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THE EFFECT OF PREY AVAILABILITY ON THE
REPRODUCTIVE OUTPUT AND FORAGING BEHAVIOR
OF A FLOWERFLY, METASYRPHUS COROLLAE (F.)

by

© SUSAN MARGARET SCOTT, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Biology
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ABSTRACT

The effectiveness of a predator depends on its foraging and reproductive responses to prey availability (number of prey and area over which prey distributed). Larvae of Metasyrphus corollae (F.) were reared with 10, 20, 40, or 60 aphids offered daily on 3 sizes of plants. When more aphids were offered, consumption increased. Production efficiency of larvae on the smallest plants was lower, although foraging costs should have been less. Fecundity was extremely variable (range 0 to 1488 eggs) and depended only on adult longevity, not on consumption or size. Flight activity affected fecundity and longevity of small, but not large, flies. Fecundity of insects that acquire most of their energy as larvae is less correlated with energy consumption than in insects which feed as adults.

A random searching model of the capture rate between a moving predator and stationary prey was constructed for M. corollae larvae. Velocities of larvae of different ages and hungers were determined in light and dark. Probabilities of

moving, capture success and time spent feeding were determined from videotapes. Larvae reared with 10 aphids per day searched a greater area and fed longer on each aphid than larvae reared with 40 aphids. Two-thirds of encountered aphids were captured. Plant size had little effect on larval behavior. The random model overestimated consumption rate. Errors in estimating each parameter do not account for the poor agreement. Instead, non-random searching behavior may explain why larvae caught fewer aphids under experimental conditions than predicted. In nature this behavior should be adaptive when prey are patchily distributed.

M. corollae larvae behave as energy maximizers when hungry and as time minimizers when aphids are abundant. Increments in larval consumption may not all have the same importance to fitness.

When aphids are abundant, M. corollae consume more, and may be more fecund, than when aphids are scarce; therefore, syrphid populations will grow faster when aphid infestations are heavy. When aphids are scarce, the great searching capacity and high production efficiency of larvae, and the

ability of adults from starved larvae to disperse
and reproduce, should enable syrphid populations to
survive.

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I. GENERAL INTRODUCTION

Recent literature abounds with discussions of optimal foraging theory (recent reviews by Pyke et al. 1977; Krebs 1978) and of optimal life history theory (reviews by Stearns 1977; Pianka 1976). Many papers present data on the efficiency of foraging or on the efficiency of reproduction, yet seldom have both areas been examined in one species under comparable conditions. This is unfortunate because reproductive success is the ultimate criterion of the efficiency of foraging. Schoener (1971) tackled the problem theoretically, recognizing two categories of foragers, time minimizers and energy maximizers. In the former fitness is maximized when time spent foraging to gather a fixed amount of energy is minimized; and in the latter fitness is maximized when a maximum amount of energy is acquired in the available time. However, there are few empirical studies.

Efficient foraging results in increased acquisition of matter and energy which, within the constraints of an organism's metabolism and the time available, will increase the number or size of offspring or enable offspring to be produced earlier (Fig. 1). Optimal searching and feeding behaviour should maximize the net energy gained and thus maximize the energy available for reproduction. For a predator,

Figure 1. Relationship between elements of foraging tactics and reproductive tactics.

Modified from Pianka (1976)

changes in prey availability change the gross energy that can be acquired as well as the costs in time and energy of acquiring it. However, there may be behavioral or physiological adjustments that minimize the effect of reduced prey availability on reproductive output. When prey are scarce, an efficient forager might concentrate its activity in areas where prey have been discovered, switch from active searching to ambushing (Matsura 1981), or extend the length of the foraging period. The first two would reduce the energy expenditure associated with locating prey, while the third would increase the amount of energy ingested. To maintain a high reproductive output when energy input has been limited, an animal might allocate a lower proportion of ingested energy to growth, produce offspring earlier in its reproductive life or allocate less energy to adult maintenance and survival. This greater reproductive effort would tend to equalize the observed reproductive output across a range of prey availabilities.

In many organisms studies of foraging and reproduction are complicated because the activities of these animals cannot be exclusively assigned to either foraging or to reproduction. However, in some insects almost all energy acquisition occurs in the larval stage while all reproduction is accomplished by adults. Thus time budgeting between foraging and reproduction

may be ignored. Many insects also have short lifespans. In addition, problems arising from the need to acquire nutrients from a variety of food types may be ignored in monophagous insects. In this thesis I examine the foraging and reproductive responses of an insect predator to changes in the availability of energy.

The larvae of the flowerfly, Metasyrphus corollae (F.), are obligate predators of aphids. The larvae are legless, eyeless, grub-like animals that rely upon touch to find aphids. A larva, when it touches an aphid, exudes a sticky saliva that helps to trap the aphid, pierces the aphid with its jaws and lifts it from the substrate. The contents of the aphid are then sucked out and an aphid carcass is left at the conclusion of feeding. The larval period lasts about eight days at 20° C, and is followed by about a week-long pupation usually in the soil. The adults feed on nectar as an energy source and adult females require pollen or some other protein source for oogenesis. Eggs are laid in aphid colonies, aphids being a necessary stimulus for oviposition. Larval M. corollae may consume as many as 100 aphids, thus M. corollae is potentially important in aphid population dynamics. The suitability of these predaceous insects as biological control agents depends on their searching ability, their voracity and their reproductive

potential at both low and high pest infestations.

I used parthenogenetic pea aphids, Acyrtosiphon pisum (Harris) as prey. This sap-sucking insect has a very high reproductive rate and can reach high densities, and can cause significant damage to pea plants (Barlow et al. 1977). The biomass of aphids that one M. corollae larva might eat can reduce pea plant net productivity by 31% (Barlow 1979). However, aphid populations are also ephemeral so syrphid larvae may also develop under conditions of prey scarcity.

Prey availability cannot be measured solely by prey density. There are many studies of the effect of prey density on the number of prey eaten or on energy consumption (eg., Holling 1965; Eveleigh and Chant 1981; Lasker et al. 1982). In these experiments, different numbers of prey were provided in an environment with constant area (or volume for aquatic animals). Consequently, gross energy available was changed as well as prey density. Gross energy availability can be held constant while prey density is manipulated by changing the area on which the prey are found and over which the predator must forage. When prey and predators are found on plants, increasing plant size also increases the complexity and heterogeneity of the foraging environment. The experiments I did involved changing both the number of prey and the area of the plants on which the prey were

placed. In this thesis, the term prey abundance refers to the number of prey while prey availability refers to the interaction between plant size and prey abundance (prey availability and prey density are not synonymous because the former includes aspects of plant structure that make prey more or less difficult for a predator to capture while prey density is simply the number of prey per unit area).

The experiments are presented in two major sections. In the first, I examine the effects of prey availability on consumption and reproduction. In the second, I develop a model of foraging behavior that predicts the levels of prey consumption observed in the first part.

II. THE EFFECT OF PREY AVAILABILITY ON CONSUMPTION AND REPRODUCTION

INTRODUCTION

Implicit in many studies of foraging behavior is that maximizing energy gain per unit time leads to increased fitness. In most organisms various aspects of life history make testing this assumption impracticable. The life history of M. corollae short and energy acquisition is concentrated in the larval period, while reproduction is confined to the adult stage. Consequently, determining which activities are foraging and which are reproductive, and calculating the time and energy budgets for foraging and reproduction, are easier.

The crucial question is "what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction?" (Fisher 1958). In particular, since the energy supply of predators probably fluctuates more than that of herbivores, how should a predator apportion energy to reproduction under different conditions of prey abundance and distribution?

Energy gained during foraging may be allocated to somatic growth, to maintenance and to reproduction. Assuming that stress-induced changes in life-history

features are adaptive (Callow 1979; Collins 1980), then changes in the pattern of energy allocation will indicate the relative importance of growth, maintenance and reproductive output to overall fitness.

In this section I report the results of laboratory experiments in which the foraging environment was manipulated and reproductive output measured. When Cornelius and Barlow (1980) offered different numbers of prey per day to syrphid larvae, different sized pupae resulted. They then recorded the average number of eggs laid by groups of females of similar size. My experiments used a wider range of prey number with the prey on plants of different sizes. Plant size affects prey density and possibly dispersion, thereby changing the energetic costs of foraging. The number of prey offered daily establishes maximum gross energy available to the predator. I also recorded the egg production and longevity of individual adult females to estimate the amount of individual variation in each of these characters and to detect any cost of reproduction expressed as decreased longevity.

I evaluated foraging success, production efficiency and reproductive efficiency under different conditions of prey availabilities. The hypotheses were that increased plant size would reduce all of these because prey would be more difficult, and therefore more costly, to locate. Therefore less energy would be

available for growth and reproduction. Similarly, restriction of gross energy available was expected to reduce growth and reproduction.

METHODS

Parthenogenetic pea aphids were reared in stock colonies on Alaska variety peas (Pisum sativum) at 20.5 °C ($\pm$ 1°C range), 60 to 90 % R.H. and 16 h photoperiod. Cohorts of aphids for use as prey were obtained by placing 200 adults from the stock colony in a 14 cm diameter, 2.5 cm deep petri dish. The bottom of the dish was lined with damp filter paper and about 12 6-day old pea seedlings were placed on the paper. Aphids born in the succeeding 24 h were transferred on the pea seedlings to 12.5 cm diameter pots containing about 60 6-day old peas. To prevent contamination of the cohorts by aphids of other ages, the plants were covered with plastic cylinders (30.5 cm high and 10.5 cm diameter). Holes, covered with organdy or plastic mesh, in the sides and tops of the cylinders allowed air to circulate. The covered pots were placed in controlled environment growth chambers. The temperature inside the cylinders was 19.5 °C ($\pm$ 1 °C range) and the photoperiod was 16 h. These cohorts of aphids were harvested and used as prey on the seventh day after their mothers had been placed in the petri dishes and were called "7-day old" aphids.

Pea plants were prepared for the experiments by transplanting 6 day old seedlings into 5 x 3 cm plastic vials filled with a soil vermiculite mixture; five days

later the plants had grown sufficiently for use. Some plants were trimmed so that only part of the first leaf remained (mean surface area = $7.5 \pm 1.5 \text{ cm}^2$) others at the two leaf stage had an average surface area of $35 \pm 6.2 \text{ cm}^2$; a third group with 2 plants per vial had an average total surface area of $73 \pm 8.4 \text{ cm}^2$.

The stock colony of M. corollae was kept as previously described (Barlow 1979). Because young syrphid larvae are difficult to handle without causing extensive mortality and because the proportion of energy consumption that occurs during the first few days is small (Barlow 1979), experiments were begun when the larvae were about 72 h old. Single larvae were transferred with a small, moist paint brush to the experimental plants and given aphids. Plastic vials with organdy covered holes in the sides and tops were inverted over the plants.

The experimental design was factorial with three plant sizes and three prey rations, for a total of nine treatments.

Each day, 7 day old aphids were provided to each syrphid larva. A larva received one of three rations: 10 aphids per day, 20 aphids per day or 40 aphids per day. When new aphids were provided, uneaten aphids were removed and the carcasses of eaten aphids were removed and counted. In one experiment, 10 larvae were offered 60 aphids per day. Half of these larvae were

on 7.5 cm² plants, half on 73 cm² plants. These individuals were followed only until they pupated.

Samples of aphids and of carcasses were freeze-dried, weighed and their energy contents determined in a Phillipson microbomb calorimeter (Gentry Instruments Inc., Aiken, S.C., U.S.A.).

When larvae pupated they were weighed and placed in individual petri dishes. The adults that emerged were kept in 450 ml glass jars with cloth tops. Honey, water and pollen were provided ad libitum. Single females were kept with one or more, usually two, males.

Reproductive output of female syrphids was measured by collecting eggs three times a week beginning four days after emergence (no flies laid eggs before the fourth day following emergence). Eggs were collected by allowing each female to oviposit in a petri dish which contained a piece of pea plant with aphids. After 4 h, females were returned to their jars and their eggs counted.

In two subsequent experiments, groups of about 30 larvae were reared on pots of 70 peas at prey levels roughly equivalent to 10 aphids per larva per day ("starved") or 40+ aphids per larva per day ("well-fed"). Adults which emerged from these larvae were marked with artist's acrylic paints on the thorax so that they could be individually identified. All the adults were kept in a large screened cage (40 cm x

40 cm x 45 cm). Eggs were collected in the same way.

Other female flies reared from "starved" or "well-fed" larvae were killed 4 days after they emerged. Their ovaries were dissected and the number of ovarioles counted.

Data were analyzed by analysis of variance after Sokal and Rohlf (1969) and using the SPSS and BMDP packaged computer programs. Most variables required transformation to meet the assumptions of ANOVA; therefore means and 95% confidence intervals calculated by back-transformation, with corrections for bias after Zar (1974) and Thoni (1969), are reported. Details of the analyses of variance are given in Appendix III.

RESULTS

When more aphids were offered, syrphid larvae ate more of them although the rate of increase in the number of aphids eaten with increasing prey abundance declined (Fig. 2). Although these data are totals for the larval period, the shape of the curve is like Holling's Type II functional response to prey density (Holling 1965). When prey abundance was low, the same percentage of prey available was consumed by larvae reared on the three different plant sizes (Table 1). However, when prey were abundant, plant size affected both the total number of prey and the percentage of available prey that were eaten.

Previously a constant value for the caloric content of an aphid carcass has been used (Barlow 1979; Cornelius and Barlow 1980) but because visible differences in carcass size existed, I weighed carcasses left by larvae in various treatments. Significant differences in mass were found (Table 2) with the largest carcasses left by young, well fed larvae. Other values were obtained by interpolation.

Consequently, the caloric value of an aphid eaten depends on the age and hunger of the predator. The formula for calculating caloric values was:

$$\begin{aligned} &\text{Dry mass of 7-day old uneaten aphid} \\ &= .300 \pm .048 \text{ mg} \end{aligned}$$

Caloric equivalent of uneaten aphid

= 5.41 cal/mg ash-free dry mass

(Randolph et al 1975)

Caloric equivalent of aphid carcass

= 5.57 cal/mg ash-free dry mass

(Barlow 1979)

3% ash assumed for both uneaten aphids

and carcasses

(Barlow 1979)

energetic value of an uneaten aphid

= (5.41 cal/mg x .300 mg x .97)

- (5.57 cal/mg x carcass mass x .97)

1 cal = 4.184 J

Application of these values gave the energy consumption of syrphid larvae under the different experimental conditions (Table 1). Prey number and plant size still had significant effects on energy consumed but the differences were less than they would have been if all larvae removed the same amount of energy from an aphid.

Increased consumption generally resulted in heavier pupae (Table 1). Plant size also had an effect but its direction was opposite to that anticipated. Within a level of prey abundance, consumption was generally greatest on the smallest plants but pupal masses were the same or lower. The ratio of pupal mass to calories consumed is analogous to a production

Table 1. Effect of the number of aphids offered per day and plants of different sizes on consumption and mass of *M. corollae*. Means and (95% confidence intervals). Total aphids available = # aphids per day x (duration of larval stage - 3 days before feeding experiment started). Identical letters indicate means within a column which are not statistically different at $p = .05$.

aphids offered per day	plant size (cm ²)	larval duration (days)	total aphids available	(mean aphids eaten ÷ total available) x 100%	consumption (calories)	pupal mass (mg)	sample size
10	7.5	9.1	61	72.1	58.7 ^a (52.5-61.6)	18.4 ^a (16.3-20.4)	10
	35	8.5	55	66.8	49.8 ^b (44.2-52.8)	17.3 ^a (15.0-19.6)	8
	73	8.1	51	73.2	51.2 ^b (45.2-54.6)	17.3 ^a (14.9-19.8)	7
20	7.5	8.8	116	52.3	76.6 ^c (69.4-79.7)	22.4 ^b (20.6-24.2)	13
	35	9.0	120	48.3	74.7 ^c (67.0-78.4)	25.5 ^c (23.5-27.6)	10
	73	8.8	116	51.4	77.3 ^c (70.2-80.2)	25.6 ^c (23.9-27.3)	14
40	7.5	8.8	232	37.9	102.2 ^d (91.7-107.3)	28.9 ^d (26.8-30.9)	10
	35	8.0	200	37.2	89.4 ^e (80.4-93.6)	31.9 ^{d,e} (29.8-34.0)	11
	73	8.4	216	33.6	92.6 ^e (83.1-97.1)	32.4 ^e (26.5-34.4)	10
60	7.5	8.2	312	33.1	111.2 ^f (99.4-124.6)	30.1 ^{d,e} (27.2-33.0)	5
	73	8.4	324	24.2	95.5 ^{d,e} (85.4-106.8)	33.3 ^e (30.4-36.2)	5
ANOVA	prey number	1.4	n.s.		106.5 ^{***}	87.1 ^{***}	
F ratios	plant size	1.3	n.s.		6.6 ^{**}	5.1 ^{**}	
	interaction	0.9	n.s.		1.3	n.s.	

*** $p < .001$; ** $p < .01$; * $p < .05$; n.s. non-significant, $p > .05$

Table 2. Mean weights of aphid carcasses left by M. corollae larvae of different ages being reared at different prey availabilities. (95% confidence intervals) (sample sizes). Identical letters indicate means not statistically different at $p = .05$. Other means differ from those at the same age but different prey number or plant size.

plant size (cm ²)	larval age (days)	number of prey offered per day		
		10	40	60
7.5	4	.085 mg (.069-.101) (18)	.108 mg (.084-.132) (24)	
	5	.069 (.054-.084) (12)	.089 (.065-.112) (15)	
	6	.060 a (.050-.070) (14)	.101 (.074-.128) (13)	
	7	.053 a (.045-.062) (11)	.074 (.068-.080) (15)	
	8	.051 a (.043-.059) (10)	.064 a (.051-.077) (15)	.085 (.070-.101) (18)
73	4	.057 a (.043-.059) (11)	.084 (.056-.112) (15)	
	5	.061 a (.050-.073) (10)	.098 (.077-.119) (18)	
	6	.056 a (.045-.066) (16)	.062 a (.053-.071) (15)	
	7	.054 a (.050-.058) (15)	.056 a (.044-.068) (14)	
	8	.066 a (.056-.076) (12)	.060 a (.052-.067) (10)	.055 a (.049-.060) (15)

Table 3. Production efficiency (= pupal mass + consumption in calories) of 176 *M. corollae* larvae reared at different prey availabilities. Means and (95% confidence intervals). Identical letters indicate means within the same sex which are not statistically different at $p = .05$.

plant size (cm ²)	sex	number of aphids offered per day			
		10	20	40	60
7.5	♀♀	.322 a (.300-.346)	.301 a,c (.283-.321)	.290 c (.270-.312)	.272 c,x (♀♀ & ♂♂) (.245-.300)
	♂♂	.324 x,y (.294-.356)	.361 y (.318-.411)	.302 x (.277-.329)	
35	♀♀	.356 b (.329-.386)	.351 b (.327-.377)	.378 b (.352-.405)	
	♂♂	.362 y (.337-.389)	.352 y (.325-.382)	.373 y (.339-.411)	
73	♀♀	.348 a,b (.320-.379)	.341 b (.321-.362)	.362 b (.337-.389)	.350 b,y (♀♀ & ♂♂) (.317-.388)
	♂♂	.348 y (.316-.384)	.343 y (.313-.375)	.360 y (.328-.394)	
ANOVA		♀♀ only	♂♂ only	♀♀ & 60	
F ratios	prey number	0.9	0.2	1.4	
	plant size	19.6 ***	3.28 *	26.1 ***	
	interaction	1.5	1.7	1.7	

efficiency ratio and such ratios reflect the energetic cost of foraging. When plants are larger, prey may be further apart and the cost of capturing each should be higher. However, the production efficiency of larvae reared on the smallest plants was usually lower than the production efficiency of larvae reared on the larger plants (Table 3). Data for males were similar to those for females.

The reproductive performance of each female syrphid fly was followed for her entire life. Total fecundity of flies within a treatment group and overall was extremely variable (Table 4). In all but one group there was at least one female that did not lay any eggs, and in six groups there was a female that laid 1000 or more eggs. The maximum number of eggs laid was 1488. Of particular interest was the weakness of relationships between fecundity and consumption ($r = .23$, $p = .05$, $N = 93$) or pupal mass ($r = .27$, $p < .05$, $N = 92$). The only important correlation was a positive one between female longevity and number of eggs laid ($r = .72$, $p < .001$, $N = 93$). Females continued to lay eggs until they died, at a rate which declined slightly with age.

Adult longevity itself was highly variable (Table 4). Flies reared as larvae at the lowest densities of each prey abundance tended to have the shortest lives. Lifespan was not related to consumption ($r = .08$,

Table 4. Effect of prey availability during the larval stage on average longevity and fecundity of adult female M. corollae. Means and (95% confidence intervals) (sample size). Flies from larvae offered 10 aphids per day laid fewer eggs in the 1st 15 days than other flies.

aphids offered per day	plant size (cm ²)	longevity (days)	total eggs laid	eggs laid in 1st 15 days
10	7.5	19.7	475	332
		(13.5-27.2)	(263-790)	(174-490)
		(10)	(10)	(6)
	35	18.3	430	298
		(11.7-26.5)	(221-974)	(141-456)
		(8)	(8)	(6)
	73	14.2	231	150
		(8.2-22.0)	(128-583)	(0 - 373)
		(7)	(7)	(3)
20	7.5	17.7	437	426
		(12.5-23.9)	(261-699)	(297-555)
		(13)	(13)	(9)
	35	23.3	622	498
		(16.4-31.5)	(362-989)	(362-635)
		(10)	(10)	(8)
	73	15.6	413	418
		(10.9-21.2)	(250-655)	(296-540)
		(14)	(14)	(10)
40	7.5	19.3	448	430
		(13.1-26.7)	(250-760)	(294-567)
		(10)	(10)	(8)
	35	20.1	685	536
		(14.0-27.3)	(417-1051)	(427-700)
		(11)	(11)	(8)
	73	14.7	434	362
		(9.5-21.3)	(237-831)	(190-536)
		(10)	(10)	(5)
ANOVA	prey number	0.13	2.20	5.09 **
F ratios	plant size	2.35	1.07	2.38
	interaction	0.27	0.43	0.55

$p > .1$, $N = 93$) nor to body size as measured by pupal mass ($r = .06$, $p > .1$, $N = 92$).

In spite of the absence of correlation between body size and the number of eggs laid, the number of ovarioles (an estimator of potential fecundity) was correlated with pupal mass ($r = .68$, $p < .01$, $N = 48$). Starved larvae produced adults with an average of 3.29 ± 0.08 S.E.M. ovarioles per mg of pupal mass ($N = 16$) which was significantly higher than flies from well-fed larvae which had 3.00 ± 0.07 S.E.M. ovarioles per mg pupal mass ($N = 32$). Thus, although small flies had fewer ovarioles per fly than large flies, the difference was not as great as might be expected from mass or energy consumption.

Energy consumption or body size have been shown to be important determinants of fecundity in a number of studies. In M. corollae such relationships were weak. However, fecundity is only one component of fitness. Survival, developmental rate and the temporal pattern of egg laying are more important than lifetime egg production. The finite rate of increase, i.e., the number of ♀ offspring/♀ /unit time, is a parameter that includes these three elements. Survival probabilities for immature stages were calculated for all larvae and pupae since their sex could not be determined during these stages. Thereafter only females were considered. I assumed a 1:1 sex ratio

since the observed ratio in emerging adults did not differ from this ($p > .05$). Egg and early larval mortality were not known but were assumed to be zero. Although unrealistic, this assumption changed only the magnitude of the rate of increase, not the pattern of differences among treatments that began after the first three days of larval life. I used the method proposed by Lenski and Service (1982) to compute the rate of increase and its variance for each group of flies. Average rates of increase (variance) varied between 1.17 (3.26) and 1.25 (0.52). T-tests revealed no significant differences ($p > .05$) between feeding regimes although flies produced by larvae offered 10 aphids per day tended to have slightly lower rates of increase.

However, the temporal pattern of egg laying did differ among treatment groups. It was impossible to differentiate among the ages at first reproduction of the different feeding regimes because eggs were collected only three times per week. In any case differences probably were small. However female syrphids that were raised at low levels of prey abundance on large plants laid fewer eggs in the first 15 days of their adult lives than females reared at higher prey availabilities (Table 4). The absence of differences in total fecundity and rate of increase resulted, therefore, from variability in the number of

Table 5. Effect of cage size on longevity and fecundity of M. corollae females reared as starved or well-fed larvae. Values for flies in small jars are averages of all flies reared at 10 (starved) or 40 (well-fed) aphids offered per day. Means and (95% confidence intervals). Identical letters indicate values not statistically different by Student-Newman-Keuls multiple range tests at $p = .05$.

larval conditions	starved		well-fed	
	small jars	large cage	small jars	large cage
pupal mass (mg)	17.7 a (16.6-18.9)	19.8 a (18.6-21.0)	31.0 b (29.7-32.4)	32.4 b (31.2-33.6)
longevity (days)	18.1 a,b (14.1-22.7)	12.0 a (8.1-16.9)	18.0 a,b (14.5-22.1)	23.0 b (18.0-28.6)
total eggs laid	369 a (252-521)	182 (118-304)	509 a,b (374-672)	670 b (476-904)
sample size	25	15	30	21

eggs laid in the late stages of adult life and that depended on the duration of this period.

Still, the effect of prey availability on reproductive output of syrphid flies seemed small. To determine whether the effects would be more noticeable if adult flies were able to fly more than was possible in small jars, starved and well-fed larvae were reared and the adults kept in a $7.2 \times 10^4 \text{ cm}^3$ cage. The pupal masses for these two groups of flies were comparable to those obtained at the regimes of 10 and 40 aphids offered per day in the previous experiments (Table 5). When kept in a large cage flies from starved larvae had shorter lives and laid fewer eggs than well-fed ones (Table 5). There was still considerable variability (coefficient of variation for combined data was 90%).

The reproductive efficiency of M. corollae females was estimated in three ways: the proportion of consumed energy present in eggs, the ratio of number of eggs laid to pupal mass, and the number of ovarioles per mg of pupal biomass (Table 6). High variability in egg number obscured any differences in the ratios involving egg number and no clear patterns were evident. Small flies have relatively more ovarioles per mg than large flies.

Table 6. Reproductive efficiency of *M. corollae* females reared as larvae at different prey availabilities. The values for adults kept in jars are not statistically different at $p = .05$.

rearing conditions	estimate of reproductive efficiency	
	<u>energy in eggs¹</u> energy consumed	<u>number of eggs</u> pupal mass
adults in jars:		
larvae reared with:		
10 aphids/day		
7.5 cm ² plants	.118	25.8
35 cm ²	.126	24.9
73 cm ²	.066	13.4
20 aphids/day		
7.5 cm ²	.083	19.5
35	.122	24.4
73	.078	16.1
40 aphids/day		
7.5 cm ²	.064	15.5
35	.107	21.5
73	.068	13.4
adults in large cage:		
larvae reared:		
starved	.047 ²	9.2
well-fed	.106 ²	20.7

¹ caloric equivalent of 1 egg = 0.0146 cal (Cornelius and Barlow 1980)

² estimated from pupal mass using pupal mass/consumption = .35

DISCUSSION

Syrphid larvae ate as many as 35 aphids in a day and more than 115 aphids during their larval stage. When only 10 aphids were present on the largest plants, larvae found and ate all of them in a few hours. The overall functional responses of syrphid larvae to prey number were similar to the negatively accelerating Type II response described by Holling (1965). Plant size influenced the upper asymptotes of the responses in a way which implies that searching as well as satiation limited the number of aphids captured. If searching time was not a limiting factor, all the functional response curves should have converged to a single maximum and this did not happen. Risch et al. (1982) have shown that increased plant density lowers the predation rate of coccinellids because the beetles spend more time foraging on plants that contain no food. Increased plant surface area may change the spatial heterogeneity or patchiness of the prey distribution (especially increasing the number of empty patches), so affecting searching success. The aphids used in this study occupied about 0.2 cm^2 . Thus the total surface area was occupied when aphid density exceeded 5 per cm^2 . This happened when 40 aphids were placed on 7.5 cm^2 of plant. When there were 40 aphids on 73 cm^2 plants about 10% of the available surface

area was occupied and aphids were able to distribute themselves on preferred parts of the plants, such as the undersides of leaves. Unless syrphid larvae locate these areas and spend proportionately more time searching in them, their overall capture success will decrease.

When prey were scarce, syrphid larvae extracted more energy from each aphid they captured. This reduced the effect of prey scarcity and is consistent with the predictions of optimal foraging theory. A single aphid can be considered to be a patch. When food is scarce, a predator should remain in a patch longer than it should in a rich environment (Charnov 1976). However, this behaviour did not eliminate the effect of reduced prey availability on energy consumption.

While prey availability affected prey consumption in an expected manner, the effect of plant size on pupal biomass was unexpected. Production efficiency was lowest on the smallest plants although the energy costs of acquiring prey on these plants should have been less and more energy should have been available for production. The close correspondence of the data for males and females suggests that this is a correct result. One possible explanation is that assimilation or digestive efficiency decreased when plant surface area was small. Support for this idea comes from a

similar trend in carcass size. Particularly when prey were abundant (40 or more available each day), larvae left larger prey carcasses. This has been included in the calculation of energy consumption but it is possible that this lower extraction efficiency was accompanied by a lower assimilation efficiency. Some studies have shown decreased assimilation efficiency with increased meal frequency or meal size (Giguère 1981; Corner et al. 1976) but there are also abundant examples of no change in assimilation efficiency (Mathavan and Muthukrishan 1976; Mukerji and Guppy 1970; Barlow 1979; Lawton 1970). If assimilation efficiency of syrphid larvae did decrease when meals were more frequent then the lowest production efficiency for each size of plant should have occurred when the most prey were captured. However, this trend only occurred on the smallest plants.

Larvae offered only 10 aphids each day may have stopped moving or moved more slowly after a period of unsuccessful searching had occurred. Other predators, when faced with starvation, may initially increase their searching activity and consequently, their respiration rate and then reduce their activity when starvation is prolonged (Matsura 1981; Tanaka and Itô 1982). The result is that production efficiencies may be as high when prey are scarce as when they are more abundant.

Another possibility is that some abiotic conditions differed in the vials with the smallest plants that increased the maintenance expenditures of syrphid larvae. This seems unlikely; smaller plants may have resulted in a lower relative humidity within the experimental chamber but temperatures did not differ among plant sizes.

These patterns of ingestion and conversion of ingested energy into pupal biomass conserved body size under low prey availabilities. Body size may affect mating success, resistance to starvation or desiccation, flying ability and fecundity (Collins 1980). In these experiments mating success and resistance to starvation or desiccation of the adults probably were not important.

When adult syrphids were kept in jars, there was no relationship between egg production and body size or larval energy consumption. Even when large cages were used, the relationships were highly variable. It is often stated that fecundity in insects is a function (usually linear) of body size or energy consumption (eg., Engelmann 1970; Evans 1982); however, I contend that this relationship is not universal but depends on the type of life history. Two kinds of data are used to establish the relationship, estimates of potential fecundity and measures of realized fecundity. The former are usually obtained by dissecting females

shortly after emergence; the second by counting the number of eggs laid in some time period. In most insects, potential fecundity is positively correlated with body size (Table 7a), and thereby with larval nutrition. However, the expression of this potential can be affected by many factors and there are only a few studies of the relationship between potential and realized fecundity. Boulétreau (1978), Heron (1955) and Collins (1980) are exceptions and in each case correlations that existed between body size and the number of ovarioles or oocytes weakened or disappeared when size and number of eggs laid were considered. Positive correlations are found in insects that feed while reproducing (Table 7b). In such insects, energy consumed by adults goes to adult maintenance or to reproduction (Figure 3) (growth in most insects being negligible after maturity). Thus, an increment in consumption should lead to a proportional increment in reproduction as it does in coccinellids (Mills 1981) and stinkbugs (Mukerji and LeRoux 1969) for example. Body size for these insects can be unrelated to reproduction (as in Mills 1981) because it sets only an upper limit on egg production through its effect on ovary size or on the number of eggs that can be contained in the abdomen (Matsura et al 1975). "Input of nymphal reserves to eggs is probably minor with respect to adult females' energy budget." (Slansky

Table 7 a. The relationship between potential fecundity and body size in arthropods.

species	size measure	potential fecundity measure	relationship	source
Homoptera				
aphids, various species	adult weight	no. of embryos, ovarioles	positive correlation	Kempton et al 1969; Dixon & Dharma 1980; Murdie 1969
Lepidoptera				
Antheraea polyphemus	pupal size	no. of immature & mature eggs	positive correlation	Miller et al. 1982
Heliconius charitonius	forewing length	no. of oocytes per ovariole at emergence	"roughly proportional"	Dunlap-Pianka et al. 1977
Hymenoptera				
Prisiphora erichsonis	adult live weight	no. of mature & immature ova and oocytes	positive correlation within populations	Heron 1955, 1966
Diptera				
Ephydra cinerea	adult mass	no. of ovarioles	positive correlation	Collins 1980
D. melanogaster	wing length	no. of ovarioles	positive correlation	Boulétreau 1978
D. mimica	thorax length	no. of ovarioles	positive correlation	Kambysellis & Heed 1971
Boopthora erythrocephala	adult weight	no. of oocytes	no correlation	Rühm & Hechler 1974
B. erythrocephala	adult weight	no. of oocytes	positive correlation	Hechler & Rühm 1976
Wilhelmia lineata				
Odagamia ornata				
Simulium sublacustre				

Table 7b. Realized fecundity of arthropods. Part 1 shows species that are predatory or herbivorous as adults.
Part 2 lists species whose adults have minimal consumption compared with their larval stages.

species	adult food	consumption or size	fecundity measure	relationship	source
Part 1					
Arachnida					
Linyphia triangularis	insects	daily food consumption of adults	no. & weight of eggs laid	increased consumption, heavier eggs but same number	Turnbull 1962
Mecynogea lemniscata	insects	no. of prey	no. of eggs	more prey, more eggs	Wise 1979
Thysanura					
Lepismodes inquilinus	detritus	weight of food eaten by adult	weight of eggs laid in lifetime	positive correlation	Watson 1967
Orthoptera					
Paratenodera angustipennis	flies	no. of prey eaten	weight of 1st & 2nd ootheca	positive correlation	Matsura & Morooka 1983
Heteroptera					
Oncopeltus fasciatus	milkweed seeds	no. of seeds given to adult; body size	no. of eggs per day; lifetime no. of eggs	less food, fewer eggs; body size had no effect	Slansky 1980 a
Podisus maculiventris	insects	no. of prey; energy consumed	no. of eggs per day	increased daily consumption, more eggs per day	Mukerji & Le Roux 1969
P. maculiventris	insects	body size	no. of eggs laid in 10, 20, 30 days	weakly correlated at day 20	Evans 1982
Orius tristicolor	thrips	no. of prey given to adults	no. of eggs laid in 14 days	more prey, more eggs	Stoltz & Stern 1978
Anthocoris confusus	aphids	no. of prey/day given to adults	no. of eggs laid per day & in life	more prey, more eggs	Evans 1976

Table 7b continued. Realized fecundity of arthropods.

species	adult food	consumption or size	fecundity measure	relationship	source
Part 1 cont.					
Heteroptera					
Notonecta undulata	mosquito larvae	no. of prey given to adults	no. of eggs laid in 4 weeks	more prey, more eggs	Toth & Chew 1972
Coleoptera					
Adalia bipunctata	aphids	weight of food eaten per day; body weight	weight of eggs laid per day	consumption & eggs positively correlated; body size & eggs not related	Mills 1981
Hippodamia convergens	aphids	no. of prey given to adults	no. of eggs laid	more prey, more eggs	Gutierrez et al. 1981
Coccinella trifasciata	aphids	prey eaten per day	no. of eggs laid per day	feeding rate & rate of egg laying positively correlated	Ives 1981
C. californica					
Part 2					
Coleoptera					
Anthrenus verbasci	nectar & pollen	body weight	no. of eggs laid	weight & fecundity correlated only when lifespan short	Blake 1961
Lepidoptera					
Pseudaletia unipuncta	nectar	larval consumption	lifetime no. of eggs laid	increased consumption, more eggs	Mukerji & Guppy 1970
Tricoplusia ni	nectar	adult weight	no. of eggs laid	weight & fecundity correlated if no. of matings constant	Shorey 1963

Table 7b continued. Realized fecundity of arthropods.

species	adult food	consumption or size	fecundity measure	relationship	source
Part 2 cont.					
Lepidoptera					
Euphydryas editha	nectar	emergent weight	weight of 1st egg mass of unfed ♀	positive correlation	Murphy et al. 1983
Dryas julia	nectar	adult size	no. of eggs laid + remaining oocytes	fecundity & size not related	Dunlap-Pianka et al. 1977
Heliconius charitonius	nectar & pollen	forewing length	no. of eggs per day	egg laying rate proportional to size	Dunlap-Pianka et al. 1977
Diptera					
Drosophila pseudoobscura	yeast	adult size	no. of eggs laid	large flies laid more eggs but correlations weak	Tantawy 1961; Tantawy & Vetukiv 1960
Ephydra cinerea	normally none	adult mass	no. of eggs laid	when food for adults, no relationship; when no adult food, medium sized flies laid most eggs; fecundity variable	Collins 1980
Wyeomyia smithii	nectar	food level of larvae; pupal weight	no. of eggs laid	food level had no effect on fecundity; pupal weight weakly correlated with fecundity only for small flies	Moeur & Istock 1980
Aedes atropalpus	blood	amount of larval food	no. of eggs matured	larval starvation reduced no. of eggs matured	Hudson 1970

Fig. 3. Energy flow through organisms. A. Adults feed and reproduce. B. Most energy acquired during larval stage and allocated to growth, larval maintenance and stored reserves. Reproduction during the adult stage draws on stored reserves while adult maintenance depends on adult consumption but may be supplemented by energy from stored reserves.

A.

B.

1980b). Body size could be directly related to reproduction if it determined the amount of tissue available to synthesize materials for eggs or the ability of the insect adult to acquire food. Even in these insects, the link between consumption and fecundity may be weak because large adults have higher maintenance requirements and so must consume more food than a small female to produce the same number of eggs (Matsura and Morooka 1983). In insects that feed as reproducing adults, increased adult maintenance costs, incurred from increased flight activity or increased foraging, will exact a cost against reproduction.

Generally, insects with minimal adult feeding show weak relationships between energy consumed by larvae or body size and realized fecundity (Table 7b). In insects with little adult feeding and egg production over a period of several to many days, adult longevity becomes the most important determinant of realized fecundity. If most larval nutrients cannot be allocated to adult maintenance, then longevity (fueled by adult consumption) (Fig. 3), and therefore realized fecundity, are independent of body size and larval consumption. Only when larvae have been severely starved or no food is available for adults do longevity and realized fecundity depend on larval ingestion. This may explain the differences from the results obtained by Cornelius and Barlow (1980) and the present

results. In the former study, lower prey levels were used and the flies were smaller. They laid fewer eggs and probably lived shorter adult lives. It seems likely that under these circumstances a more direct relationship between larval consumption and adult reproduction existed. Short adult lives will accentuate the importance of ovary size to total realized fecundity since egg production during the first part of the reproductive period was found to be related to pupal weight for the flies in this study.

There are data suggesting that flight activity and fecundity are interrelated in flies (Roff 1977; Rygg 1966). Large M. corollae females in large cages had about the same lifespan and fecundity as large females kept in small jars. However, small females laid fewer eggs and died sooner in large cages. These inverse relationships between flight and fecundity show that there can be a trade-off between adult maintenance and egg production. This cost of reproduction, or alternatively, cost of dispersal, is relatively less for large flies than for small ones.

The basis of the trade-off is in the use of a common resource, the nutrients accumulated by the larvae. Moeur and Istock (1980) claimed that "nutrients stored during larval life provide negligible energy for adult maintenance" because, in the absence of a carbohydrate source, pitcher-plant mosquitoes

(which do not blood-feed) live only a few days and lay virtually no eggs. Syrphid flies also cannot live more than a few days without access to sugar. But the ability to live for a few days means that at least some larval resources do go to adult maintenance. Even within dipterans, the requirement for adult carbohydrate and hence the reliance on larval reserves for adult maintenance varies. In Ephydra cinerea (Collins 1980) and Musca domestica (Engelmann 1970) access to carbohydrates is not required for survival and reproduction. Any larval nutrients that do go to adult maintenance will represent a bigger sacrifice for small flies than for large ones. Consequently, their reproduction should be more greatly affected.

Flight activity in small syrphids had a greater effect on fecundity than on lifespan. This may indicate that dispersal is more important to fitness than preserving fecundity. Since aphid populations are both spatially and temporally patchy, it is important for a syrphid female to live long enough to locate suitable patches of aphids for oviposition and to distribute eggs over several patches even if this requires some sacrifice of fecundity.

Ovarioles and oocytes are probably energetically inexpensive to produce until yolk must be deposited. In both M. corollae and Ephydra cinerea (Collins 1980) small flies have more ovarioles per unit of pupal or

adult mass than large flies. By this criterion, small flies make a larger reproductive investment than large flies. But because realized fecundity depends heavily on longevity, and longevity in M. corollae and sometimes in E. cinerea, has a separate energy source, this higher reproductive investment may be obscured in its expression when lifespans are long. Under field conditions this potential to produce relatively more eggs may be important because lifespans are probably shorter.

For M. corollae preserving body size through efficient foraging behaviour and metabolism, may result in increased egg production when dispersal draws significantly on stored reserves. But the importance of body size in these flies should not be overemphasized. A wide range of body mass occurred. Survival through the pupal stage approached 100% at masses which exceeded the threshold value of about 25 mg. Successful pupation and emergence and considerable reproduction occurred at masses less than 50% of the maximum observed mass or energy ingestion. The larval period was extended by less than 15% when prey availability was limited during the third instar. This contrasts with E. cinerea which extended its larval period several hundred percent (Collins 1980) and the pitcher-plant mosquito which extended its larval period by 50% at low ration (Moeur and Istock 1980).

Extending the larval period may increase mortality more in M. corollae or the cost of delaying reproduction may be greater than the gains resulting from increased energy ingestion. Lastly, unless small flies must use larval reserves for flight, their fitness as measured by their contribution to population growth is not significantly less than that of large flies. Hence populations of M. corollae that develop when aphids are scarce may have almost the same capacity for increasing as those that develop with more abundant prey. However if aphids are scarce during the oviposition period of a population of small flies, energy may be expended on dispersing to more favorable locations with concomittant reduction of egg production. This plasticity of energy allocation is important in an animal for which food supply during the feeding period may be an unreliable predictor of abundance for its offspring. It would be interesting to know to what extent adult consumption can compensate for low larval consumption.

When and how much to reproduce are the central themes life-history theory. The basic premises are that there is a cost to reproduction and that reproductive effort should be maximized over a lifetime. Unfortunately, life-history models make predictions about the evolutionary responses of populations to different environments and these cannot

be extrapolated to the question I have investigated which involves phenotypic responses. Woollhead and Calow (1979) predicted that semelparous species should increase their reproductive effort as food supply decreases and thus their total reproductive output should be relatively insensitive to food limitation. While the latter appears to hold for M. corollae over a wide range of prey availabilities, there is no adequate measure of reproductive effort since I have shown that dispersal costs must be included. I have presented evidence that there may not be a cost of reproduction measured as decreased survival unless populations are energetically stressed. This adds to a number of studies that show that individuals capable of living longer are also capable of laying more eggs (eg., Browne 1982; Tallamy and Denno 1982).

The effects of larval food supply on reproduction in predators have been poorly researched. For insect predators food supply may be highly variable. When ingestion and energy storage occur at one time and reproduction later, flexible energy allocation tactics are essential. It seems reasonable to predict that individuals developing at low prey densities should make a higher mass-specific investment in the structures necessary for reproduction so that they have the potential to lay many eggs if conditions improve, i.e., prey increases and dispersal is not required.

The occurrence of phenotypic responses of life history parameters to the availability of energy is a problem for the evaluation of evolutionary models of reproductive tactics. These models are often tested by comparing populations living in environments with different levels of food resources. Differences between populations are attributed to adaptive genetic responses to the particular environments. But this is done without testing each population for phenotypic shifts in the same life history traits in response to different environments.

The extreme variability of fecundity, longevity and the rate of increase as well as the insensitivity of reproductive output to prey availability complicate attempts to construct predator-prey models. At least for insects that acquire most of their energy while larvae, models which rely on a simple relationship between prey number and predator rate of increase without incorporation of the variance in this parameter should be treated cautiously.

III. THE EFFECT OF PREY AVAILABILITY ON FORAGING BEHAVIOR

INTRODUCTION

A vast and growing body of literature suggests that some animals forage to increase the rate of net energy gain above that expected if foraging were strictly random. Choice of which foods to eat (eg., Goss-Custard 1977; Heinrich 1978), allocation of time among patches of different food abundance or quality (Charnov 1976; Pyke 1978), choice of which prey sizes to eat (Thompson 1978), and of what sorts of search paths to pursue (Pyke 1974; Smith 1974a,b) have all been investigated theoretically and the predictions tested empirically especially in birds and arthropods. For example, many arthropods, eg., mites (Eveleigh and Chant 1982b), coccinellid larvae (Carter and Dixon 1982), lacewing larvae (Bond 1980) and first instar syrphid larvae (Chandler 1969) show "area-restricted searching" behavior immediately after capturing a prey. This type of searching is characterized by reduced velocity and increased turning which tends to keep a predator within a patch where prey have been found. The thoroughness of such searching decays with time after the last prey capture into more extensive searching (Bond 1980; Murdie and Hassell 1973) which will take the predator to another area. Thus more time will be spent in energy-rich patches and less time in

poor patches or traveling between patches of prey. Energy acquisition should therefore be greater than if time were allocated randomly among all points in the habitat. This sort of foraging behavior is probably most efficient when prey are clumped (Eveleigh and Chant 1982b).

Aphids are patchily distributed on plants; they are more abundant on stems and the undersides of leaves (Dixon 1973) and probably are patchily distributed among plants. Syrphid larvae probably also exhibit area-restricted searching behavior. However random searching models are the simplest ones for predicting encounter rates between predator and prey. Such a model could predict prey consumption at various prey availabilities. This is a necessary component for modeling the impact of syrphids on aphid populations. In addition, a random encounter model can serve as a null hypothesis for evaluating the efficiency of syrphid larval foraging behavior. Random searching in the context of these models means that the path of the predator is not affected by the location of prey (Royama 1971) and there is an equal probability of visiting each point in the foraging area. The search path will have no directionality (Pyke 1974).

I used a model developed by Laing (1938 cited in Schoener 1971) for moving predators and stationary prey. The search path of a moving animal has a width

equal to $2 \times (R_1 + R_2)$, where R_1 is the radius of the objects to be encountered and R_2 is the perceptual radius of the predator (Fig. 4). The area searched in any time is thus the product of the path width and the distance travelled. More conveniently, the rate of searching is the path width $\times$ speed, V . For randomly distributed stationary prey and a randomly moving predator the probability of encountering a prey item is proportional to the density of prey, D . Hence the expected number of encounters per unit time, N , is given by the formula

$$N = 2 \times (R_1 + R_2) \times V \times D$$

Predictions of prey consumption by M. corollae larvae were made and compared with the predation rate observed during the experiments on the effect of prey availability on consumption and reproduction.

METHODS

1. Area searched per minute

The area searched per minute (A) is given by the formula

$$A = 2 \times (R_1 + R_2) \times V$$

where R_1 = prey radius in cm

R_2 = predator searching radius in cm

V = predator speed in cm/min

The length and width of aphids settled on pieces of pea plant were measured under a dissecting microscope with a calibrated eyepiece micrometer. An average rectangular area for 7 day old aphids was calculated as mean length x mean width. The radius of a circle of equal area was used as the prey radius, R_1 .

Syrphid larvae search by waving the front part of their bodies from side to side as they move. The parameter R_2 was taken as the distance from the longitudinal body axis to the furthest point reached by the sideways waving (Fig. 4). Larvae were reared at either 10 or 40 aphids provided per day on pea plants. Five, six and seven day old larvae were placed singly in a 14 cm diameter petri dish which was placed on 1 mm grid graph paper. The dish was moved so that the location and orientation of the larva's body axis stayed constant with respect to the graph paper while

Fig. 4. Search path width of a moving predator. R_1 = radius of prey; R_2 = searching radius of predator; V = velocity of predator; Area searched = $2 \times (R_1 + R_2) \times V$

Area searched

the larva moved in the dish. The extent of the waving motions was recorded as points on a matching grid. The predator searching radius was then measured as the distance required to encompass these points. Resting body length was also measured.

Speed of larvae was determined by tracing the paths of crawling larvae. Larvae that had been fed ad libitum for the first four days of their larval lives were obtained from the stock culture (Barlow 1979). All experiments were done at 20 °C ($\pm$ 1 °C range). Individual larvae were placed in a 15 cm diameter, 2.5 cm deep, plastic petri dish with the plastic floor replaced by a floor of taut organdy netting. A grid of 1 cm squares was inked on the lid. This facilitated recording the paths of larvae on paper with a corresponding grid. A larva placed in the dish was allowed 2 to 3 min. to acclimatize; then its path was recorded for 10 min. Larvae that did not move were prodded gently with a fine paint brush. If they did not move within 5 minutes they were discarded. The lengths of the paths were determined with a map measurer. Because hunger, light intensity and the presence or absence of aphids might affect the speed of syrphid larvae speed was measured under the following conditions:

1. three larval ages - 5, 6, and 7 days after hatching
2. two hunger levels - satiated larvae were kept in

cages with aphids until testing. Other larvae were removed from the stock culture 24 h before testing and placed in small dishes with 2 to 3 fresh pea stems on damp filter paper but no aphids. These were called "24 h starved".

3. two light intensities - satiated and 24 h starved larvae were tested under two 15 watt cool-white fluorescent tubes suspended 40 cm above the experimental chamber (giving about 3×10^3 lux) or under one red incandescent light bulb at a height of 30 cm (about 400 lux). The latter treatment was used to simulate dark conditions.
4. aphid presence or absence - most experiments were done in the absence of aphids. To test the effect of aphid presence the experimental chamber with its organandy floor was placed on top of a second uncovered petri dish containing aphids. Thus syrphid larvae could smell but not touch the aphids.

The speeds measured in these experiments were those of moving larvae because larvae that failed to move were discarded. But larvae on plants do not move all the time. Therefore these speeds had to be corrected by a probability of moving (PM). The rate of search A' , thus becomes

$$A' = 2 \times (R_1 + R_2) \times V \times PM$$

Since speed had been determined during a ten minute

period, the necessary probability of moving was the chance of moving during a similar 10 min interval. The activity of syrphid larvae was recorded with a time-lapse videotape recorder (Panasonic Time Lapse recorder NV-8050) with a videocamera with high sensitivity to red wavelengths (Panasonic videocamera WV-1850). Larvae were reared at two food levels (10 or 40 aphids offered per day) on two plant sizes (7.5 cm^2 or 35 cm^2) as has been described previously. Larger plants could not be used because there were too many overlapping leaves for good visibility. The activity of larvae was recorded when they were 5, 6, and 7 days old. These days were chosen because they were the days with the highest consumption of aphids. The high sensitivity of the camera allowed recording under almost dark conditions. For the 8 h "dark" part of the photoperiod an, infrared transmitting, visible absorbing filter (Corning Laboratory Products #2540) was placed in front of a high-intensity incandescent light source that was surrounded by a metal housing that prevented unfiltered light from escaping. The resulting light level was less than 0.5 lux. During the "light" part of the photoperiod, fluorescent tubes and incandescent bulbs provided light in excess of 9×10^3 lux. Videotapes were made with an interval of 0.2 sec between videorecords (24 h mode) and played back for analysis with 1/60 sec or 1/120 sec between

videorecords (i.e., 12x or 24x normal speed).

Each 10 minute interval of the recorded period was scored as either with locomotion or without locomotion. Sequences of 6, 10 min intervals were grouped to give an average probability of moving during each hour. Thus diurnal activity patterns for larvae of different ages and rearing conditions were constructed.

To measure activity during the morning light hours positions of larvae were noted directly at 10 min intervals. This provided data equivalent to those obtained from the videotapes.

2. Capture Success

The encounter rate (N) between a searching predator and its prey is

$$N = 2 \times (R1 + R2) \times V \times PM \times D$$
 where D = density but not all encounters between syrphid larvae and aphids resulted in an aphid being captured and eaten. The proportion of encounters that ended in capture, the capture success (CS), was estimated from the videotapes. An encounter was defined as an aphid that was touched by a searching larva. This excluded two types of syrphid-aphid interactions, moving aphids that encountered resting larvae and aphids that escaped by moving away or dropping off the plant without actually being touched by a syrphid. A capture was defined as

an encounter in which the larva held the aphid for more than one minute. The proportions of encounters that resulted in capture were averaged for all larvae of the same age and rearing condition.

3. Time spent feeding

The time that a predator spends handling and feeding on prey is not available for searching and therefore reduces the encounter rate. For M. corollae larvae handling time is indistinguishable from feeding time. Feeding times were determined from the videotaped observations of larvae. The time of capture of an aphid was subtracted from the time at which the syrphid larva dropped the aphid carcass.

4. Computer simulation of the random searching model

The equation predicting the rate of captures made by syrphid larvae with modifications for periods of inactivity and aphid escapes is

$$N = 2 \times (R_1 + R_2) \times V \times PM \times D \times CS$$

Since predator age had an effect on the values of several model parameters, the model was evaluated for 24 h periods and compared with daily prey consumption data obtained during the experiments on the effect of prey availability on consumption and reproduction (Section II). Since prey were not replaced during each 24 h period, prey density changed as each aphid was eaten. Consequently the time required to encounter

each successive aphid increased. Thus, the number of aphids captured was calculated iteratively using a BASIC computer program (Appendix I). The computer simulation began with the number of aphids provided daily, the surface area of the cage and pea plant(s) on which the aphids were placed, the total time available, and the values for prey radius and predator searching behavior (Fig. 5). Then the average expected time between captures, including the expected time between captures spent motionless and the probability of not capturing an aphid and having to locate another, was calculated as the inverse of the capture rate (time between captures, $TS = 1/N$) (Fig. 5). This time and the time spent feeding on a captured aphid were subtracted from the total time available to give the time remaining (Fig. 5). The number of prey remaining was used to revise the prey density; then the expected time for capturing the next aphid was calculated and the time remaining and prey remaining revised. This sequence was continued until all the aphids were captured or until there was no time remaining.

The model was run for 8 h with values of predator behavior in the light, for another 8 h with values for the dark period and the number of prey remaining after the first 8 h, and then continued for a further 8 h with values for the light period. This corresponded with the photoperiod cycle and procedures of the first

Fig. 5. Flow chart of computer simulation of random searching model in which the encounter rate,

$$N = 2 \times (R_1 + R_2) \times V \times PM \times CS \times D$$

where R_1 = prey radius

R_2 = predator searching radius

V = predator velocity

PM = probability of moving

CS = proportion of encountered prey
that are captured

D = prey density

series of experiments in which the daily ration of aphids was provided during a 2 h period in the middle of the light phase (Fig. 6). These three periods are called "afternoon", "night", and "morning". When 40 aphids were used as the initial number of prey, the speeds for satiated larvae were used; when 10 aphids were used, the speeds for 24 h starved larvae were used. To test the model against more observations, values of the parameters were estimated for larvae being reared on 73 cm² plants.

The success of this model in predicting prey consumption by syrphid larvae was evaluated for the afternoon, night and morning periods. The number of aphids eaten every 2 h during the light hours by larvae being reared at 10 or 40 aphids offered per day on 7.5 cm² or 73 cm² plants was recorded. A second source of data was the number of prey eaten in the afternoon by larvae used in the videotaped experiments. These data were averaged to give the number of aphids eaten in afternoon and morning periods; the number of aphids eaten during the night was obtained by subtracting these from the average total daily consumption determined in the 3 series of experiments (i.e., effect of prey availability on consumption and reproduction; videotaped experiments; and diel pattern of prey consumption experiments).

RESULTS

1. Area searched per minute

The average length of a 7-day old aphid was 0.47 ± 0.12 (S.E.M.) cm ($N=10$), the average width was 0.40 ± 0.17 cm. Thus the average rectangular area was 1.88 cm^2 and the radius of a circle of the same area was 0.24 cm.

The searching radius (R_2) of M. corollae larvae increased with body length. Well-fed larvae had searching radii of 0.6 ± 0.02 , 0.8 ± 0.03 and 1.0 ± 0.01 cm when they were 5, 6, and 7 days old respectively. Larvae being reared with only 10 aphids per day were smaller at any age, but searched a wider path for their length than the well-fed larvae. Their searching radii were 0.5 ± 0.02 , 0.7 ± 0.03 and 0.9 ± 0.04 cm at 5, 6, and 7 days of age.

Satiated larvae of all ages moved faster in the dark than in the light as did 7 day old larvae that had been starved for 24 h. Younger starved larvae moved at the same speed in both light and dark (Table 8). In the light, starved larvae moved more quickly than satiated ones. In the dark, satiated larvae moved faster than starved ones when they were 5 and 6 days old but at the same speed when 7 days old. Aphid presence did not generally affect the speed of movement of larvae.

Table 8. Effect of hunger, light, and aphid presence or absence on the velocity (cm/min) of *M. corollae* larvae. Means $\pm$ S.E.M. (sample size). Letters indicate values within an age which are not statistically different by Student-Neumann-Kuels Multiple Range Tests at $p = .05$.

larval age	treatment	satiated	24 h starved
5 days	light; no aphids	1.5 $\pm$ 0.21 a (18)	2.6 $\pm$ 0.29 c (14)
	light; with aphids	1.2 $\pm$ 0.27 a (11)	2.7 $\pm$ 0.32 c (8)
	dark; no aphids	3.9 $\pm$ 0.26 b (12)	2.7 $\pm$ 0.40 c (11)
6 days	light; no aphids	2.0 $\pm$ 0.24 a (25)	2.9 $\pm$ 0.25 a (22)
	light; with aphids	1.6 $\pm$ 0.32 a (14)	3.8 $\pm$ 0.71 b (8)
	dark; no aphids	4.3 $\pm$ 0.37 b (15)	2.5 $\pm$ 0.36 a (14)
7 days	light; no aphids	0.8 $\pm$ 0.09 a (24)	3.7 $\pm$ 0.53 b (17)
	light; with aphids	0.5 $\pm$ 0.16 a (10)	5.1 $\pm$ 1.0 b (6)
	dark; no aphids	4.4 $\pm$ 0.73 b (15)	5.3 $\pm$ 0.57 b (13)

Larvae being reared at 40 aphids per day had a low probability of moving during the light hours (Table 9, Fig. 6). After the lights were turned off, activity increased sharply with another increase later in the night (Fig. 6). These larvae reduced their activity after the lights were turned on in the morning. Larvae being reared with only 10 aphids per day moved almost constantly in the dark and morning hours although most or all aphids had been eaten. Plant size did not affect the probability that a larva moved (Mann-Whitney U-tests, Table 9).

The product of search path width, speed and probability of moving gives the rate of searching. M. corollae larvae are capable of searching large areas very quickly (Table 10). During the night they searched as much as 12 cm^2 per minute or 720 cm^2 per hour. Given that the largest plant surface area used was only 73 cm^2 and the cage surface area was 168 cm^2 , these larvae were able to search the entire foraging environment several times each hour.

2. Capture success

M. corollae larvae captured approximately two-thirds of the aphids which they encountered. Generally, larval rearing conditions had little effect on capture success rate. Because very few captures were observed during the dark period for larvae

Table 9. Effect of prey availability on proportion of 10 min intervals with locomotion by M. corollae larvae.
Means of (N) larvae. Identical letters indicate means within the same time which are not statistically different by Mann-Whitney U tests at $p = .05$.

aphids offered per day	plant size (cm ²)	larval age							
		5 days				6 days			
		afternoon	night	morning	afternoon	afternoon	night	morning	afternoon
10	7.5	.14 a	.63 a,b	.54 a	.31 a	.97 a	.86 a	.41 a	.98 a
		(3)	(5)	(4)	(2)	(6)	(4)	(4)	(6)
									.34 a
35	7.5	.33 a	.78 b	.86 b	.87 b	1.0 a	.77 a,b	.48 a c	1.0 a
		(3)	(6)	(4)	(3)	(5)	(4)	(2)	(5)
									.15 a
40	7.5	.21 a	.25 c	.19 c	0 a	.55 b	.33 b	0 b	.55 b
		(3)	(5)	(3)	(3)	(5)	(3)	(4)	(5)
									.03 a
35	7.5	.08 a	.51 a	.12 c	.05 a	.53 b	.15 c	0 b	.43 b
		(6)	(6)	(4)	(5)	(6)	(4)	(4)	(6)
									.02 a
									(4)

Fig. 6. Diel activity of M. corollae larvae of different ages being reared at 10 aphids offered per day (top row) or 40 aphids per day (bottom row) on 7.5 cm² plants (closed circles, solid line) or 35 cm² plants (open circles, dashed line). The duration of the dark period is shown by the thickened segment of the X-axis. Frequency of locomotion is the average proportion of 10 min intervals with locomotion (sample sizes are in Table 9).

Table 10. Effect of prey availability on the average rate of searching of M. corollae larvae.
 Area searched (cm^2/min) = $2 \cdot V \cdot (R1 + R2)$. PM where V = velocity, $R1$ = prey
 radius, $R2$ = predator searching radius and PM = probability of moving

aphids offered per day	plant size (cm^2)	time of day and larval age									
		afternoon					night				
		5 days	6 days	7 days	5 days	6 days	7 days	5 days	6 days	7 days	morning
10	7.5	0.55	1.7	3.5	2.5	4.6	11.8	2.1	4.7	2.9	
	35	1.3	4.7	4.0	3.1	4.7	12.1	3.5	4.2	1.3	
40	7.5	0.50	0	0	1.6	4.9	6.0	0.46	1.4	0.06	
	35	0.19	0.21	0	3.2	4.7	4.7	0.29	0.62	0.04	

provided only 10 aphids per day, the probabilities of capturing an encountered aphid for these larvae were determined for all observed encounters. For larvae offered 40 aphids per day, a small sample of encounters during the light period was averaged for larvae of all ages to give a capture success rate during the light of 0.4, which was slightly lower than that calculated for the dark period (Table 11).

3. Time spent feeding on a prey

Five day old larvae tended to spend longer feeding on each aphid than older larvae (Table 12). Feeding times also tended to be longer for larvae offered only 10 aphids per day. When 40 aphids were provided per day, feeding times were affected by plant size but the pattern is not clear. While 5 day old larvae with 40 aphids on small plants fed longer on each aphid than similar larvae on large plants, older larvae fed slightly longer when aphids were on larger plants.

4. Diel pattern of prey consumption

The daily ration of aphids was provided between 1400 and 1500 h which was approximately the middle of the photoperiod. In the next 7 to 9 h of light, syrphid larvae ate relatively few aphids (Fig. 7). Although no direct measurements of the rate of prey consumption were made during the dark, the difference

Table 11. Effect of prey availability on the capture success of *M. corollae* larvae. Capture success = proportion of encountered aphids captured. Means and (sample sizes). Identical letters indicate values within an age which are not statistically different by Mann-Whitney U tests at $p = .05$.

aphids offered per day	plant size (cm ²)	larval age		
		5 days	6 days	7 days
10	7.5	.63 a (8)	.89 a,b (6)	.83 a (8)
	35	.67 a (9)	.88 a,b (7)	.67 a (7)
40	7.5	.42 a (5)	.80 a (5)	.39 b (5)
	35	.51 a (6)	.49 b (5)	.54 a,b (6)

Table 12. Effect of prey availability on time spent feeding
(min) on individual aphids by M. corollae larvae.
Means and (95% confidence intervals) (sample size).
Lines connect means within an age which are not
statistically different by Student-Newman-Keuls
multiple range tests at $p = .05$.

aphids offered per day	plant size (cm ²)	larval age		
		5 days	6 days	7 days
10	7.5	12.5 (10.6-14.6) (18)	9.9 (8.4-11.7) (17)	10.2 (8.9-11.8) (23)
	35	13.9 (12.2-15.9) (26)	10.2 (10.5-15.0) (15)	9.5 (7.9-11.3) (14)
40	7.5	10.6 (9.5-11.8) (38)	5.7 (5.3-6.1) (91)	5.3 (4.9-5.8) (60)
	35	7.9 (7.2-8.6) (58)	6.9 (6.2-7.6) (45)	6.0 (5.5-6.6) (59)

Fig. 7. Diel pattern of prey consumption by M. corollae larvae of different ages being reared at different prey availabilities. The dark period is shown by the thickened segment of the X-axis. The daily ration of aphids was provided between 1400 and 1500 h (■).

- x — x 10 aphids per day, 7.5 cm² plants
- — — — ● 10 aphids per day, 73 cm² plants
- ····· ○ 40 aphids per day, 7.5 cm² plants
- ▲ — — ▲ 40 aphids per day, 73 cm² plants

Fig. 7. continued. Diel pattern of prey consumption

between the number of aphids eaten when the lights went off and the number that had been eaten when the lights came on 8 h later, showed a marked increase in the rate of consumption by all but 4 day old larvae. Larvae offered 40 aphids per day caught between 5x and 10x more aphids per hour at night than in the afternoon although the aphid density had declined. During the morning, consumption was very low even when aphids remained. Only when larvae were provided 10 aphids per day on 73 cm² plants did larvae capture a large proportion of their daily intake during the afternoon light period (Fig. 7). These patterns of consumption correspond in a general way with those of locomotory activity (Fig. 6). Consumption at night was always greater than that in the other two periods. Actual values and values predicted by the model are given in Tables 13 and 14 and compared in Fig. 8.

5. Computer simulation and evaluation of the random searching model

The model based on a capture rate given by

$$N = 2 \times (R_1 + R_2) \times V \times PM \times CS \times D$$

was evaluated using the appropriate values from Tables 8 to 12. An example of the output of the computer program of the model is given in Appendix II. It became obvious that the model would not accurately predict prey consumption unless the density was

Table 13. Number of aphids eaten by *M. corollae* larvae during different parts of the day. Means $\pm$ S.E.M. (N).

No. of aphids eaten at night = average total consumption - (no. eaten in afternoon + morning).

aphids offered	plant size per day	age cm ² days	mean number of aphids eaten			mean total number of aphids eaten				
			afternoon	night	morning	series 1	series 2	series 3	average	
10	7.5	5	3.0 ± 0.65 (7)	5.5	0.2 ± 0.18 (6)	8.7 ± 0.60 (17)	9.0 ± 0.63 (6)	8.6 ± 0.33 (26)	8.7	
		6	2.6 ± 0.69 (8)	6.8	0 (6)	9.2 ± 0.59 (17)	10.0 ± 0.26 (6)	9.4 ± 0.37 (25)	9.4	
		7	3.5 ± 1.12 (10)	5.7	0.2 ± 0.18 (6)	9.6 ± 0.24 (17)	9.7 ± 0.33 (6)	9.2 ± 0.44 (24)	9.4	
	35	5	4.5 ± 1.19 (4)	4.0	(0.5)*	9.5 ± 0.35 (21)		8.7 ± 0.38 (29)	9.0	
		6	6.3 ± 0.88 (3)	3.4	0 *	10.0 ± 0.12 (21)		9.4 ± 0.15 (28)	9.7	
		7	4.6 ± 1.03 (5)	4.8	0 *	8.8 ± 0.67 (21)		9.8 ± 0.09 (29)	9.4	
40	7.5	5	2.2 ± 0.49 (5)	6.3	1.2 ± 0.37 (5)	9.9 ± 0.16 (14)	9.2 ± 0.37 (5)		9.7	
		6	4.8 ± 1.28 (5)	4.9	0 (5)	9.7 ± 0.22 (14)	9.6 ± 0.40 (5)		9.7	
		7	5.2 ± 1.51 (5)	4.4	0 (5)	9.4 ± 0.31 (14)	10.0 ± 0.32 (5)		9.6	
	35	5	3.7 ± 0.92 (7)	14.8	0.8 ± 0.37 (5)	19.5 ± 2.3 (18)	19.6 ± 1.0 (5)	19.2 ± 1.2 (27)	19.3	
		6	1.4 ± 0.75 (8)	24.3	0.4 ± 0.24 (5)	25.8 ± 2.5 (18)	27.0 ± 1.4 (5)	26.2 ± 0.99 (27)	26.4	
		7	2.2 ± 0.76 (13)	20.7	0.2 ± 0.20 (5)	18.4 ± 2.9 (18)	29.2 ± 1.7 (5)	25.2 ± 0.86 (27)	23.1	
73	7.5	5	3.0 ± 1.5 (3)	13.2	1 *	20.4 ± 0.95 (18)		15.1 ± 1.05 (27)	17.2	
		6	3.0 ± 1.0 (2)	19.9	1 *	25.2 ± 0.97 (18)		23.1 ± 1.05 (27)	23.9	
		7	2.0 ± 1.0 (3)	15.8	1 *	14.2 ± 2.1 (18)		21.9 ± 0.85 (27)	18.8	
	35	5	2.3 ± 0.82 (6)	12.5	1.5 ± 0.22 (6)	17.2 ± 1.7 (18)	11.8 ± 1.4 (6)		15.8	
		6	2.5 ± 0.85 (6)	21.3	1.2 ± 0.79 (6)	25.6 ± 2.0 (18)	23.0 ± 1.8 (6)		24.9	
		7	1.2 ± 0.47 (10)	15.4	2.0 ± 0.93 (6)	18.3 ± 2.4 (18)	21.0 ± 2.8 (6)		18.9	

1 series 1: reproduction experiments; series 2: time of prey consumption experiments; series 3: videotaped experiments

* estimated by interpolating between values for 7.5 and 73 cm² plants

Table 14. Predicted prey consumption by *M. corollae* larvae based on two models. (1) capture rate = $2 \cdot (R1 + R2) \cdot V \cdot PM \cdot CS \cdot D$
 (2) capture rate = $2 \cdot (R1 + R2) \cdot V \cdot PM \cdot CS \cdot D \cdot X$, where
 X chosen such that predicted = observed consumption

aphids offered per day	plant size cm ²	age days	predicted number of aphids eaten					
			model (1)			model (2) (X)		
			afternoon	night	morning	afternoon	night	morning
10	7.5	5	6	4	-	3 (.5)	6 (.6)	0 (.2)
		6	10	-	-	3 (.1)	7 (.4)	-
		7	10	-	-	5 (.1)	5 (.2)	-
	35	5	8	2	-	5 (.4)	4 (.5)	1 (.4)
		6	10	-	-	6 (.1)	4 (.3)	-
		7	10	-	-	5 (.13)	5 (.2)	-
	73	5	8	2	-	2 (.15)	6 (.2)	1 (.2)
		6	10	-	-	5 (.1)	5 (.3)	-
		7	10	-	-	5 (.15)	5 (.2)	-
40	7.5	5	13	18	3	4 (.2)	14 (.4)	1 (.1)
		6	0	40	-	1 (1)	24 (.13)	2 (.1)
		7	0	39	0	0 (1)	21 (.15)	1 (1)
	35	5	6	30	1	3 (.5)	14 (.15)	1 (.3)
		6	6	32	1	3 (.5)	20 (.2)	1 (.2)
		7	0	39	0	0 (1)	17 (.1)	0 (1)
	73	5	6	27	1	2 (.4)	13 (.17)	1 (.2)
		6	5	32	1	2 (.4)	21 (.25)	2 (.3)
		7	0	38	0	0 (1)	16 (.12)	0 (1)

Fig. 8. Comparison of observed and predicted prey consumption by M. corollae larvae of different ages being reared with either 10 or 40 aphids offered per day on plants with 7.5, 35 or 73 cm² surface area. Predicted consumption exceeded observed except when all aphids had been eaten earlier.

calculated as the number of aphids / total surface area including both plant surface area and cage surface area. The cage surface area was 168 cm^2 ; the areas, corresponding to the three plant sizes, were 175, 200 and 240 cm^2 . Nevertheless, the predictions of the model exceeded the observed predation rate (Tables 13 and 14 and Fig. 8). This was true for all parts of the diel cycle, except when larval activity had been measured as zero, where the model predicted that no aphids would be eaten, when in fact a small number were. These aphids were most likely ones that were moving and encountered larvae who were opportunistic in capturing them.

Both time spent feeding and time between captures determined the rate at which syrphid larvae used the time available. Since feeding times were measured directly, the poor agreement of the model is ascribed primarily to overestimation of the capture rate. To determine the correction required, the model was re-run to find the best adjustment factor (i.e., find x , such that the new capture rate, $N' = N \cdot x$ and therefore $TS' = 1/N' = TS/x$, where $x < 1$ and the total number of prey captured = observed number). The encounter rate was found to be overestimated by somewhat less than an order of magnitude in most cases (Table 14); there were no clear patterns in the amount of correction required.

DISCUSSION

M. corollae larvae move by stretching the anterior part of the body forward, grasping the substrate, and pulling the rest of the body forward. Periodically they lift the front part of the body from the substrate and strike out to the side or front. They turn frequently while moving so that they re-search the same area. On plants they often crawl along the edges of leaves and search both leaf surfaces.

Hungry M. corollae larvae had relatively wider search paths and were more active in the light with both faster and more frequent movement than satiated larvae. Although these increased the area searched and therefore should increase the probability that larvae encounter aphids, they may also entail increased energy expenditure and increased exposure to visually hunting predators. Starved larvae increased their speed in the dark only when they were 7 days old. Satiated larvae of all ages moved faster in the dark and their speed in the dark was greater or the same as that of starved larvae. Satiated larvae were bigger than starved larvae of the same chronological age. These facts suggest that the speeds of syrphid larvae in the dark and in the light when starved are the greatest or most efficient for their size. Larger individuals should have faster optimal travel speeds during foraging (Pyke

1981).

Bigger M. corollae larvae had a wider search path and were capable of faster locomotion, thus they were capable of searching a larger area than smaller larvae. Thus the probability of their encountering aphids should be greater. This means that success in finding and capturing aphids early in larval life will affect the chance of later success. Thus the first part of the larval period may be critical in determining larval survival and growth, as well as future reproductive success.

Larvae continued to search for many hours after all aphids had been eaten. The speed, path width and frequency of activity were such that larvae could search large areas every hour. The entire surface of the largest plants could be searched in less than 20 min by 5 day old larvae and in less than 10 minutes by 7 day old larvae if they moved continuously. Under these conditions there was a low probability that aphids moved into an area before it was revisited by a larva. Larvae moved up and down the plants several times, eventually reaching the base of the stem and leaving the plant. Similar movements have been described for coccinellid larvae (Dixon 1959). In Adalia decempunctata, well-fed larvae made more visits to the apex of an artificial stem and the tendency to revisit the apex decreased as the period of starvation

increased (Dixon 1959). Thus, hungry larvae will "waste" (Dixon 1970) less time revisiting areas they have searched unsuccessfully. After leaving the plant, syrphids moved along the cage bottom until they reached a vertical surface which they usually climbed. In a field of peas this behavior would result in larvae moving quickly from plants without aphids to plants with aphids. Here they would stay longer if they exhibited area-restricted searching after finding prey as many insect predators do (Carter and Dixon 1982, Bond 1980).

The pattern of feeding times generally corresponded with that of carcass weights determined in the earlier experiments on the effect of prey availabilities on consumption and reproduction (Table 2), although precise comparisons are not possible because different plant sizes were used. Generally, longer feeding times were related to smaller carcasses and this trend is confirmed by unpublished data that showed that within an age, longer feeding times resulted in smaller carcasses and greater energy extraction. Foraging theory predicts that animals in poor quality prey habitats should spend longer feeding in a patch of prey than animals in richer habitats to maximize their rate of net energy gain (Charnov 1976). An aphid can be considered a patch, and the number and density of aphids offered per day set the expected rate

of energy gain in the habitat. Thus larvae offered only 10 aphids per day should, according to foraging theory, and did, feed longer on each aphid than larvae offered 40 aphids per day. When 40 aphids were offered per day, 6 and 7 day old larvae spent longer feeding on each aphid when aphids were present on large plants. This implies that syrphid larvae responded to both the number of prey and to prey density in 'evaluating' habitat quality. But this does not apply to 5 day old, well-fed larvae. Syrphid larvae that respond to prey scarcity by feeding longer on each aphid will increase their energy intake with very little increase in energy expenditure.

The random searching model based on these behavior variables predicted that M. corollae larvae would capture more aphids more quickly than was observed. This apparently means that syrphid larvae searched less efficiently than they would if they moved randomly. Within the adaptationist framework, this conclusion seems surprising and other explanations may be possible.

Obvious sources of error in the model are the values of the parameters. Velocity of larvae moving over the flat, homogeneous surface of a petri dish may be greater than that of larvae crawling over a pea plant. Leaf edges, branching points, and places where leaves overlap may be intensively explored with more

turning and waving of the body. This might reduce the average velocity. However, larvae were observed to search plants very rapidly and probably can come close to achieving the velocities seen in petri dishes where frequent turning and waving also occurred. Overestimation of velocity probably does not therefore, account entirely for the model's overestimation of the predation rate.

The width of the searching path of older larvae may have exceeded the dimensions of parts of the plants. Most pea leaf laminae were less than 1.5 cm in any direction, the circumference of pea stems was less than 0.6 cm while the search path width of 7 day old larvae was 1.24 cm. But larvae also moved on the cage where the full path width could be searched. It seems unlikely that overestimation of search path width is a significant source of error.

The frequency of movement was measured directly from videotaped observations of larvae. Because the probability of movement was determined in an all-or-none manner for 10 min. intervals it overestimates the actual time spent moving. This is most severe when only a few intervals had movement and these intervals were interspersed among periods without movement. Then as little as 0.5 min might have had movement although 10 min would have been incorporated in the model. However, larvae in the experiments to

measure velocity also stopped moving during the 10 min for which their path lengths were traced. Also, when aphids were dense, larvae could capture several of them without any locomotion being recorded.

Another model parameter that may contribute in a small way to the poor fit of the model is the capture success of M. corollae larvae. The values used were based on clearly seen, narrowly defined direct encounters and captures. Aphids have escape responses apart from those initiated by direct contact with a predator (Clegg and Barlow 1982). Disturbed aphids secrete an alarm pheromone from their cornicles to which other aphids usually respond by moving their antennae. When vibration of the plant stem preceded presentation of pheromone, aphids responded by backing up, running, or dropping off the plant as well as by waving their antennae (Clegg and Barlow 1982). If aphids began to move in response to vibrations caused by the advance of a syrphid larva or alarm pheromone released by other aphids, the larva would move into an area which the aphids had just vacated. In addition, antennal waving may touch nearby aphids, exciting them and increasing their tendency to respond to other stimuli by moving away. These aphid behaviors would reduce the overall probability of encounter from the random expectation. The model for encounter rate cannot be corrected for this type of aphid movement.

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simply by adding a term for average aphid velocity. Doing this assumes random aphid movement, and would actually increase the encounter rate (Holling 1965).

Even if each predator behaviour parameter in the model (i.e., V , R_2 , PM , CS) had been overestimated by 100%, the model would still overestimate the predation rate in some cases and such a large error for each parameter seems unlikely. An additional and potentially important source of error lies in the assumptions of random prey dispersion and random predator searching inherent in the model. Syrphid larvae probably do not or cannot search randomly. Rather, they respond to patchiness which under experimental conditions may have led to less efficient predation but under natural conditions may lead to greater efficiency in energy acquisition. Syrphid larvae turn frequently while they move. Increased turning, decreased velocity and longer sequences of turns in the same direction, following prey capture or encounter, are characteristic of area-restricted searching and ensure that a predator stays near the place where prey have been found. Aphids are clumped in their dispersion and area-restricted searching seems to be an effective way of harvesting clumped prey (Eveleigh and Chant 1982b). Many insects, including first instar syrphid larvae (Chandler 1969) show area-restricted searching, so it seems likely that M.

corollae larvae also do. Thus the velocities after prey capture may be slower than those measured in a petri dish. When many aphids had been eaten and prey density reduced to a low level so that the time between captures was long, M. corollae larvae became more active and appeared to search less thoroughly. They moved up and down plants rapidly. If they also made fewer turns, fewer casts and had less tendency to travel sideways along branches (all things predictable from the behavior of other aphid-eating insects), then some parts of the plant, particularly the leaves, would rarely be searched after the prey density had become sufficiently low that it would be more profitable for a syrphid larva to leave that plant for another. Under the experimental conditions, the next vertical surface encountered was usually the cage wall which larvae usually climbed. Leaves of 35 and 73 cm² plants touched the cage and larvae were able to get on the plants from the cage. But the prey density on these plants was already low and the probability of the larvae encountering an aphid and thus switching to more intensive searching behavior, would also be low. Hence after prey density has been reduced, the the probability of the remaining aphids being found is lower than their average density might suggest.

Plants impose a structure on the foraging environment which limits the routes along which a crawling animal can travel. When a syrphid larva reaches the apex of a branch or the tip of a pea leaf, it can only turn around and travel over the area it has just searched. It may travel on the other surface of the leaf but since aphids prefer the undersides of leaves, searching both upper and lower surfaces equally would be inefficient (Dixon 1970). This effect of plant structure may be thought of as almost halving the area searched. When larvae moved on the cage their movement was not similarly restricted. However, few aphids were on the cage surfaces and those were usually moving and almost impossible for larvae to catch.

Habitat structure and complexity have been found to limit predator effectiveness in a few other studies. Banks (1957) found that the alternate arrangement of bean leaves on the stem resulted in coccinellid larvae not searching some leaves. Tamaki et al. (1981) found that predator consumption per plant was lower in field cages with more than one plant. The encounter rate of a predaceous mite, Phytoseilus persimilis, with prey mites was lower in arenas with more internal barriers (Kaiser 1983). In this case, the lower encounter rate appeared to result not just from impeded searching but also because greater total length of barriers increased the number of places that prey preferred and thus

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increased prey dispersion. Eveleigh and Chant (1982a) have also found that the predation rate of some mites was lower when prey were more dispersed than when they were clumped. How many of these findings are applicable to M. corollae larvae under the conditions of the experiments is uncertain. On a daily basis, increased plant size had only a small effect on the number of aphids eaten (Table 13). However, it may be that any amount of structure and heterogeneity decreases predator effectiveness relative to the random expectation while further increases have only small added effects.

Such predator responses to spatial complexity as shown by M. corollae larvae are difficult to incorporate into a model of encounter rates. Added to this is the dependence on hunger level of most of the model parameters. Holling (1965) dealt with this problem when modelling the functional response of a praying mantis by finding the functional relationships between each component and hunger. For M. corollae larvae, however, plant size as well as prey number is sometimes a determinant of at least two model parameters, feeding time and activity. Since daily prey consumption differed only slightly among plant sizes, it is not clear how much 'hunger' measured in conventional ways (i.e., as hours of starvation or quantity of food in the gut) also differed.

Constructing a general model that predicts the predation rates of M. corollae larvae may be much more difficult than directly measuring the functional response under a variety of conditions.

IV. GENERAL DISCUSSION

My aim was to determine the effect of prey availability on consumption and reproduction of an insect predator and then to develop a model, based on the behavior of the predator, to predict consumption at different prey availabilities. With these components it would be possible to predict reproduction given prey conditions. The relationships between prey availability, predator consumption and reproduction are essential elements for assessing the biological control potential of an insect predator.

Two aspects of prey availability were manipulated, prey abundance and prey density. When I began there were no published studies of the effect of plant size (or an equivalent) on foraging effectiveness. Also there were few studies on the effect of larval nutrition on reproduction. It was logical to expect that when more prey were provided on a constant area, more would be eaten, foraging costs would be lower, and thus more energy would be available for reproduction. When plant size was increased and prey abundance held constant, I expected that fewer prey would be eaten, foraging costs per prey would be higher and less energy would be available for reproduction. These ideas were tested with the aphidophagus flower fly, Metasyrphus corollae, which

was provided with pea aphids, Acyrtosiphon pisum presented on pea plants, Pisum sativum.

The number of aphids eaten was higher when more were provided. Increased plant size only reduced prey consumption when 40 or more aphids were offered. However, prey consumption did not fall as much as the change in prey density would predict. At lower abundances, M. corollae larvae searched longer and at greater speed and managed to catch the same number of prey on any size of plant which was used. When prey were very scarce, larvae extended their active foraging into the light hours which would likely increase their risk of being eaten under natural conditions. When aphids were scarce, larvae increased the amount of energy that they extracted from each aphid they caught.

The expected pattern of foraging costs was not reflected in the production efficiency of M. corollae larvae. Production efficiencies were lowest when prey were abundant on the smallest plants. High production efficiency when prey are scarce is adaptive because more energy is thus available for growth, adult maintenance and reproduction. How this was achieved is not clear. Larvae did not conserve energy by ceasing to search for prey after a long time had elapsed since the last capture. Increased assimilation efficiency with decreased rate of consumption remains a possible mechanism. When prey are abundant a low efficiency of

assimilation of energy may not be critical. Ingestion of more prey than are necessary to satisfy energy requirements may result in greater acquisition of nutrients with slower absorption rates or lower assimilation rates.

The number of eggs laid by M. corollae females was extremely variable. Small flies made a relatively greater investment in ovarioles; however, large flies had a higher total number of ovarioles. Only when flies were kept in a cage that allowed them to fly freely did large females live longer and lay more eggs than small flies. To this extent, different prey availabilities during the larval period did affect fitness. Changes in foraging behavior that tend to minimize the effects of prey scarcity on energy consumption can increase adult female size and thereby increase fitness.

Schoener (1971) linked foraging to fitness with the concept of energy maximizers and time minimizers. The results from my study of M. corollae suggest that these terms can not be applied to a species but describe responses by individuals to different energy availabilities. When aphids were scarce and M. corollae larvae hungry, larvae did not minimize the time they spent searching. They kept searching even in the light, a period that probably entails increased risk of predation. Under natural conditions, this high

level of activity should increase energy consumption. Thus hungry larvae appear to behave as energy maximizers. When aphids were abundant, however, larvae stopped searching almost entirely during the light hours although aphids remained in the environment. These larvae thus appear to be time minimizers. This may be because each increment in energy does not contribute equally to fitness (Caraco 1980). To a starving animal, acquisition of another unit of energy may increase its survival probability, dispersal ability, body size, or fecundity, more than the addition of the same unit of energy to an animal that is nearly satiated. The relationship between reproduction and energy consumption is unlikely to be linear. It may be sigmoid, with a threshold of energy that must be obtained before any reproduction can occur, while at higher levels of energy consumption, factors other than energy may limit lifespan and reproduction. These include aging processes, the cumulative probability of surviving periods of bad weather, etc.

The effectiveness of a predator as a biological control agent depends on its voracity, searching efficiency and power of increase relative to that of its prey. M. corollae larvae consumed many aphids when they were abundant. They also left larger carcasses than when aphids were scarce, so that when aphids are

abundant larvae kill more of them than are necessary to satisfy their energy requirements. Thus their impact on heavy infestations is greater than if they extracted the maximum amount of energy from each aphid but ate fewer of them. When control of a pest population is effective (i.e., pest density is low), the searching ability of the predator becomes very important in maintaining stability (Huffaker et al. 1974). M. corollae larvae can search more than $1 \text{ m}^2/\text{day}$; they can survive and reproduce when they eat only 10 aphids/day. Thus they have the potential to survive at very low aphid densities. This will tend to add to the stability of the predator-prey relationship.

When aphids were abundant, syrphid larvae did not capture them all. It seems likely that plant structure and aphid dispersion on plants and among plants make the foraging environment of syrphid larvae spatially heterogeneous. The larvae probably forage non-randomly in such an environment like so many other aphidophagus predators. Models of predator-prey population dynamics that incorporate such foraging show greater persistence of both species (Hassell 1978). This spatial heterogeneity and the reaction of syrphid larvae to it create prey refuges (which need not be fixed entities). Such refuges for a small proportion of a pest population contribute to the feasibility of biological control (Beddington et al. 1978).

M. corollae in the laboratory produce large numbers of eggs but the mortality rate of young larvae in the field must be very high. Females lay their eggs in aphid colonies and when aphids are scarce in an area they will disperse. More eggs will thus be laid in areas of heavy infestation. Over a large area this may contribute to stability because low density aphid populations will have a chance to survive while denser populations will be subjected to greater predation.

Low, stable depression of the equilibrium pest density is the aim of biological control. Successful control is achieved when there is spatial heterogeneity, patchily distributed pests, and differential exploitation of patches both for foraging and oviposition (Beddington et al. 1978). These conditions seem to apply to M. corollae and pea aphids. However, much more knowledge about the interaction of these species at different temperatures and on larger and multiple plant systems is needed before predictions about the potential for control can be made.

V. CONCLUSIONS

1. Prey availability affected the number of prey eaten by M. corollae larvae. Both prey abundance and plant size affected foraging behavior and prey consumption.
2. A random encounter model overestimated the rate of prey consumption by M. corollae larvae. Evidence suggests that this is because larvae did not search randomly for patchily distributed aphids. Plant structure and aphid escape responses may contribute to the failure of larvae to capture all aphids.
3. The effects of prey scarcity were reduced by extracting more energy from each captured aphid, higher production efficiency, and a higher mass-specific investment in ovarioles. Under natural conditions the higher rate of searching when larvae are hungry should also decrease the effects of prey scarcity.
4. Lifespan and reproduction of adult female M. corollae were extremely variable. Adult rearing conditions determined the significance of low energy consumption during the larval period on reproductive output. In particular, dispersal appears to exact a cost against reproduction for small flies.

5. Under natural conditions, M. corollae populations that develop when aphids are abundant should grow faster than when aphids are scarce.

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VII. APPENDIX I: COMPUTER PROGRAM FOR SIMULATION
OF A RANDOM ENCOUNTER MODEL

```

IBASIC ENCOUNTER
10 READ X$,Y$,Z$
20 DATA AFTERNOON,NIGHT,MORNING
30 PRINT "ENTER CONDITIONS"
40 PRINT "ENTER INITIAL # OF PREY, TOTAL AREA"
50 INPUT AI,AREA
60 NE = 0
80 PRINT "ENTER 3 TIME PERIODS, AFTERNOON,NIGHT,MORNING"
90 INPUT ATIME,NTIME,MTIME
100 PRINT "ENTER VELOCITIES FOR EACH TIME PERIOD"
110 INPUT VA,VN,VM
120 PRINT "ENTER PROBABILITIES OF MOVING"
130 INPUT PMA,PMN,PMM
140 PRINT "ENTER CAPTURE SUCCESSES"
150 INPUT CSA,CSN,CSM
160 PRINT "ENTER PREDATOR SEARCHING RADIUS,PREY RADIUS"
170 INPUT R1,R2
180 PRINT "ENTER FEEDING TIME PER PREY"
190 INPUT TF
200 PRINT "      "
210 PRINT "*****"
220 PRINT "*"
230 PRINT "*" INITIAL # OF PREY",AI,"AREA",AREA
240 PRINT "*"

```

```
250 PRINT "*****"  
260 PRINT " "  
280 NE = 0  
285 DENSITY = AI/AREA  
290 PRINT " "  
300 PRINT " "  
320 PRINT " "  
330 FOR I = 1 TO 3 STEP 1  
340 IF (I=3) GO TO 480  
350 IF (I=2) GO TO 420  
360 TIME = ATIME  
370 PERIOD$ = X$  
380 V = VA  
390 PM = PMA  
400 CS = CSA  
410 GO TO 540  
420 TIME = NTIME  
430 PERIOD$ = Y$  
440 V = VN  
450 PM = PMN  
460 CS = CSN  
470 GO TO 540  
480 TIME = MTIME  
490 PERIOD$ = Z$  
500 V = VM  
510 PM = PMM  
520 CS = CSM
```

```

530 GO TO 540
540 PRINT " "
550 PRINT " "
560 PRINT " "
570 PRINT "-----"
580 PRINT " "
590 PRINT "PREDATOR PARAMETERS","TIME IS",PERIOD$
600 PRINT " "
610 PRINT "VELOCITY",V,"PROBABILITY OF MOVING",PM
620 PRINT "CAPTURE SUCCESS RATE",CS,"FEEDING TIME",TF
630 PRINT " "
640 PRINT "-----"
650 PRINT " "
660 PRINT "PREY # SEARCH PREY TIME LEFT DENSITY"
670 PRINT " TIME LEFT"
680 PRINT " "
690 FOR K = 1 TO AI STEP 1
700 NT = 2 * V * PM * (R1 + R2) * DENSITY * CS
710 TS = 1/NT
720 TIME = TIME - TS - TF
725 IF (TIME < 0) GO TO 810
730 NE = NE + 1
740 A = AI - NE
750 DENSITY = A/AREA
760 PRINT K,TS,A,TIME,DENSITY
770 IF (NE = AI) GO TO 850
780 IF (TIME = 0) GO TO 810

```

```
790 IF ((TIME-TS) = 0 OR (TIME-TS) < 0) GO TO 810
800 NEXT K
810 NEXT I
820 PRINT "      "
830 PRINT "A 24 HOUR DAY HAS BEEN COMPLETED"
840 GO TO 860
850 PRINT "ALL APHIDS HAVE BEEN EATEN"
860 PRINT "      "
880 PRINT "      "
890 PRINT "ENTER 1 FOR ANOTHER EXPERIMENT;  0 TO STOP"
900 INPUT Q
910 IF (Q = 1) GO TO 30
920 END
```

VII. APPENDIX II: OUTPUT FROM COMPUTER SIMULATION
OF RANDOM ENCOUNTER MODEL

```
*****
*
* INITIAL # OF PREY      10          AREA      200
*
*****
```

```
-----
PREDATOR PARAMETERS      TIME IS      AFTERNOON

VELOCITY      2.6          PROBABILITY OF MOVING      .33
CAPTURE SUCCESS RATE      .88          FEEDING TIME      13.2
-----
```

PREY #	SEARCH TIME	PREY LEFT	TIME LEFT	DENSITY
1	17.8977	9	448.902	.045
2	19.8864	8	415.816	.04
3	22.3722	7	380.244	.035
4	25.5682	6	341.475	.03
5	29.8296	5	298.446	.025
6	35.7955	4	249.45	.02
7	44.7444	3	191.506	.015
8	59.6592	2	118.647	.01
9	89.4887	1	15.958	.005

```
-----
PREDATOR PARAMETERS      TIME IS      NIGHT

VELOCITY      2.7          PROBABILITY OF MOVING      .78
CAPTURE SUCCESS RATE      .88          FEEDING TIME      13.2
-----
```

PREY #	SEARCH TIME	PREY LEFT	TIME LEFT	DENSITY
1	72.9167	0	393.883	0

ALL APHIDS HAVE BEEN EATEN

```
*****
*
* INITIAL # OF PREY      40                AREA      175
*
*****
```

```
-----
PREDATOR PARAMETERS          TIME IS      AFTERNOON

VELOCITY      2              PROBABILITY OF MOVING      .01
CAPTURE SUCCESS RATE      .4              FEEDING TIME      5.5

-----
```

PREY #	SEARCH TIME	PREY LEFT	TIME LEFT	DENSITY
1	262.921	39	211.579	.222857

```
-----
PREDATOR PARAMETERS          TIME IS      NIGHT

VELOCITY      4.3           PROBABILITY OF MOVING      .55
CAPTURE SUCCESS RATE      .8           FEEDING TIME      5.5

-----
```

PREY #	SEARCH TIME	PREY LEFT	TIME LEFT	DENSITY
1	1.14022	38	473.36	.217143
2	1.17023	37	466.69	.211429
3	1.20185	36	459.988	.205714
4	1.23524	35	453.252	.2
5	1.27053	34	446.482	.194286
6	1.3079	33	439.674	.188571
7	1.34753	32	432.826	.182857
8	1.38964	31	425.937	.177143
9	1.43447	30	419.002	.171429
10	1.48229	29	412.02	.165714
11	1.5334	28	404.987	.16
12	1.58816	27	397.898	.154286
13	1.64699	26	390.751	.148571
14	1.71033	25	383.541	.142857
15	1.77874	24	376.262	.137143
16	1.85286	23	368.909	.131429
17	1.93342	22	361.476	.125714
18	2.0213	21	353.955	.12
19	2.11755	20	346.337	.114286
20	2.22343	19	338.614	.108571

21	2.34045	18	330.773	.102857
22	2.47048	17	322.803	9.71429E-2
23	2.6158	16	314.687	9.14286E-2
24	2.77929	15	306.408	8.57143E-2
25	2.96457	14	297.943	.08
26	3.17633	13	289.267	7.42857E-2
27	3.42066	12	280.346	6.85714E-2
28	3.70572	11	271.14	6.28571E-2
29	4.0426	10	261.598	5.71429E-2
30	4.44686	9	251.651	5.14286E-2
31	4.94096	8	241.21	4.57143E-2
32	5.55858	7	230.151	.04
33	6.35266	6	218.299	3.42857E-2
34	7.41144	5	205.387	2.85714E-2
35	8.89372	4	190.993	2.28571E-2
36	11.1172	3	174.376	1.71429E-2
37	14.8229	2	154.053	1.14286E-2
38	22.2343	1	126.319	5.71429E-3
39	44.4686	0	76.3505	0

ALL APHIDS HAVE BEEN EATEN

IX. APPENDIX III. ANALYSES OF VARIANCE

1. Number of aphids eaten

transformation used: log X

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	3	.508	162.28	<.001
plant size	2	.041	13.19	<.001
interaction	5	.006	1.91	>.1
within groups	92	.003		

2. Carcass masses

transformation used: log X

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
age	4	.1498	7.11	<.001
prey number	1	.6432	30.50	<.001
plant size	1	.2022	9.59	<.01
age x number	4	.0300	1.42	>.2
age x plant	4	.0851	4.04	<.01
number x plant	1	.0548	2.60	>.1
age x no. x pl.	4	.0467	2.21	>.05
within groups	263	.0211		

3. Energy consumption

transformation used: log X

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	.339	106.49	<.001
plant size	2	.021	6.60	.002
interaction	5	.004	1.26	>.2
within groups	91	.003		

4. Pupal Mass

transformation used: none

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	3	934.79	87.11	<.001
plant size	2	54.50	5.08	<.01
interaction	5	16.14	1.50	>.1
within groups	91	10.73		

5. Production Efficiency - females only

transformation used: $\log X$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	.0022	0.90	>.4
plant size	2	.0487	19.64	<.001
interaction	4	.0037	1.48	>.2
within groups	83	.0025		

6. Production Efficiency - males only

transformation used: $\log X$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	.0008	0.24	>.7
plant size	2	.0102	3.28	<.05
interaction	4	.0054	1.73	>.1
within groups	64	.0031		

7. Production Efficiency - females and 60 aphids/day
transformation used: $\log X$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	3	.0033	1.40	>.2
plant size	2	.0630	26.01	<.001
interaction	5	.0040	1.67	>.1
within groups	91	.0024		

8. Lifespan of females in jars
transformation used: $\sqrt{X}$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	0.223	0.13	>.8
plant size	2	3.910	2.35	.101
interaction	4	0.451	0.27	>.8
within groups	84	1.662		

9. Total number of eggs laid by females in jars

transformation used: $\sqrt{(X + 0.5)}$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	132.076	1.07	>.3
plant size	2	270.442	2.20	.117
interaction	4	52.473	0.43	>.7
within groups	84	123.067		

10. Number of eggs laid in first 15 days

transformation used: none

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	2	187979.36	5.09	<.01
plant size	2	87782.91	2.38	.103
interaction	4	20461.26	0.55	>.6
within groups	54	36946.08		

11. Lifespan of females in large cage

transformation used: $\sqrt{X}$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	1	6.518	3.696	.06
cage size	1	0.031	.018	>.8
interaction	1	10.540	5.976	.02
within groups	88	1.764		

12. Fecundity of females in large cage

transformation used: $\sqrt{(X + 0.5)}$

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	1	13.971	13.971	<.001
cage size	1	27.633	0.255	>.6
interaction	1	673.116	6.214	<.01
within groups	88	108.330		

13. Velocity

transformation used: $\log (X + 1)$

note: For each age, separate ANOVAs were done
for hunger X light level and
hunger X aphid presence.

A. 5 day old larvae, aphids absent:

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	.054	2.250	.14
light/dark	1	.477	19.747	<.001
interaction	1	.222	9.210	<.01
within groups	50	.024		

B. 6 day old larvae, aphids absent:

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	.012	0.413	>.5
light/dark	1	.309	10.940	.001
interaction	1	.376	13.312	<.001
within groups	71	.028		

C. 7 day old larvae, aphids absent:

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	1.124	32.589	<.001
light/dark	1	1.459	42.300	<.001
interaction	1	0.339	9.832	<.01
within groups	65	.034		

D. 5 day old larvae, lights on:

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	.452	17.858	<.001
aphid presence	1	.0003	.013	>.9
interaction	1	.009	.350	>.5
within groups	46	.0253		

E. 6 day old larvae, lights on:

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	.548	18.558	<.001
aphid presence	1	.020	0.685	>.4
interaction	1	.101	3.427	.07
within groups	63	.030		

F. 7 day old larvae, lights on:-

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
hunger	1	2.499	109.671	<.001
aphid presence	1	.0003	.013	>.9
interaction	1	.106	4.654	<.05
within groups	55	.069		

14. Time spent feeding

transformation used: log X

note: Separate analyses were done for each age.

A. 5 day old larvae

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	1	.938	31.438	<.001
plant size	1	.176	5.904	<.05
interaction	1	.221	7.394	<.01
within groups	136	.030		

B. 6 day old larvae

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	1	1.131	58.354	<.001
plant size	1	.186	9.594	<.01
interaction	1	.031	1.610	>.2
within groups	152	.019		

C. 7 day old larvae

ANOVA TABLE

Source	d.f.	Mean Square	F ratio	P
between groups				
prey number	1	1.715	87.279	<.001
plant size	1	.049	2.515	>.1
interaction	1	.055	2.784	.1
within groups	152	.020		

END

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FIN