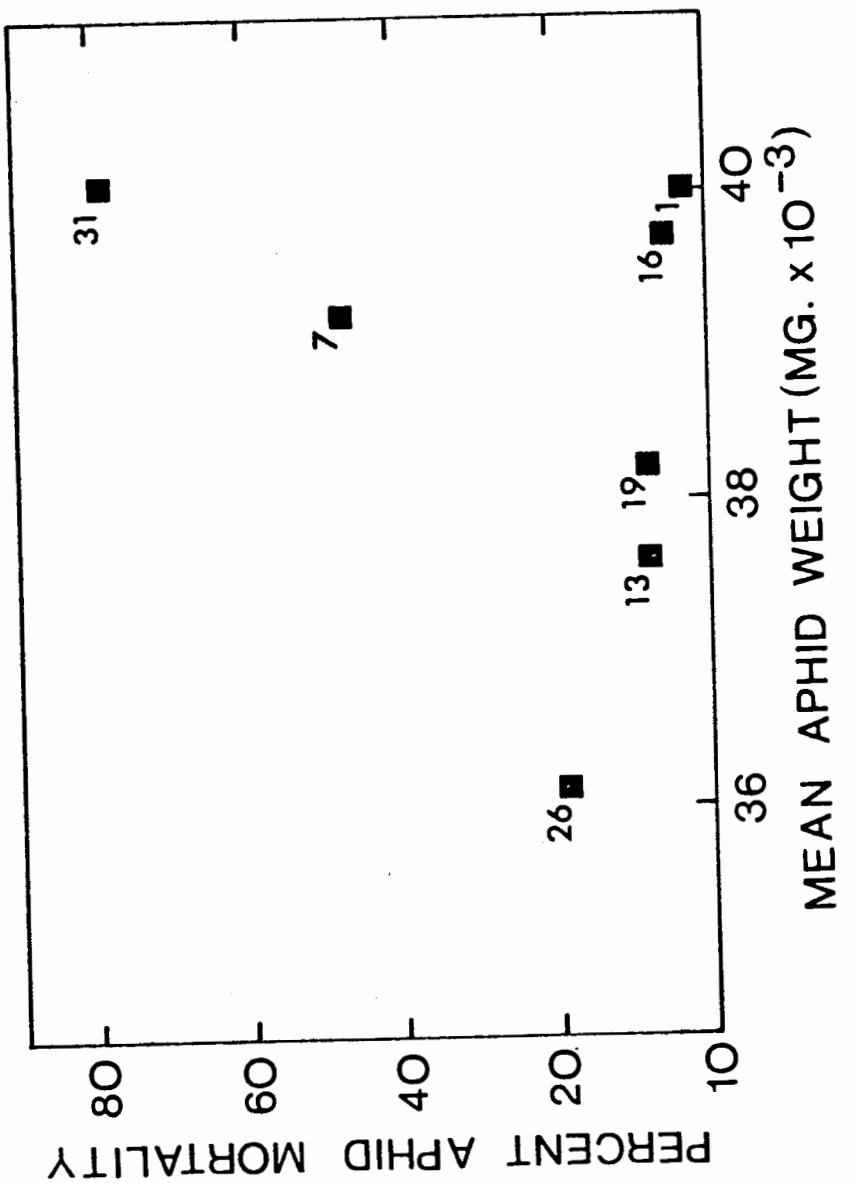

PERCENT APHID MORTALITY
10
20
40
60
80
36
38
40
MEAN APHID WEIGHT (MG. x 10⁻³)
31
7
26
13
19
16
1

Figure 5. Mean mortality within 24 h of first-instar *A. pisum* (Harris), per deprivation time (probit-$\log_{10}$ transformation) of female *A. asychis* (Walker).

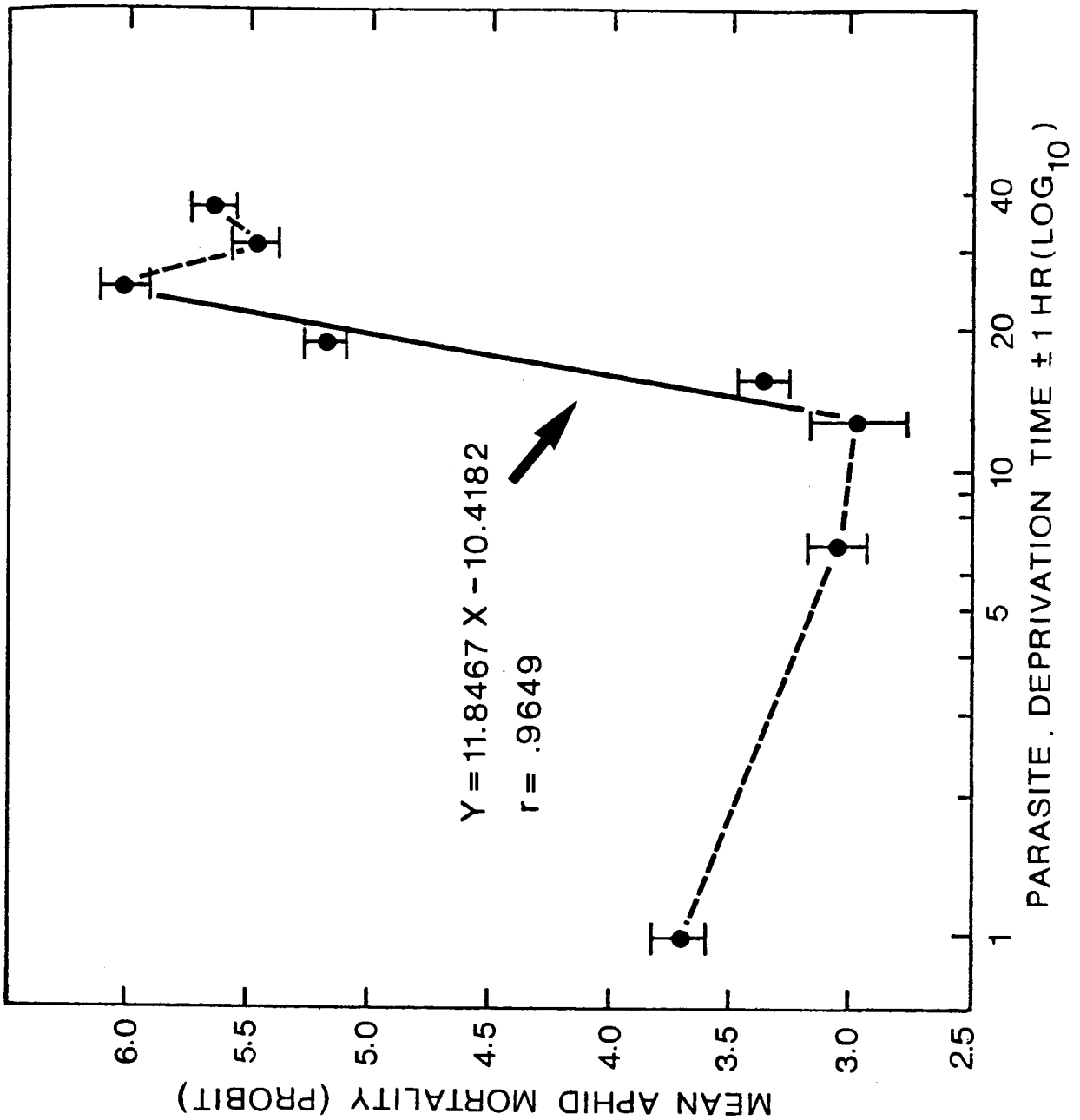
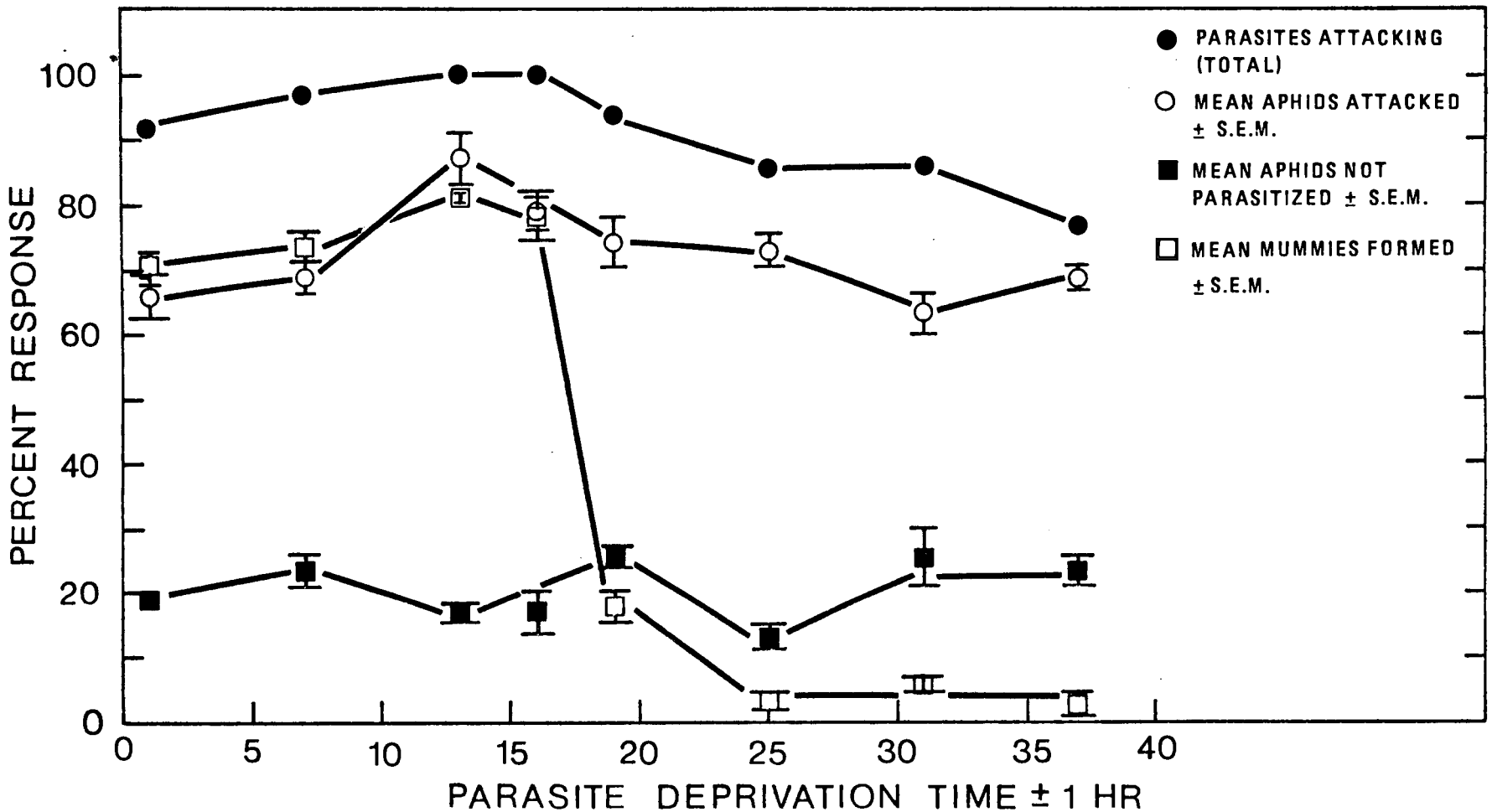

MEAN APHID MORTALITY (PROBIT)
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
Y = 11.8467 X - 10.4182
r = .9649
1
5
10
20
40
PARASITE. DEPRIVATION TIME ± 1 HR (LOG10)

Figure 6. Percent response of female A. asychis (Walker) with increase in deprivation time to first-instar A. pisum (Harris).


PARASITES ATTACKING (TOTAL)
MEAN APHIDS ATTACKED ± S.E.M.
MEAN APHIDS NOT PARASITIZED ± S.E.M.
MEAN MUMMIES FORMED ± S.E.M.
PERCENT RESPONSE
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
PARASITE DEPRIVATION TIME ± 1 HR

In run 1 the proportion of mummies formed was relatively constant ($\bar{x}$= 0.633, S.E.= 0.023) between deprivation times 1 h to 16 h; the exception being at 7 h. Here, the mean mummy formation was 0.349 (S.E.= 0.028). A negative correlation (r= -0.859, P= 0.07) exists for the decrease in mummy formation between deprivation times 16 h to 25 h; mummification decreasing from 0.627 to 0.541. In run 2 (Fig. 6) the proportion of mummies formed was constant ($\bar{x}$= 0.758, S.E.= 0.015) as the deprivation time was increased from 1 h to 16 h. A negative correlation (r= -0.973, P= 0.014) was evident as the proportion of mummies decreased from 0.81 to 0.03 from deprivation times 13 h to 25 h. The mean proportion of mummies formed remained constant at 0.03 with additional increases in the deprivation times. In both runs, where a negative correlation exists between mummification and deprivation time, this relationship was non-linear (F_1= 5.635, P_1= 0.141; F_2= 6.384, P_2= 0.086). No correlation or linear regression appears to exist, in either run, between the proportion of aphids not parasitized and the increase in deprivation time.

The proportion of female A. asychis emerging in the F1 generation ranged from 0.60 to 1.00 in run 1 and 0.75 to 0.77 in run 2, as the deprivation time was increased. A heterogeneity-χ^2 test (χ^2_1 = 2.661, $P_1 > 0.5$, df = 6: χ^2_2 = 3.433, $P_2 > 0.5$, df = 6) was not significant. The proportions and their deviations from the assumed 1:1 sex ratio are each homogeneous. The overall mean proportion of females emerging in the F1 generation was 0.86 (S.E.= 0.027) in run 1; in run 2 this mean was 0.77

(S.E.= 0.003).

3. Summary.

No changes occurred in the total first-instar pea aphid mortality (i.e. the number of mummies formed plus the number of aphids dead within 24 h) as the deprivation time was increased. However, the parasite's method of causing host mortality did change with the increase in deprivation time. As deprivation time increased the host mortality due to oviposition decreased while the host mortality due to paralysis increased. The sex ratio of the F1 generation of parasites remained in favour of females as the deprivation time increased. The total number of parasite progeny in the F1 generation decreased as the deprivation time was increased.

(C). Increase in parasite deprivation time. Host = second-instar pea aphid (48 ± 2 h).

1. Host weight and data-collection intervals.

Aphid dry weights were not significantly different for each deprivation time interval (Table VII). In addition, no linear regression existed. The four one-half-hour data-collection intervals (DCI) and the parasite deprivation times (PDT) had a significant effect on the dependent variables, in both runs (Tables VIII & IX). The increase in PDT affected (1) aphid mortality within 24 h, (2) mummification of aphids, and (3) aphids not parasitized. The data for the proportion of aphids attacked was not collected in run 1 and only the total number of aphids attacked, for each deprivation time, was collected in run 2.

In run 1 the proportion of mummies formed was significantly affected by the DCI (Table VIII). Mummification was negatively correlated with DCI at the deprivation times of 1 h, 19 h, and 25 h. No significant correlations were found with the five remaining deprivation times (Table X). Because aphid dry weight was not measured and the temperature was recorded only once during each deprivation time, of this run, it was difficult to establish the source of the variation.

In run 2 the proportion of mummies formed and the proportion of aphid mortality within 24 h (Table IX) were affected by the DCI. In the former, only the 15 h deprivation time showed a negative correlation of slight significance, so it was ignored. With the latter, deprivation times of 1 h, 7 h, and 31 h had

significant positive correlations (Table X). Though temperature was kept as constant as possible between the DCI and was approximately the same for each PDT, the environmental conditions were not constant. These could have affected the parasites' behaviour within any one deprivation time interval, causing significant variance within the DCI. Even with the added variance from the DCI, the change in deprivation time still affects the behaviour of the parasites.

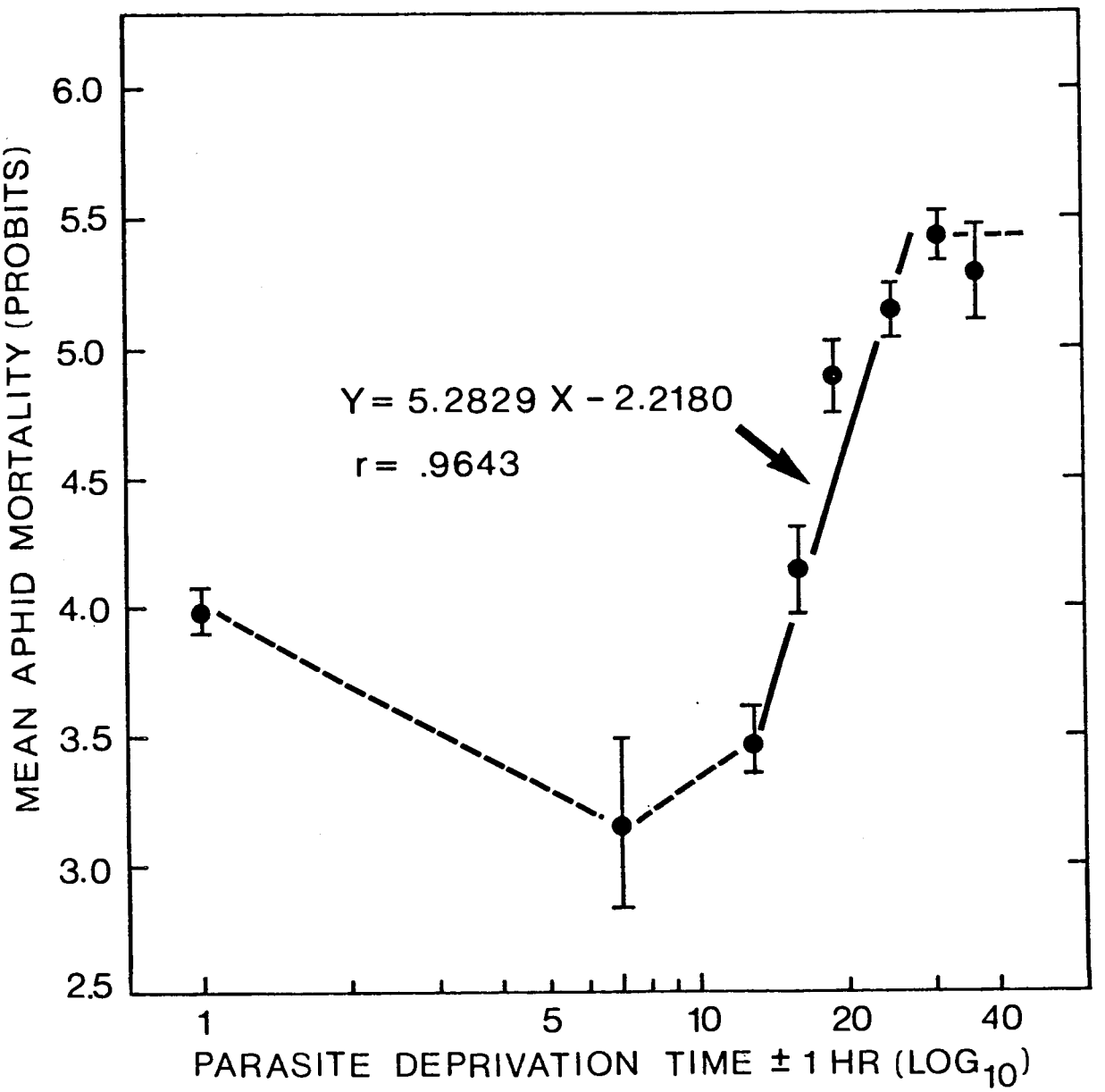
2. Influence of the deprivation times.

In run 2 the mean proportion of aphids attacked showed some variability, ranging from 0.881 to 1.00 ($\bar{x}$=0.946, S.E.= 0.015) as the deprivation time was increased. The mean proportion of parasites attacking remained relatively constant, the mean being 0.840 (S.E.= 0.031); the large standard error was due to all the parasites attacking at the 20 h deprivation time interval.

The mean proportion of aphids dead within 24 h was variable ranging from 3.431 probits (0.058) to 4.005 probits (0.160) ($\bar{x}$= 0.096, S.E.= 0.020) between deprivation times of 1 h to 13 h. Aphid mortality then increased from 3.528 probits (0.071) to 5.432 probits (0.667) for deprivation times of 13 h to 31 h. Here, a strong positive correlation exists (r= 0.922, P= 0.013) with linear regression accounting for 85% of the variance.

In run 2 the mean proportion of aphids dead within 24 h increased linearly from 3.976 probits (0.153) to 5.376 probits (0.646) as the deprivation time increased from 13 h to 26 h. Here, linear regression accounted for 81% of the variance.

Figure 7. Mean mortality within 24 h of second-instar A. pisum (Harris), per deprivation time (probit-$\log_{10}$) transformation of A. asychis (Walker).


6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
MEAN APHID MORTALITY (PROBITS)
Y = 5.2829 X - 2.2180
r = .9643
1
5
10
20
40
PARASITE DEPRIVATION TIME ± 1 HR (LOG10)

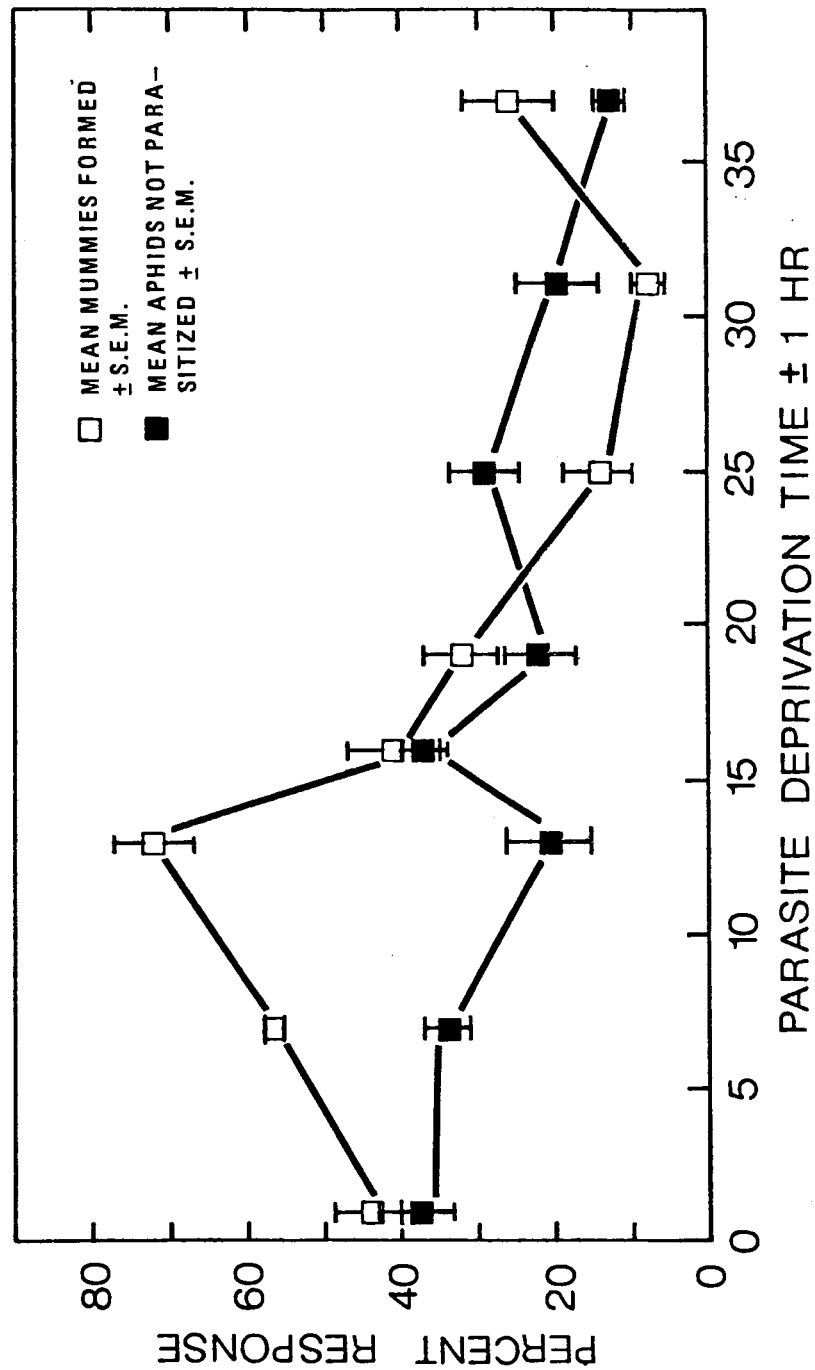
After 31 h the mean aphid mortality within 24 h becomes highly variable, either leveling off or decreasing.

The proportion of mummies formed was primarily affected by the increase in deprivation time (Tables VIII & IX). In run 1 deprivation time accounted for 85% of the variability; in run 2 it accounted for 86% of the variability. In both runs mummy formation exhibited a triphasic relationship (Fig. 8) with the increase in deprivation time. Mummification decreased as deprivation time increased from 13 h to 31 h, in run 1 ($r= -0.9587$, $P= 0.005$) and run 2 ($r= -0.8826$, $P= 0.024$). In the former, regression accounts for 91% of the variance from linearity; in the latter it accounts for 78% of the variance.

The proportion of aphids not parasitized was significantly affected by the increase in deprivation time (Tables VIII & IX; Fig. 8). In run 1 it decreased from 0.386 to 0.126 while in run 2 it decreased from 0.473 to 0.197. An increase in deprivation time accounted for 58% of the variability of the mean proportion of aphids not parasitized in run 1 and 72% of that variability in run 2.

The proportion of female parasites which emerged in the F1 generations ranged from 0.74 to 1.00 in run 1 and from 0.69 to 1.00 in run 2. The heterogeneity- χ^2 test was non-significant for both runs ($\chi^2_1= 5.736$, $P_1 > 0.5$, $df= 7$; $\chi^2_2 = 6.009$, $P_2 > 0.1$, $df= 6$). The proportion of female parasites produced in the F1 generation was 0.832 (S.E.= 0.030) in run 1 and was 0.818 (S.E.= 0.039) in run 2.

Figure 8. Percent response of female A. asychis (Walker), with increase in deprivation time, towards second-instar A. pisum (Harris).


□ MEAN MUMMIES FORMED ± S.E.M.
■ MEAN APHIDS NOT PARASITIZED ± S.E.M.
PERCENT RESPONSE
0
20
40
60
80
0
5
10
15
20
25
30
35
PARASITE DEPRIVATION TIME ± 1 HR

3. Summary.

The total number of parasites attacking remained relatively constant as the deprivation time was increased. However, the mean number of aphids attacked, per group of parasites, increased after the 19 h deprivation time. This suggests that individual parasites are attacking more aphids at the longer deprivation times.

With the increase in deprivation time the parasite changes its method of causing aphid mortality; oviposition being replaced by host paralysis. This becomes evident with deprivation times greater than 12 h.

The increase in deprivation time does not alter the ratio of male to female parasites of the F1 generation. At each deprivation time there are significantly more females than males being produced.

CHAPTER IV. APHELINUS ASYCHIS WITH THE POTATO APHID.

(A). Response of the parasite, when starved for 24 h, to five age-groups of potato aphids.

1. Relationship between aphid age and weight.

With an increase in aphid age from 24 h to 84 h there is an increase in aphid weight (Table XI). Significant deviations from linearity were found only in run 2 and accounted for 68.8% or the variance. The SNK analysis for groupings placed all weights independent of one another in run 1. Three weight groupings were found in run 2. These were 0.0431 mg, 0.0579 mg to 0.0609 mg, and 0.1191 mg to 0.1196 mg.

Increase in host weight was strongly correlated with the increase in host age (r_1= 0.987, P_1= 0.002; r_2= 0.929, P_2= 0.022). In run 1 this relationship was primarily linear (Fig. 9), while in run 2 it appeared quadratic. The deviations from linearity accounted for 69% of the variance in run 2.

2. Influence of data-collection intervals and host weight.

The data collected during the 4 one-half-hour data-collection intervals were comparable to each other; no added variance coming from the DCI (Tables XII & XIII). This applies to: (1) aphid mortality within 24 h, (2) mummies formed, and (3) aphids not parasitized. In both runs the DCI add variance to the aphids attacked.

In run 1 (Fig. 10) the mean proportion of aphids dead within 24 h was 0.095 and 0.063 ($\bar{x}$= 0.079, S.E.= 0.019) for host weights of 0.0521 mg and 0.0714 mg. This mortality increased

Figure 9. Mean dry weight, per host age of apterous *M. euphorbiae* (Thomas).

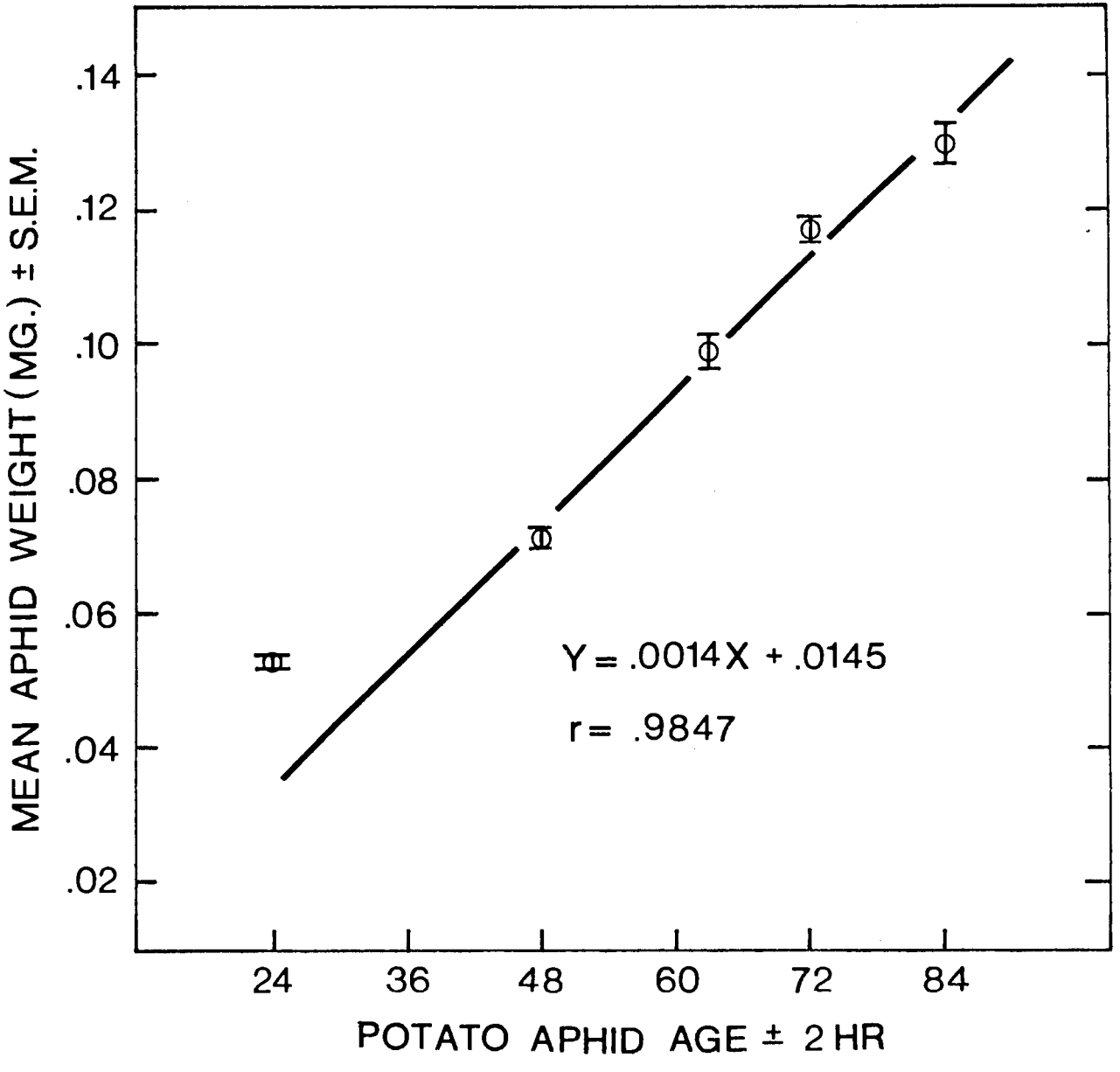
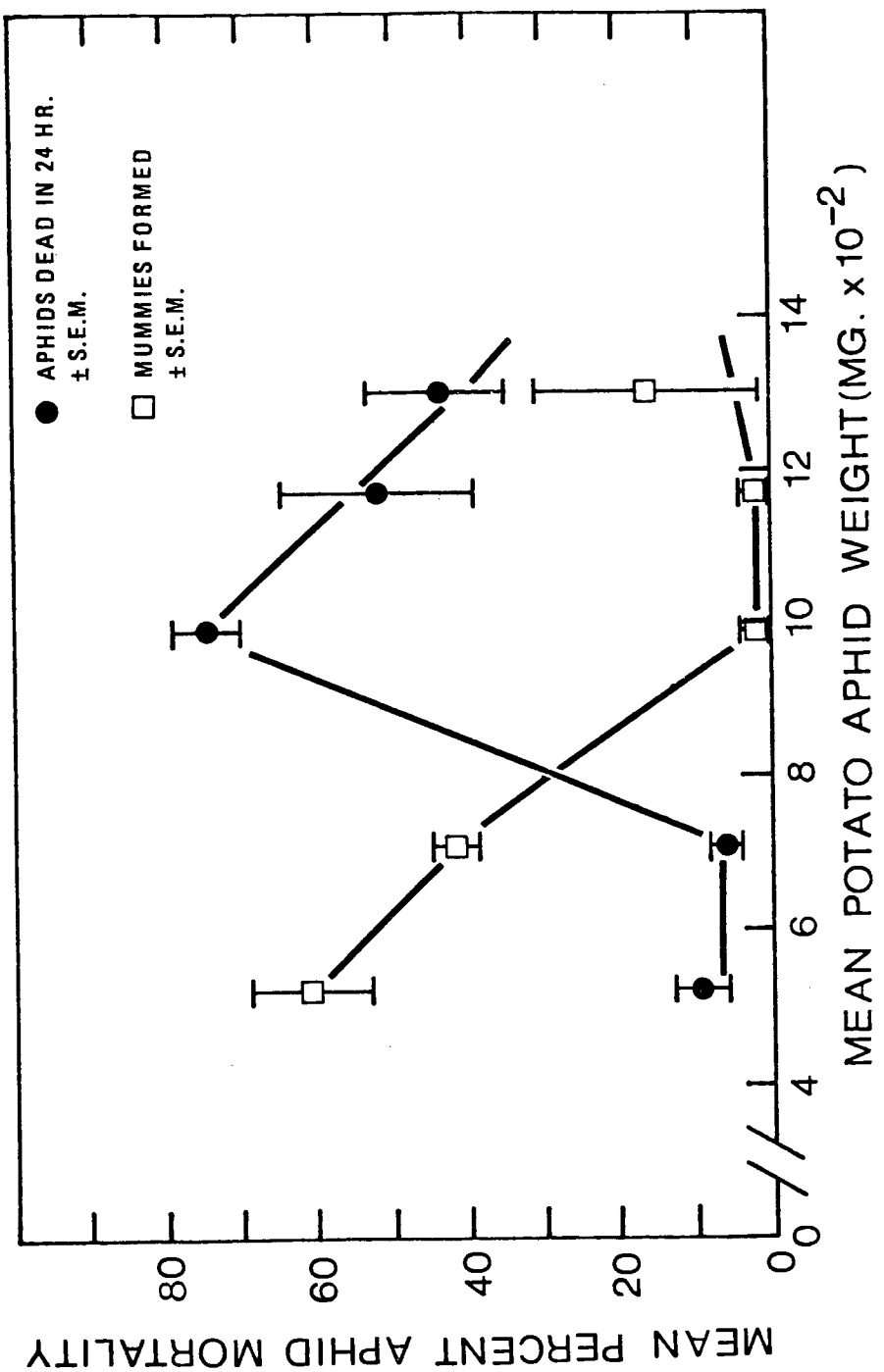

MEAN APHID WEIGHT (MG.) ± S.E.M.
.14
.12
.10
.08
.06
.04
.02
24
36
48
60
72
84
POTATO APHID AGE ± 2 HR
Y = .0014X + .0145
r = .9847

Figure 10. Mean percent mortality of M. euphorbiae (Thomas), with increase in host weight, due to attack by female A. asychis (Walker). Parasites deprived from host for 24 h prior to attack.


APHIDS DEAD IN 24 HR. ±S.E.M.
MUMMIES FORMED ±S.E.M.
MEAN PERCENT APHID MORTALITY
0
20
40
60
80
0
4
6
8
10
12
14
MEAN POTATO APHID WEIGHT (MG. x10^{-2})

to 0.749 at a host weight of 0.099 mg and then it subsequently decreased to 0.524 and 0.437 ($\bar{x}$= 0.481, S.E.= 0.076) at heavier host weights of 0.1144 mg and 0.1264 mg, respectively. The mean proportion of aphids attacked was relatively constant, ranging from 0.219 to 0.25 ($\bar{x}$= 0.236, S.E.= 0.017) for host weights of 0.0521 mg to 0.1144 mg. It then decreased to 0.1206 at a host weight of 0.1264 mg.

The proportion of mummies formed (Fig. 10) decreased from a mean of 0.609 to 0.049 with host weights one (0.0521 mg) to three (0.099 mg). Mummification then ranged from a mean of 0.049 (S.E.= 0.151) to 0.219 (S.E.= 0.149) at the heavier host weights.

Aphid mortality within 24 h and mummification of aphids in run 2 were similar to those of run 1. The mean proportion of aphid mortality within 24 h was 0.149 (S.E.= 0.033) at a potato aphid weight of 0.058 mg. This mortality then increased to 0.819 at a host weight of 0.061 mg. At host weights of 0.1191 mg and 0.1196 mg the proportion of aphid mortality decreased to 0.731 and 0.246, respectively. Mummy formation was constant, the mean proportion being 0.521, up to a host weight of 0.058 mg. This decreased to 0.038 at a host weight of 0.071 mg. Mummification was then variable, ranging from 0.0605 to 0.145 ($\bar{x}$= 0.1206, S.E.= 0.0196), with the heavier host weights.

The proportion of aphids attacked, though initially low ($\bar{x}$= 0.144, S.E.= 0.032) increased to a mean of 0.344 (S.E.=0.041) at a host weight of 0.1191 mg; thereafter it decreased to a mean of 0.157 (S.E.= 0.041) at a host weight of 0.1196 mg.

In run 1 the proportion of female parasites produced in the

F1 generation ranged from 0.42 to 1.00; in run 2 this ranged from 0.69 to 1.00. In either run the sex ratio data were homogeneous ($\chi^2_1 = 2.499$, $P_1 > 0.5$, df= 4; $\chi^2_2 = 1.754$, $P_2 > 0.5$, df=4) and the deviations from the assumed 1:1 sex ratio were in the same direction. Therefore the overall mean proportion of females produced in the F1 generation was 0.84 (S.E.= 0.114) for run 1, and 0.91 (S.E.= 0.061) for run 2.

(B). Increase in parasite deprivation time. Host = first-instar potato aphid (24 ± 2 h).

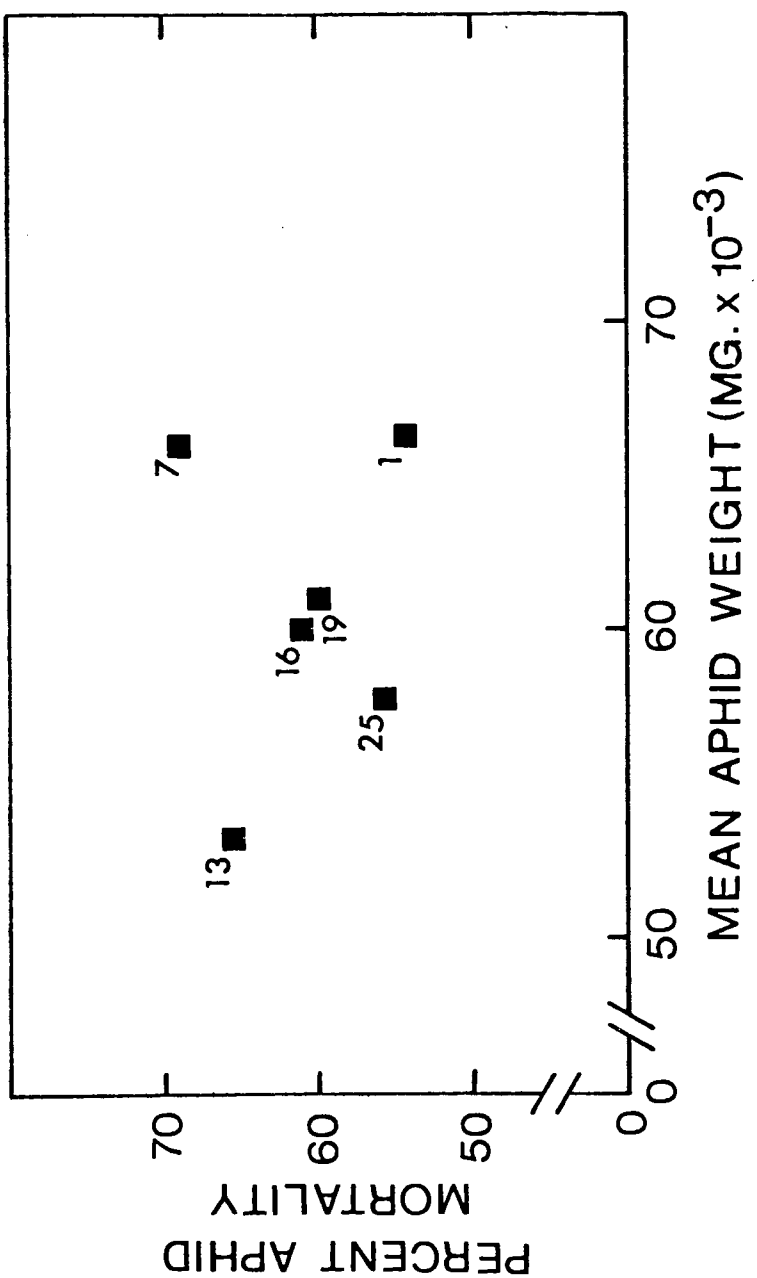
1. Host weight for each deprivation time.

In both runs significant differences exist between the mean aphid weights for each deprivation time interval (Table IV). In run 1 the mean potato aphid dry weight ranged from 0.053 mg to 0.066 mg ($\bar{x}$= 0.061, S.E.= 0.001); in run 2 this range was from 0.065 mg to 0.077 mg ($\bar{x}$= 0.070, S.E.= 0.001). This difference in aphid weights had a random affect on the mean aphid mortality within 24 h (Fig. 11), therefore this variation in host weight was ignored.

2. Influence of the data-collection and deprivation time intervals.

The 4 one-half-hour data-collection intervals (DCI) added some variance to some of the dependent variables (Tables XV & XVI). In run 1 the proportion of aphid mortality within 24 h and the proportion of mummies formed had an added variance due to the DCI. In run 2 the proportion of aphid mortality within 24 h, the proportion of aphids attacked, and the proportion of aphids not

Figure 11. Mean mortality within 24 h of first-instar *M. euphorbiae* (Thomas), at each host weight, per deprivation time for female *A. asychis* (Walker).


PERCENT APHID MORTALITY
70
60
50
0
50
60
70
MEAN APHID WEIGHT (MG. x 10⁻³)
7
1
16
19
25
13

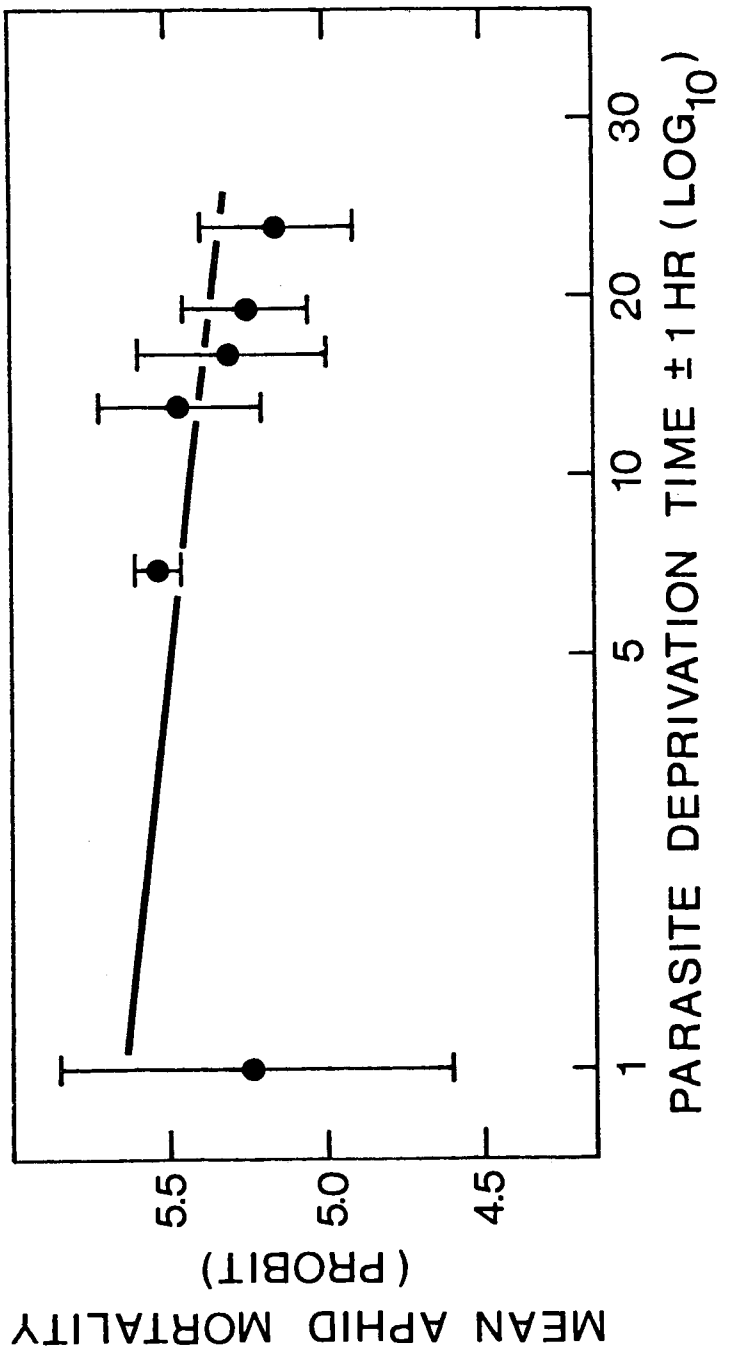
parasitized had an added variance due to the DCI.

The increase in deprivation time also significantly affected some of the dependent variables (Tables XV & XVI). In run 1 the mean proportion of aphids attacked increased from 0.179 to 0.693 as the deprivation time increased from 1 h to 19 h; at the 25 h deprivation time it decreased to 0.469. In run 2 the mean proportion of aphids attacked increased from 0.256 to 0.515 as deprivation time was increased from 13 h to 25 h. At the 31 h deprivation time the mean proportion of aphids attacked decreased to 0.478. In both runs the mean proportion of aphids attacked was correlated to the increase in deprivation time (r_1= 0.658, P_1= 0.078; r_2= 0.894, P_2= 0.053) but the relationship in each is non-linear (F_1= 3.05; P_1= 0.15; F_2= 7.98, P_2= 0.10).

A probit-$\log_{10}$ transformation was used on the mean proportion of aphid mortality within 24 h, at each deprivation time. First-instar potato aphid mortality within 24 h , in run 1 (Fig. 12), ranged from 5.5 probits (69%) to 5.15 probits (56%) from deprivation times of 1 h to 25 h. This mortality was negatively correlated (r= -0.971, P= 0.003) with deprivation times between 7 h and 25 h. In run 2 the mean aphid mortality within 24 h increased from 5.11 probits (54.7%) to 5.71 probits (76.2%) for deprivation times between 13 h and 31 h. Altough the observed mortality appeared to be positively correlated (r= 0.848, P= 0.053) with the increase in deprivation time, the correlation coefficient was not significant.

The proportion of mummies formed was highly variable as deprivation time was increased. In run 1 the proportion of mummies formed ranged from a mean of 0.036 to a mean of 0.345

Figure 12. Mean mortality within 24 h of first-instar *M. euphorbiae* (Thomas) for deprivation times (probit-$\log_{10}$ transformation) of *A. asychis* (Walker).


MEAN APHID MORTALITY
(PROBIT)
5.5
5.0
4.5
1
5
10
20
30
PARASITE DEPRIVATION TIME ± 1 HR (LOG10)

($\bar{\bar{x}}$= 0.202, S.E.= 0.037) over all deprivation times; in run 2 this ranged from a mean of 0.089 to 0.263 ($\bar{\bar{x}}$ = 0.160, S.E.=0.029).

The increase in deprivation time had no systematic effect on the mean proportion of aphids not parasitized; no correlation was evident with the increase in deprivation time (r_1= 0.021, P= 0.484; r_2= 0.491, P_2= 0.255). In run 1 the mean proportion of aphids not parasitized ranged from 0.061 to 0.423 ($\bar{\bar{x}}$ = 0.211, S.E.= 0.030) over all increases in deprivation time; in run 2 this range was from 0.176 to 0.293 ($\bar{\bar{x}}$ = 0.245, S.E.= 0.033).

In run 1 the proportion of female parasites in the F1 generation ranged from 0.57 to 1.00 with the increases in deprivation time; in run 2 this range was from 0.50 to 1.00. A heterogeneity-χ^2 test showed that these proportions were homogeneous (χ^2_1 = 2.758, $P_1 > 0.5$, df= 5; χ^2_2 = 1.247, $P_2 > 0.5$, df= 3). The overall mean of the proportion of female parasites of the F1 generation is therefore 0.75 (S.E.= 0.080) in run 1, and 0.755 (S.E.= 0.102) in run 2.

(C). Increase in parasite deprivation time. Host= second-instar potato aphid (48 ± 2 h).

1. Host weight for each deprivation time interval.

In both runs the mean second-instar potato aphid dry weight for each deprivation time are significantly different from one another (Table XVII). There was no systematic increase or decrease in aphid dry weight as deprivation time was increased. In run 1 the mean aphid dry weight ranged from 0.076 mg to 0.092 mg ($\bar{x}$ = 0.082, S.E.= 0.002) while in run 2 the mean aphid dry weight

ranged from 0.066 mg to 0.093 mg ($\bar{\bar{x}}$= 0.078, S.E.= 0.003).

2. Influence of data-collection and deprivation time intervals.

The 4 one-half-hour data-collection intervals (DCI) affected only the mean proportion of aphids attacked (Tables XVIII & XIX). In run 1 the proportion of aphids attacked increased within the DCI in each of the 7 h, 13 h, 16 h, and 31 h deprivation times; in run 2 it increased within the DCI of the 7 h and 13 h deprivation times (Table XX).

The increase in deprivation time affected the proportion of aphids dead within 24 h and the proportion of aphids attacked (Tables XVIII & XIX). The mean proportion of aphids attacked tends to increase as the deprivation time is increased. In run 1 the mean proportion of aphids attacked increased from 0.148 (at 1 h) to 0.514 (at 25 h); in run 2 it increased from 0.078 (at 1 h) to 0.203 (at 32 h).

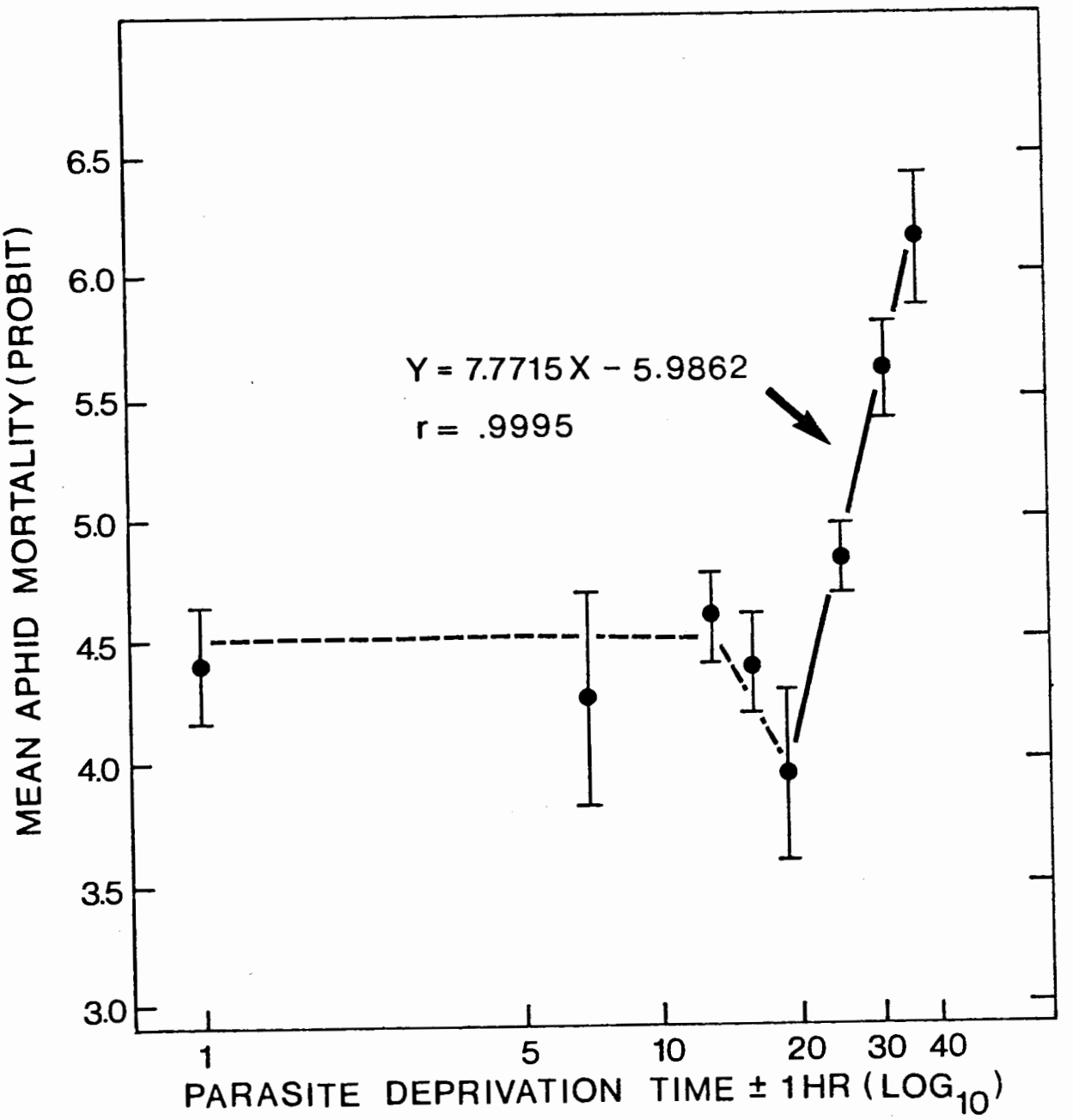
There was a slight increase in the mean proportion of aphids dead within 24 h between deprivation times of 1 h and 16 h, for both runs. In run 1 this increase was from 4.429 probits (28%) to 4.631 probits (35%) ($\bar{\bar{x}}$ =0.3075, S.E.= 0.0357); in run 2 this increase was from 3.735 probits (10%) to 4.055 probits (17%) ($\bar{\bar{x}}$ =0.138, S.E.= 0.024). In run 1 aphid mortality increased linearly (r= 0.987, P= 0.007; F=73.1, P= 0.013) from 4.107 probits (18%), at 19 h, to 6.094 probits (86%), at 37 h. In run 2 aphid mortality within 24 h increased linearly (r= 0.991, P= 0.042; F= 57.88, P= 0.083) from 3.419 probits (6%), at 19 h, to 5.383 probits (65%), at 31 h. Run 1 with the regression equation and regression coefficient is found in Figure 13.

In run 1 the mean proportion of mummies formed decreased from 0.5208 (S.E.=0.1679), at 1 h, to 0.1027 (S.E.= 0.0465), at 31 h, and then 0.00 at 37 h. In run two the mean proportion of mummies formed increased from 0.3095 (S.E.=0.1349), at 7 h, to 0.6905 (S.E.=0.0957), at 16 h. It then decreased from 0.50 (S.E.=0.0794), at 19 h, to 0.1598 (S.E.=0.0624), at 31 h.

In run 1 the proportion of aphids not parasitized remained relatively constant, the mean being 0.3316 (S.E.=0.0534) from deprivation times of 1 h to 13 h. This proportion then decreased from 0.4568 (S.E.=0.153), at 16 h, to 0.1222 (S.E.=0.062), at 37 h. In run 2 the mean proportion of aphids not parasitized decreased from 0.6547 (S.E.=0.1651), at 7 h, to 0.3314 (S.E.= 0.0160) at 37 h.

In run 1 the proportion of female parasites in the F1 generation was relatively constant, ranging from 0.66 to 0.88 as the deprivation time was increased; in run 2 this ranged from 0.60 to 1.00. A heterogeneity- χ^2 showed that the data in each of the runs were homogeneous (χ^2_1 = 1.731, $P_1 > 0.9$, df= 6; χ^2_2 = 2.424, $P_2 > 0.5$, df= 5) and that the deviations from the assumed 1:1 sex ratio are in the same direction. The overall mean proportion of females emerging was 0.745 (S.E.= 0.036) in run 1 and 0.885 (S.E.= 0.061) in run 2.

Figure 13. Mean mortality within 24 h of second-instar *M. euphorbiae* (Thomas), per deprivation time (Probit-$\log_{10}$ transformation) for female *A. asychis* (Walker).


MEAN APHID MORTALITY (PROBIT)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
Y = 7.7715 X - 5.9862
r = .9995
1
5
10
20
30
40
PARASITE DEPRIVATION TIME ± 1HR (LOG10)

(D). Summary.

The response of female A. asychis to potato aphid hosts is highly variable. The following trends are evident even though the reasons for the observed variability are not clear:

(1) Female A. asychis upon coming in contact with progressively heavier hosts, kill a greater proportion of the hosts by paralysis than by oviposition.

(2) A greater proportion of the hosts, be they first- or second-instar aphids, are attacked as the deprivation time is increased. The upper limit of the attack rate is reached at the 25 h deprivation time with first-instar hosts and the 32 h deprivation time with second-instar potato aphid hosts.

(3) The pattern for aphid mortality within 24 h is markedly different between the two instars as the deprivation time is increased. First-instar aphid mortality within 24 h ranged from 69% to 56% as the deprivation time was increased from 1 h to 25 h. In contrast, second-instar hosts had a lower mortality (14% to 35%) with deprivation times less than 19 h; from 19 h to 37 h this mortality increased linearly. In run 1 this increase was from 19% to 86%; in run 2 it was from 6% to 65%.

(4) Neither changing the weight of the host, the host-instar or the parasite deprivation time altered, to any degree, the sex ratio of the parasite progeny in the F1 generation; the ratio averaged 3 females to 1 male.

CHAPTER V. ALTERNATE HOST AND NYMPHAL DEVELOPMENT.

1. Alternate host.

The alternate host species experiment was repeated once on a different day. The weights of the second-instar pea aphids differ from each other on the two days. This was also true of the weights of the second-instar potato aphid. This within-species weight difference accounted for only 3.7% of the total variability in host dry weight. The weight of each host species was therefore combined to calculate the mean of either host dry weight. The mean dry weight of second-instar pea aphids was 0.0558 (S.E.= 0.0008) while for second-instar potato aphids the mean dry weight was 0.0866 (S.E.= 0.0019). These mean weights are significantly different from each other (F= 297.95; P 0.01).

The differences in test-days and host species had a significant effect on the proportion of aphids attacked, the proportion of aphids dead within 24 h and the proportion of mummies formed. The proportion of aphids not parasitized was not affected by either test-days or host species (Table XXI). It is inevitable that the different test-days would add variance to the results. This is most likely due to differences in environmental conditions between the two tests.

The behaviour of the parasite differed between the host species. A greater proportion of pea aphids ($\bar{x}$= 0.693;S.E.=0.027) that potato aphids ($\bar{x}$= 0.205,S.E.= 0.019) were attacked by the parasite. Of those hosts attacked, a greater proportion of the potato aphids ($\bar{x}$= 0.657, S.E.= 0.045) than pea aphids ($\bar{x}$=0.366;

S.E.= 0.095) died within 24 hours. Consequently, a greater proportion of mummies were formed from pea aphid hosts ($\bar{x}$ =0.323; S.E.= 0.084) than potato aphid hosts ($\bar{x}$ = 0.158, S.E.= 0.021). Finally, there was no significant difference in the proportion of aphids not parasitized between the pea aphid hosts ($\bar{x}$ = 0.318, S.E.= 0.032) and the potato aphid hosts ($\bar{x}$ = 0.2004, S.E.= 0,047).

2. First- and second-instar developmental time.

The developmental time of the first-instar pea aphid ranged from 28.62 h to 49.62 h, with a mean of 39.12 h (S.E.= 0.39). The developmental time of the first-instar potato aphid ranged from 40.29 h to 52.24 h, with a mean of 46.62 h (S.E.= 0.91). The variance of the mean developmental time of the first-instar pea aphids (s^2= 10.515) and that of the first-instar potato aphids (s^2= 12.568) are very similar. A t-test showed that the mean developmental time of these hosts are significantly different (t= -7.762, $t_{.05}$= 1.989); first-instar potato aphids having a longer developmental time than first-instar pea aphids. The 95% confidence limits of the difference between the means are -9.171 to -5.429, the zero point (i.e. no difference) being excluded from the range.

The developmental time of the second-instar pea aphids ranged from 28.06 h to 47.56 h, with a mean of 37.81 h (S.E.=0.4) while that of the second-instar potato aphid ranged from 38.44 h to 66.69 h, with a mean of 52.56 h (S.E.= 1.802). The variances of the mean of second-instar pea aphids (s^2= 11.025) and that of second-instar potato aphids (s^2= 48.709) are unequal therefore an

approximate t-test was used to take into account this heteroscedasticity (Sokal and Rohlf 1969). The approximate t-test was significant ($t' = -7.987$, $t'_{.05} = 2.138$); therefore the means were significantly different. The developmental period of the second-instar potato aphid was significantly longer than that of the second-instar pea aphid.

CHAPTER V. DISCUSSION AND CONCLUSION.

(A). General.

The age of the parasite and its hunger level, as discussed below, were standardized just prior to the start of each experiment. Still, parasite behavioural differences are evident in the results of the two runs of each experiment. These differences are presumably due to environmental factors which could not be controlled. In addition, the nutritional quality of the bean plants could not be controlled. This may have affected the physiology of the aphids and hence their response to paralysis.

The primary factors which influence the behaviour of adult female A. asychis towards its hosts are: (1) the age of the parasite, (2) the number of hosts exposed to the parasite for 24 h, (3) the number of generations the parasite has been in association with its host, (4) the age of the host, and (5) the nutritional stress imposed on the parasite (Michel 1967; Monadjemi 1972). The age of the parasite and the number of hosts exposed to the parasite for 24 h were incorporated into each experiment; the former, to standardize the parasite age and the latter, to standardize the hunger level of the parasite. The predatory, host-feeding behaviour of A. asychis, just after emergence appears to be the consequence of the female requiring some essential nutrients needed for öogenesis. The post-emergence feeding was observed to last up to 5-days (Esmaili & Wilde 1972; Hamilton 1973; Michel 1967). Monadjemi (1972) has further demonstrated that 6-to-15-day-old females would attack and cause the mummification of the greatest number of aphids. In my experiments 7 ± 2-day-old parasites were used to ensure that the parasites

were in their oviposition cycle. In addition, 24 hours prior to any experiment, the parasites were exposed to hundreds of first- and second-instar nymphs. this allowed those parasites which were above a minimum hunger level to feed on as many hosts as they desired. Any response of the parasite to an increase in hunger level would be due to the hunger level imposed on the parasite during the experiment; the hunger level prior to the experiments in effect being zero. Any change in the parasite's response to the host weight or host species would primarily be due to the change in these variables.

The third factor, the number of generations that the parasite is associated with its host will influence the behaviour of the parasite on the host. Michel (1970) in her studies with A. asychis, attacking various aphid hosts, including the pea aphid, found that when the parasite was exposed for the first time to an alternate host species, the fecundity and longevity of the parasite and the mummification of the alternate host all decreased. Furthermore, she found that after three generations on the alternate host, the fecundity and longevity of the parasite and the mummification of the alternate host all returned to levels which were comparable to that of the initial host species.

In my studies involving the increase in aphid weight or the increase in deprivation time, the parasites were reared on the pea aphid or potato aphid for over 10 generations. In the alternate host experiments at least 7 generations elapsed on the

initial hosts before the parasites were exposed to the alternate hosts. This should have nullified any effect of the initial host on the behaviour of the parasites. The last two factors, the age of the host and the nutritional stress imposed on the parasite are main factors considered in this study.

(B). Host age.

Various authors have stated that Aphelinus prefers first-or second-instar aphids either for oviposition or for parasite feeding (Cate et al. 1977; Griswold 1929; Hagen and van den Bosch 1968; Hamilton 1973; Hartley 1922; Raney et al. 1971; Schlinger and Hall 1959). The preference for either instar is likely due to the weight (or size) and shape of the instar; these physical characteristics being different between one instar and the next, both within and between host species.

For A. pisum and M. euphorbiae the relationship between host age and weight was primarily linear over the first 84 hours of host-age (Figs.1,9). A comparison of the regression lines indicates that at the same host-age, A. pisum is always significantly lighter in weight than M. euphorbiae. This may be one of the reasons why A. asychis attacked more pea aphid hosts than potato aphid hosts, at every increase in host age.

Host weight (or size) is probably the main deterrent to the adult parasite when attacking heavier hosts since the larger aphids can ward off attack by kicking the parasite. However, this would not explain the large difference in the attack rate between the two host species at the lighter host weights. For example,

at a host weight of approximately 0.05 mg only 22% of M. euphorbiae hosts were attacked while 87% of A. pisum hosts were attacked. The parasite, prior to attack, scans its host using its antennae (Boyle and Barrows 1978). Antennal receptors may relay information to the parasite about the kind and the general quality of the host. Differences in host quality, if any, may explain the observed differences in the attack rates of the parasites.

The manner by which the parasite caused host mortality changes as the parasite comes in contact with heavier (or larger) hosts. With either host species, host mortality due to oviposition decreases while mortality within 24 h, due to non-recovery from host paralysis, increases with an increase in host weight. Both types of mortality follow a curvilinear relationship (Figs. 3, 10). The female parasite moves its head from side to side and taps the host with its antennae upon coming in contact with the host. This behaviour of A. asychis has also been noted by Boyle and Barrows (1978). Moran et al. (1969) presume that such behaviour serves in olfactory identification of the host by the wasp. The head movements may also be used to evaluate the size of the host. Host size (or weight) may possibly trigger either of two responses: (1) oviposition or (2) parasite feeding. Some selective process, with respect to the manner by which the parasite causes host mortality, appears to occur between host weights of 0.04 mg and 0.06 mg of the pea aphid and 0.07 mg and 0.09 mg of the potato aphid (Figs. 3, 10). Somewhere within these ranges the weight (or size) of the host appears to influence the

parasite's manner of causing aphid mortality.

Potato aphid mortality is primarily due to oviposition at weights of about 0.07 mg whereas above 0.09 mg, mortality is mainly due to paralysis. Pea aphid mortality is mainly due to oviposition at weights between 0.04 mg and 0.05 mg. Aphids weighing less than 0.04 mg presumably do not contain sufficient quantities of hemolymph to dilute the venom to a level from which they can successfully recuperate from paralysis. Pea aphid mortality at weights above 0.06 mg is mainly due to paralysis.

(C). Nutritional stress of the parasite.

1. A. asychis with the pea aphid.

The level of nutritional stress of the parasite influences the response of the parasite to its hosts. Total aphid mortality, which is the number of mummies formed and the number of aphids dead within 24 h, for both first- and second-instar pea aphids is relatively constant as deprivation time is increased, being 78% and 70% respectively. Where change occurs is in the parasite's method of causing aphid mortality. With both instars, mortality due to mummification is replaced by mortality due to paralysis as the deprivation time is increased (Figs. 5-8).

The increase in mortality within 24 h (paralysis) was presumably due to the quantity of venom injected into the host. After the parasite has inserted its ovipositor into the host, the host changed color from the usual green to yellow-green. Boyle and Barrows (1978) had observed this change in coloration when A. asychis attacked S. graminum and attributed this to a

paralyzing venom or substances introduced during parasite feeding. Parasite feeding was not allowed to occur in my study. It is therefore believed that a venom is causing the color change. Piek and Spanjer (1978) have characterized the venom of the solitary wasp Microbracon hebetor (Say) as containing protein toxins of high molecular weight. Possibly the venom of A. asychis is like that of M. hebetor.

The relationship between aphid mortality within 24 h and the increase in parasite deprivation time it triphasic, with both instars. Each have low levels of mortality within 24 h, at deprivation times less than 13 h. The amount of venom is probably being sufficiently diluted throughout the host's hemolymph allowing a majority of the hosts to recover from the paralysis. At deprivation times longer than 25 h, mortality within 24 h remained high, appearing to level off. It is speculated that the maximum amount of venom, defined by the maximum storage capacity of the parasite's acid gland, is most likely being injected into the host at the 25 h deprivation time. Further increases in deprivation time would not produce additional increases in the amount of venom being injected into the hosts.

Aphid mortality within 24 h increases linearly between deprivation times of 13 h to 25 h (Figs. 5,7). The parasite's hunger level probably influences the quantity of venom which is injected into the host. An increase in deprivation time will increase the quantity of venom being injected causing greater proportions of aphids to be killed. The slopes of aphid mortality within 24 h, with deprivation time, are not equal. The slope of

first-instar pea aphid mortality is 11.847 while that of second-instar pea aphid mortality it 5.283; hence the rate of mortality of first-instar hosts is greater than that of second-instar hosts.

The mean weight of first-instars ($\bar{x}$ = 0.038 mg, S.E.= 0.0001) is significantly lower than that of second-instar aphids ($\bar{x}$ = 0.0673, S.E.= 0.0016). This difference in weights (and sizes) of the two instars may explain the differences in the rates of aphid mortality. The amount of hemolymph in first-instar hosts is less than that in second-instar hosts,therefore the dilution of venom is less in first- than second-instars.

Nutritional stress can also directly affect the parasite with respect to egg production. Öosorption or termination of öogenesis may result; the parasite conserving energy for its own survival (Flanders 1942; Boyle and Barrows 1978). In these studies with A. asychis attacking the pea aphid, there does not appear to be any selective pressure imposed on fertilized or non-fertilized eggs; the sex ratio remaining in favour of females with each increase in deprivation time.

2. A. asychis with the potato aphid.

The large variability in the data has made analysis and subsequent interpretation of the results, at times, very difficult. It is believed that this variability is largely due to a non-preference of the wasp for the potato aphid. Behavioural trends still exist, primarily with the proportion of aphids attacked and the proportion of aphids dead within 24 h, for both instars.

The variability in the data, at each deprivation time, was sufficiently great as to obscure group differences, if any, that might exist in the proportion of aphids attacked. Still, a trend does exist; the mean number of aphids attacked decreases with the increase in deprivation time. This trend is curvilinear, with both host instars. Even though A. asychis appears not to prefer the potato aphid, the increase in nutritional stress (deprivation time) induces the parasite to attack.

First-instar potato aphid mortality within 24 h remains relatively high (Fig. 12) with each increase in deprivation time. These hosts appear incapable of tolerating any amount of venom which the parasite injects. In contrast, second-instar aphid mortality within 24 h (Fig. 13) increased, but only for deprivation times from 19 h to 31 h (or 37 h). In run 1 the mortality within 24 h increased from 19% to 86% between these deprivation times; in run 2 this mortality increased from 6% to 65%. At deprivation times less than 19 h mortality within 24 h, in run 1, ranged from 28.4% to 35.6%, with a mean of 30.7% (S.E.= 0.036); in run 2 it ranged from 10.2% to 17.2%, with a mean of 13.8% (S.E.= 0.024).

The heavier (and larger) second-instar hosts could better withstand the amount of venom that the parasite injects at deprivation times less than 19 h. This would explain the lower levels of second-instar aphid mortality within 24 h as compared to that of first-instar hosts. Deprivation times which are above 19 h presumably cause greater levels of stress in the parasite. At each increase in deprivation time, more hosts are being used for

a food source rather than for oviposition; the parasite attempting to increase its longevity at the expense of its fecundity.

Though the increase in deprivation time affected the parasite's manner of causing host mortality, it does not appear to alter the production of fertilized or non-fertilized eggs; the sex ratio always favouring the female progeny at each increase in deprivation time.

(D). Alternate host study.

The influence of the initial host species may affect the behaviour of the parasite on the alternate host species. When A. asychis is in the presence of an alternate host for the first time, the mummification of hosts decreased and the host mortality within 24 h increased (Michel 1970, 1973; Monadjemi 1972).Michel (1970) found that after the parasite was reared on alternate hosts for three generations, A. asychis would cause mummification in hosts which were comparable to that on the initial host, Rhopalosiphum padi Linnaeus.

Here, A. asychis was initially reared on A. pisum and then transferred to M. euphorbiae. Both colonies were maintained for over 7 generations before the alternate host studies were performed. Presumably both colonies of parasites were well adapted to their respective hosts. Any effect of the founder colony (i.e. A. pisum) prior to host transfer would no longer be of any consequence.

Here, A. asychis prefers to attack second-instar A. pisum ($\bar{x}$= 0.6935) rather than second-instar M. euphorbiae ($\bar{x}$= 0.2049).

In addition, A. asychis causes a greater proportion of mummy formation ($\bar{x}$ = 0.3234) in the pea aphid than the potato aphid ($\bar{x}$ = 0.1525). Finally, the proportion of aphids dead within 24 h is greater in the potato aphid ($\bar{x}$ = 0.6583) than that in the pea aphid ($\bar{x}$ = 0.3664).

(E). Conclusions.

Boyle and Barrows (1978) in studying the oviposition and feeding behaviour of A. asychis on S. graminum noted that a gradual color change occurred in the host from the usual green to yellow-green, to yellow and finally to brown. They felt that a paralyzing agent or other substances introduced during the wasps feeding, or both, brought about this color change. Cate et al. (1973) also noticed this in the same host. Here, wasps after retracting their ovipositor from either the pea aphid or potato aphid hosts, were removed from the aphids, thus ensuring that no parasite feeding could occur. While the parasite's ovipositor was inserted into the host, a host color change was observed. The color of the pea aphid changed from green to yellow-green while the color of the potato aphid changed from pink to orange. It would appear to be the paralyzing agent rather than feeding which causes the change in host coloration.

Aphid mortality within 24 h is attributed here to female A. asychis paralyzing its hosts. Paralysis, in all probability, is due to venom injection and not to damage inflicted upon the host by insertions of the parasite's ovipositor; the wasp was allowed to insert its ovipositor into the host only once. It is concluded

that host paralysis is a third method by which the parasite causes aphid mortality; the other methods being oviposition and parasite-feeding. Thus, at least three factors are influencing the relative impact of host paralysis on aphid mortality.

First is the degree of nutritional stress imposed on the parasite. It is speculated that the wasp injects greater amounts of venom into the host as the level of stress (or deprivation time) is increased. There are likely lower and upper limits to this phenomenon. The lower limits would be governed by the need for a minimum hunger level to be surpassed, while the upper level would possibly be governed by the maximum storage capacity of the acid gland; the gland believed to produce the venom.

Second is the weight of the host. It is the lighter, first-instar hosts, within either host species, which have higher levels of aphid mortality within 24 h (paralysis) with each increase in deprivation time. When deprivation time is constant at 24 h and host weight is increased, it is the older (or heavier hosts) which have a higher level of mortality within 24 h.

Third is the host species. A. asychis, on coming in contact with a host, was observed to tap the host with its antennae and also to sway its head back and forth. This has also been noted by Boyle and Barrows (1978) and Hamilton (1973). Moran et al. (1969) presumed that such behaviour functions in olfactory identification of the host by the wasp. The wasp would also be evaluating the host with respect to size. Here, A. asychis prefers to attack the smaller host, the pea aphid, over the potato aphid. A. asychis can be induced to attack a greater

proportion of potato aphids by increasing the deprivation time but at no time does it surpass the attack rate on the pea aphid.

The significance of the results of this study lies in the creation of modeling systems for biological control. These systems attempt to predict and assess the degree to which parasites and predators are effective control agents. In modeling systems involving aphelinids, the hunger level of the parasite should be taken into account. This is especially true if one is attempting to assess the immediate impact of this parasite on its host. The parasite's hunger level appears to determine the manner by which the parasite causes host mortality; oviposition appears to be favoured over paralysis at the lower hunger levels whereas the opposite occurs at the higher hunger levels.

APPENDIX

Table I. Anova-1 and linear regression of pea aphid age versus weight.

RUN ONE

SOURCE	df	MS	F
Among groups	5	0.0280	446.66**
linear	1	0.1360	136.00**
deviations	4	0.0010	16.67*
Within groups	114	0.00006	
Total	119		

*= significant at $P < 0.05$
**=significant at $P < 0.01$

Regression equation: $Y = 0.0102 + 0.0016X$

RUN TWO

SOURCE	df	MS	F
Among groups	5	0.0149	186.25**
linear	1	0.0726	181.50**
deviations	4	0.0004	5.00*
Within groups	103	0.00008	
Total	108		

*= significant at $P < 0.05$
**=significant at $P < 0.01$

Regression equation: $Y = 0.0209 + 0.0012X$

Table II. Anova-2 of the 4 one-half hour data-collection intervals versus pea aphid dry weight, for each dependent variable: A. asychis females deprived of host for 24 hours prior to attack.(Run One).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0208	1.202
	Weight	5	0.1589	9.185*
	Error	15	0.0173	
	Total	23		
Aphids attacked	Intervals	3	0.0132	2.095
	Weight	5	0.0642	10.206*
	Error	15	0.0063	
	Total	23		
Mummies formed	Intervals	3	0.0014	0.378
	Weight	5	0.1833	49.540*
	Error	15	0.0037	
	Total	23		
Aphids not parasitized	Intervals	3	0.0225	2.163
	Weight	5	0.0265	2.548
	Error	15	0.0104	
	Total	23		

*= significant at $P < 0.05$

Table III. Anova-2 of the 4 one-half hour data-collection intervals versus pea aphid dry weight, for each dependent variable: A. asychis females deprived of host for 24 hours prior to attack (Run Two).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0027	0.391
	Weight	5	0.1180	17.101*
	Error	15	0.0069	
	Total	23		
Aphids attacked	Intervals	3	0.0018	0.486
	Weight	5	0.0211	5.703*
	Error	15	0.0037	
	Total	23		
Mummies formed	Intervals	3	0.0031	0.659
	Weight	5	0.2808	59.745*
	Error	15	0.0047	
	Total	23		
Aphids not parasitized	Intervals	3	0.0048	0.727
	Weight	5	0.0609	9.227*
	Error	15	0.0066	
	Total	23		

* = significant at $P < 0.05$

Table IV. Anova-1 and linear regression of first-instar pea aphid dry weight versus parasite deprivation time.

RUN ONE

SOURCE	df	MS[a]	F
Among groups	6	0.4783	3.702*
linear	1	0.1950	0.364
deviations	5	0.5350	4.141*
Within groups	133	0.1292	
Total	139		

RUN TWO

SOURCE	df	MS[a]	F
Among groups	7	0.5008	3.946*
linear	1	0.0678	0.118
deviations	6	0.5730	4.515*
Within groups	152	0.1269	
Total	159		

a; MS x 10^{-4}

* = significant at $P < 0.05$

Table V. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time for each dependent variable: Host= first-instar pea aphid (Run One).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0061	1.848
	Times	6	0.3261	98.818**
	Error	18	0.0033	
	Total	27		
Aphids attacked	Intervals	3	0.0025	0.675
	Times	6	0.0179	4.837*
	Error	18	0.0037	
	Total	27		
Mummies formed	Intervals	3	0.0021	0.389
	Times	6	0.2123	39.315**
	Error	18	0.0054	
	Total	27		
Aphids not parasitized	Intervals	3	0.0128	2.612
	Times	6	0.0228	4.653*
	Error	18	0.0049	
	Total	27		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table VI. Anova-2 of the 4 one-half hour data-collection Intervals versus parasite deprivation time, for each dependent variable: Host = first-instar pea aphid (Run Two).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0012	0.428
	Times	7	0.5941	212.178**
	Error	21	0.0028	
	Total	31		
Aphids attacked	Intervals	3	0.0078	2.108
	Times	7	0.0249	6.729*
	Error	21	0.0037	
	Total	31		
Mummies formed	Intervals	3	0.0007	0.437
	Times	7	0.5517	344.812**
	Error	21	0.0016	
	Total	31		
Aphids not parasitized	Intervals	3	0.0028	1.12
	Times	7	0.0087	3.48*
	Error	21	0.0025	
	Total	31		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table VII. Anova-1 and linear regression of second-instar pea aphid dry weight versus parasite deprivation time. (Run Two)[a].

SOURCE	df	MS[b]	F
Among groups	7	0.2639	0.306
linear	1	0.2958	1.144
deviations	6	0.2586	0.299
Within groups	72	0.8623	
Total	79		

a; no data for Run one.
b; MS x 10^{-3}

Table VIII. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = second-instar pea aphid (Run One)[a].

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0057	0.663
	Times	7	0.2533	29.453**
	Error	21	0.0086	
	Total	31		
Mummies formed	Intervals	3	0.0277	4.328
	Times	7	0.1836	28.687**
	Error	21	0.0064	
	Total	31		
Aphids not parasitized	Intervals	3	0.0110	1.571
	Times	7	0.0355	5.071*
	Error	21	0.0070	
	Total	31		

a; data not collected for aphids attacked.
* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table IX. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = second-instar pea aphid (Run Two)[a].

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0557	9.772*
	Times	7	0.1500	26.316**
	Error	21	0.0057	
	Total	31		
Mummies formed	Intervals	3	0.0229	3.094*
	Times	7	0.2032	27.459**
	Error	21	0.0074	
	Total	31		
Aphids not parasitized	Intervals	3	0.0037	0.7115
	Times	7	0.0440	8.461*
	Error	21	0.0052	
	Total	31		

a; data not collected for aphids attacked.
* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table X. Pearson correlation coefficients of the dependent variables for the 4 one-half hour data-collection intervals, for each parasite deprivation time. Host = second-instar pea aphid.

RUN ONE

DEPENDENT VARIABLE		PARASITE DEPRIVATION TIME (hours)							
		1	7	13	16	19	25	31	37
Mummies formed	r	-0.9479	-0.2763	-0.6556	-0.7636	-0.9319	-0.9884	-0.7494	-0.0352
	P	0.026	0.362	0.172	0.118	0.034	0.006	0.125	0.482

RUN TWO

DEPENDENT VARIABLE		PARASITE DEPRIVATION TIME (hours)							
		1	7	13	15	20	26	31	37
Mummies formed	r	0.0250	-0.7783	-0.3685	-0.8830	-0.5622	-0.1308	-0.1846	0.7239
	P	0.487	0.111	0.316	0.058	0.219	0.435	0.408	0.138
Aphid mortality within 24 h.	r	0.9870	0.8472	0.2748	0.7837	0.5604	-0.0080	0.9225	0.5010
	P	0.007	0.076	0.363	0.108	0.220	0.496	0.039	0.250

Table XI. Anova-1 and linear regression of potato aphid age versus weight.

RUN ONE

SOURCE	df	MS	F
Among groups	4	0.0201	59.118**
linear	1	0.0780	97.50**
deviations	3	0.0008	2.353
Within groups	90	0.00034	
Total	94		

** = significant at $P < 0.01$

Regression equation: $Y = 0.0145 + 0.0014X$

RUN TWO

SOURCE	df	MS	F
Among groups	4	0.0245	128.947**
linear	1	0.0184	0.694
deviations	3	0.0265	139.474**
Withing groups	90	0.00019	
Total	94		

** = significant at $P < 0.01$

Regression equation: $Y = \bar{0}.0055 + 0.0018X$

Table XII. Anova-2 of the 4 one-half hour data-collection intervals versus potato aphid dry weight, for each dependent variable: A. asychis females deprived of host for 24 hours prior to attack (Run One).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0094	0.352
	Weight	5	0.3419	12.805*
	Error	15	0.0267	
	Total	23		
Aphids attacked	Intervals	3	0.0108	3.857*
	Weight	5	0.0114	4.071*
	Error	15	0.0028	
	Total	23		
Mummies formed	Intervals	3	0.0395	1.881
	Weight	5	0.2395	11.405**
	Error	15	0.0210	
	Total	23		
Aphids not parasitized	Intervals	3	0.0615	1.557
	Weight	5	0.0537	1.359
	Error	15	0.0395	
	Total	23		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table XIII. Anova-2 of the 4 one-half hour data-collection intervals versus potato aphid dry weight, for each dependent variable: A. asychis females deprived of host for 24 hours prior to attack (Run Two).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0222	1.247
	Weight	4	0.4355	23.466**
	Error	12	0.0178	
	Total	19		
Aphids attacked	Intervals	3	0.0161	7.318*
	Weight	4	0.0340	15.454**
	Error	12	0.0022	
	Total	19		
Mummies formed	Intervals	3	0.0032	0.262
	Weight	4	0.2393	19.615**
	Error	12	0.0122	
	Total	19		
Aphids not parasitized	Intervals	3	0.0360	1.558
	Weight	4	0.1440	6.234*
	Error	12	0.0231	
	Total	19		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table XIV. Anova-1 and linear regression of first-instar potato aphid dry weight versus parasite deprivation time.

RUN ONE

SOURCE	df	MS[a]	F
Among groups	5	0.2467	5.930*
linear	1	0.5112	2.830
deviations	4	0.1806	4.341*
Within groups	54	0.0416	
Total	59		

RUN TWO

SOURCE	df	MS[a]	F
Among groups	3	0.2359	3.709*
linear	1	0.0941	0.307
deviations	2	0.3064	4.894*
Within groups	36	0.0626	
Total	39		

a; MS x 10^{-3}

* = significant at $P < 0.05$

Table XV. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = first-instar potato aphid (Run One).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.1387	5.615*
	Times	5	0.0129	0.522
	Error	15	0.0247	
	Total	23		
Aphids attacked	Intervals	3	0.0300	0.716
	Times	5	0.1477	3.525*
	Error	15	0.0419	
	Total	23		
Mummies formed	Intervals	3	0.0828	4.381*
	Times	5	0.0458	2.423
	Error	15	0.0189	
	Total	23		
Aphids not parasitized	Intervals	3	0.0220	2.417
	Times	5	0.0616	6.769*
	Error	15	0.0091	
	Total	23		

* = significant at $P < 0.05$

Table XVI. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = first-instar potato aphid (Run Two).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0839	5.344*
	Times	3	0.0581	3.701
	Error	9	0.0157	
	Total	15		
Aphids attacked	Intervals	3	0.0479	6.221*
	Times	3	0.0558	7.247*
	Error	9	0.0077	
	Total	15		
Mummies formed	Intervals	3	0.0008	0.077
	Times	3	0.0281	2.702
	Error	9	0.0104	
	Total	15		
Aphids not parasitized	Intervals	3	0.0484	4.792*
	Times	3	0.0098	0.970
	Error	9	0.0101	
	Total	15		

* = significant at $P < 0.05$

Table XVII. Anova-1 and linear regression of second-instar potato aphid dry weight versus parasite deprivation time.

RUN ONE

SOURCE	df	MS[a]	F
Among groups	7	3.766	3.816*
linear	1	0.9290	0.219
deviations	6	4.239	4.295*
Within groups	72	0.987	
Total	79		

RUN TWO

SOURCE	df	MS[a]	F
Among groups	5	0.1243	207.167**
linear	1	0.0007	0.004
deviations	4	0.1552	258.667**
Within groups	114	0.0006	
Total	119		

a; MS x 10^{-4}

* = significant at $P < 0.05$

**= significant at $P < 0.01$

Table XVIII. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = second-instar potato aphid (Run One).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0022	0.092
	Times	6	0.1247	5.196*
	Error	18	0.0240	
	Total	27		
Aphids attacked	Intervals	3	0.0728	20.222**
	Times	6	0.0509	14.139**
	Error	18	0.0036	
	Total	27		
Mummies formed	Intervals	3	0.0715	2.207
	Times	6	0.0643	1.984
	Error	18	0.0324	
	Total	27		
Aphids not parasitized	Intervals	3	0.0711	2.867
	Times	6	0.0358	1.443
	Error	18	0.0248	
	Total	27		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table XIX. Anova-2 of the 4 one-half hour data-collection intervals versus parasite deprivation time, for each dependent variable: Host = second-instar potato aphid (Run Two).

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h.	Intervals	3	0.0069	0.585
	Times	5	0.1797	15.229**
	Error	15	0.0118	
	Total	23		
Aphids attacked	Intervals	3	0.0160	13.333**
	Times	5	0.0094	7.833*
	Error	15	0.0012	
	Total	23		
Mummies formed	Intervals	3	0.0109	0.480
	Times	5	0.1017	4.480*
	Error	15	0.0227	
	Total	23		
Aphids not parasitized	Intervals	3	0.0223	0.695
	Times	5	0.1394	4.343*
	Error	15	0.0321	
	Total	23		

* = significant at $P < 0.05$
**= significant at $P < 0.01$

Table XX. Pearson correlation coefficients of the dependent variables for the 4 one-half hour data-collection intervals, for each parasite deprivation time. Host = second-instar potato aphid.

RUN ONE

DEPENDENT VARIABLE		PARASITE DEPRIVATION TIME (hours)						
		1	7	13	16	19	25	31
Aphids attacked	r	a	0.991	0.983	0.942	0.585	0.837	0.963
	P	a	0.004	0.009	0.029	0.208	0.082	0.019

RUN TWO

DEPENDENT VARIABLE		PARASITE DEPRIVATION TIME (hours)					
		1	7	13	16	19	25
Aphids attacked	r	a	0.924	0.996	0.750	0.638	0.791
	P	a	0.038	0.017	0.125	0.181	0.104

a; values could not be computed.

Table XXI. Anova-2 of the 2 test-days versus the 2 host species, for each dependent variable.

DEPENDENT VARIABLE	SOURCE	df	MS	F
Aphid mortality within 24 h	Days	1	0.1603	15.437 **
	Hosts	1	0.3409	32.823 **
	Interaction	1	0.3408	32.811 **
	Error	12	0.0104	
	Total	15		
Aphids attacked	Days	1	0.0195	5.597 *
	Hosts	1	0.9550	274.663 **
	Interaction	1	0.0001	0.032
	Error	12	0.0035	
	Total	15		
Mummies formed	Days	1	0.1873	35.532 **
	Hosts	1	0.1168	22.154 **
	Interaction	1	0.1711	32.465 **
	Error	12	0.0053	
	Total	15		
Aphids not parasitized	Days	1	0.0001	0.001
	Hosts	1	0.0496	3.653
	Interaction	1	0.0194	1.431
	Error	12	0.0136	
	Total	15		

* = significant at $P < 0.05$.
** = significant at $P < 0.01$.

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