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EFFECT OF HUNGER ON THE ALLOCATION OF TIME AMONG PEA PLANTS BY THE LARVAE OF AN APHIDOPHAGOUS HOVER FLY, *EUPEODES COROLLAE* [*DIPT : SYRPHIDAE*]

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We observed the movement of predatory larvae of the syrphid fly *Eupeodes corollae* (F.) (formerly *Metasyrphus corollae*) among small pea plants with and without aphids. Starved larvae spent longer time than well-fed larvae on similar plants and both groups of larvae stayed longer on plants with aphids than on plants without aphids. On plants with aphids, larvae which failed to capture prey left the plant sooner than those which captured aphids. The capture of at least one aphid on a plant increased the persistence of syrphid larvae. The average rate of energy gain was higher for well-fed larvae than for starved larvae because starved larvae stayed on plants even when their rate of return was lower. When larvae that had captured aphids left plants, their rate of energy gain tended to be lower than at any time following capture of the 2nd aphid. The 1st aphid was captured in less time than similar larvae spent on plants without aphids. Time between captures of aphids by well-fed larvae was less than the time such larvae spent on plants without aphids. Among starved larvae, the intercatch intervals were similar to the time on plants without aphids. We discuss the significance of these results relative to current predator foraging theory and the efficiency of *E. corollae* as a biological control agent.

KEY-WORDS : syrphid larvae, hunger, searching time on plants.

Prey are often patchily distributed so that predators may face the problem of allocating foraging time among patches to maximize prey capture rates. **Charnov** (1976) predicted that the net energy gained from foraging would be maximized if a predator reduced all patches to the same marginal rate of net energy gain. To do this a predator must remain longer in better patches because it will take longer to reduce better patches to the same marginal rate of energy gain. The rate of net energy gain at which a predator should leave a patch depends on the average quality of patches within the predator's habitat. Thus, a predator should leave a patch of a given quality in a good habitat sooner than in a poor habitat. In other words, a predator should remain in a patch longer if its expected return outside the patch is less (**Munger**, 1984). Animals with limited memories can show this pattern through area-restricted searching (**Waage**, 1979 ; **Bond**, 1980 ; **Hassell**, 1978) i.e., frequent turning and slow speed after prey encounter. However, with the exception of some work by **Kohler** (1984) on an Ephemeroptera larva, it has seldom been shown that simple animals actually distribute their foraging effort in accordance with Charnov's predictions.

Much controversy has surrounded the method by which a forager decides when to leave a patch. **Krebs** *et al.* (1974) argued that the giving-up time which is the time between the last prey capture and the time at which a predator leaves a patch is inversely proportional to the marginal rate of return when the predator leaves the patch and thus that the giving-up time should be the same in all patches. But **McNair** (1982) claimed that the giving-up time should be greater in better patches. This latter prediction suggests that a predator should be more persistent in better quality patches.

We, and others, have documented changes in speed and turning in response to captures of aphids and periods of starvation in several species of syrphid larvae (**Scott & Barlow,** in prep ; **Rotheray & Martinat,** 1984 ; **Chandler,** 1969) but it remained to examine how their movement on and between plants bearing various numbers of aphids influenced the allocation of time among plants.

For some predators a patch of prey lacks clear boundaries and is merely a nebulous area around captured prey, but for predators that forage on plants, such as aphid predators, each plant may be considered a patch because when prey are not found on a plant, or if the capture rate is too low, the predator must leave the plant and seek another. Thus, when observing predators in such a structured environment it is possible to measure the time spent in patches of different qualities and thereby examine the predictions of foraging theory.

The validity of these tests depends on the validity of the premise that maximizing net energy gain maximizes fitness. In the aphid predator, *Eupeodes corollae* (F.) (formerly *Metasyrphus corollae*), 2 characters linked to fitness, survival to reproduction and fecundity, increase with increased consumption (**Barlow,** 1979 ; **Cornelius & Barlow,** 1980 ; **Scott & Barlow,** 1984). This is consistent with the energy maximization premise. Also larval *E. corollae* are obligate aphid predators so considerations arising from the need for a varied diet can be safely ignored. These features, along with the absences of activities other than foraging and resting during the larval stage, make *E. corollae* larvae very suitable for testing predictions about allocation of time among patches.

Well-fed and starved *E. corollae* larvae were placed on an arena with small plants, some of which bore aphids. We hypothesized that larvae would spend more time on plants with the most aphids and that starved larvae i.e., larvae with a history of living in a poor quality habitat, would spend longer on plants with a given number of aphids than well-fed (good-habitat) larvae.

MATERIALS AND METHODS

Stock cultures of *E. corollae* and parthenogenetic pea aphids, *Acyrthosiphon pisum* (Harris) were maintained at 20° ± 1 °C and 16h light (**Barlow,** 1979). All experiments were done in controlled environment chambers at 20° ± 1 °C. Uniformly sized, 7-day old aphids for use as prey were obtained by placing adult aphids in a Petri dish with pea seedlings on damp filter paper. Offspring born in the next 24h were transferred to pots of young peas and reared at 20 °C for another 6 days before they were used as prey.

The foraging environment was a 25.5 × 25.5 cm square of opaque white perspex with 7 holes, 0.8 cm diameter, spaced equidistantly around a central hole. The holes were 8 cm apart. A 0.5 cm wide, 0.5 cm deep moat filled with water surrounded the arena and was intended to keep both larvae and aphids within the experimental area. Eight vial lids, also with 0.8 cm diameter holes, were fastened to the underside of the arena with the holes of the lids and arena aligned. Six-day old pea seedlings were transplanted into a soil-vermiculite mixture in small plastic vials. The seedlings were gently eased through the holes in the arena and held in place by snapping the vials into their lids. After 3 to 4 days of growth at 20 °C under fluorescent lights, the peas were about 10 cm tall, had 2 fully expanded leaves and were used in the experiments. Adjacent plants did not touch.

We obtained syrphid larvae for the experiments by collecting eggs from the stock culture on aphid-infested pea seedlings. The eggs and, subsequently, larvae were kept in large Petri dishes lined on the bottom with moist filter paper and containing 3 to 5 pea seedlings. Seedlings were replaced as needed and aphids were provided *ad libitum*. About 4 days after they hatched, we culled the syrphid larvae so that about 15 remained. We used 6 day-old larvae for these foraging experiments because this is a period of high consumption and activity (**Barlow,** 1979 ; **Scott,** 1983). To mimic a good habitat, larvae were enclosed in a Petri dish with an abundance of aphids on small pea seedlings. Aphids were numerous enough that they repeatedly contacted larvae that were not even actively foraging. A poor habitat was simulated by keeping larvae with aphids until 5 days after hatching, then transferring them to another Petri dish with aphid-free pea seedlings. They were used 24h later and called "starved" larvae.

Before each experiment we placed 7 day old aphids in plastic cages which we inverted over the individual pea plants in the arena. Within 3h the aphids were on the plant and stationary and we could carefully remove the cages. At the start of each experiment one 6 day old larva was selected haphazardly and placed on the arena between plants. It was then free to move over the arena and encounter plants and aphids.

We tested both well-fed and starved larvae under each of the following conditions : all 7 plants without aphids ; 4 plants without aphids and 3 plants with 5, 10, 20 or 35 aphids per plant. We intended to test equal numbers of larvae under each condition ; however, more starved larvae drowned in the moat (perhaps because they were more active) and the activities of larvae on plants with aphids disturbed the aphids so that many aphids left the plants. Consequently, aphid density changed during an experiment. We wanted to observe the same larva both on plants with and without aphids but many larvae visited only 1 or 2 plants before escaping across the moat or drowning in it. We therefore lumped all observations of larvae on plants with aphids and compared these to observations of larvae on plants without aphids.

Because *E. corollae* larvae are more active in the dark (**Scott,** 1983), the arena was illuminated with only one red incandescent bulb about 40 cm above the arena which gave about 400 lux with 89 % of radiation emitted above 725 nm and only 0.3 % below 625 nm. Time-lapse videotapes of larval activity were made using a Panasonic videocamera, model WV-1850 fitted with an Opticon 12.5 F 1.3 infrared sensitive lens mounted 40 cm above the plants. For each plant visited by a syrphid larva we recorded the following variables : time onto the plant, time off the plant, method of leaving the plant (crawling off stem or falling), starting and finishing times of feeding, and number of aphids leaving the plant during a visit. We analyzed only the first 3 visits made by any larva to plants except when determining whether larvae changed their persistence as successive plants without aphids were visited. Thus each larva contributed between 1 and 3 observations to the data set. This reduced the bias that might have resulted because larvae that spent only a short time on each plant were able to visit more plants during an experiment.

When required the data were transformed to eliminate significant heterogeneity of variances. Analyses of variance were done using the MANOVA program of SPSS. For presentation in the tables, data were backtransformed with corrections for bias (**Sokal & Rohlf,** 1968 ; **Thoni,** 1969).

RESULTS

TIME ON PLANTS

Initial differences in hunger, resulting from 24 h starvation, presumably persisted at least until larvae captured aphids. Most larvae encountered a plant within 1h of the start of an experiment. Starved larvae did not take significantly longer time than well-fed larvae to locate a plant (82 vs 64 min ; Mann-Whitney $U_s = 596.5$, $p > 0.05$).

E. corollae larvae not only left plants by crawling down the stem but also frequently fell off plants. Syrphid larvae search by lifting the anterior part of the body off the substrate and waving it from side to side. Sometimes this casting behavior is very vigorous and the larva flings itself off the plant ! Falling occurred more frequently when larvae were starved or on plants without aphids (table 1). Other larvae did not leave the last plant visited during the experiment ; both well-fed and starved larvae had a greater tendency to remain on plants when aphids were present (table 1). Only the results from larvae that left plants by crawling from the stem, not falling, were used for analysis of patch residence times and giving-up time.

TABLE 1

Frequencies of different ways in which well-fed and 24 h starved E. corollae *larvae left plants. Values are numbers of visits to plants ending in a particular way*

Method of leaving plant	plants with aphids		plants without aphids	
	well-fed	24 h starved	well-fed	24 h starved
Crawled from stem	28	8	49	33
Fell	5	8	8	13
Did not leave	5	5	1	2

Overall : $G^1 = 23.4304$, $p < 0.01$.
Tests of independence :
aphid presence vs leaving method : $G = 10.718$, $p < 0.01$;
larval hunger vs leaving method : $G = 8.699$, $p < 0.05$;
aphid presence vs larval hunger : $G = 1.475$ ns.
[1] G test for goodness of fit (**Sokal & Rohlf**, 1968).

The presence of aphids had a significant effect on the patch residence time of larvae (SPSS MANOVA, $p < 0.05$) as follows : $t_{fw} < t_{sw} < t_{fa} < t_{sa}$ where

t = time on a plant
f = well-fed larvae
s = starved larvae
w = plants without aphids
a = plants with aphids.

Both starved and well-fed larvae stayed longer on plants with aphids than on plants without aphids (table 2). This difference was not due entirely to time spent feeding. Indeed, after we substracted time spent feeding, well-fed larvae still spent 2x longer on plants with aphids and starved larvae almost 3x longer than on plants without aphids. Thus, *E. corollae* larvae stayed longer in better quality patches.

TABLE 2

Time spent on plants by well-fed and starved E. corollae *larvae foraging for aphids. All times are in minutes*

	Well-fed	24 h starved
Plants without aphids		
total residence time	49.2 (1)	78.1
	38.9-62.1 (2)	58.5-104
	49 (3)	33
Plants with aphids		
total residence time	112.9	318
	82.3-155	161-628
	28	8
Plants with aphids		
total time - feeding time	99.1	289
	69.4-141	134-622
	28	8

(1) Mean calculated by backtransforming and correcting for bias after analysis of log transformed data (**Sokal & Rohlf,** 1968 ; **Thoni,** 1969).
(2) 95 % confidence interval.
(3) Sample size = number of plant visits.

The 2nd prediction of the marginal value theorem is that patch residence time will vary inversely with average habitat quality. Consistent with this hypothesis, starved larvae spent longer than well-fed larvae on plants with and without aphids (SPSS MANOVA, $F = 11.46$, $p < .01$; table 2). This is not because starved syrphid larvae moved less rapidly than well-fed larvae. In fact, they usually move more rapidly unless starvation is extreme (**Scott & Barlow,** in prep ; **Rotheray & Martinat,** 1984).

GIVING-UP TIME

Giving-up time (= time from last meal to time leaving plant) estimates a predator's persistence or "willingness" to continue searching within a patch rather than moving to another. The giving-up time was longer for starved larvae than for well-fed ones regardless of plant type or larval experience (Mann-Whitney U-test, $U_s = 85.5$, $t_s = 3.019$, $p < .05$; table 3). The time spent on a plant without aphids can be thought of as the giving-up time in an extremely poor patch. For both well-fed and starved larvae, the giving-up time on plants with aphids was usually greater than the time spent on plants without aphids (table 3). This is consistent with McNair's model that animals should continue to search patches on which they had recent success longer before moving to another patch.

A few *E. corollae* larvae on plants with aphids failed to capture any. Comparing successful to unsuccessful larvae showed that regardless of hunger, unsuccessful larvae stayed on plants for less time than did comparably treated larvae which captured aphids (tables 2 & 3). In addition, the total residence time of unsuccessful syrphid larvae was shorter than the giving-up time of larvae successful in capturing aphids (SPSS MANOVA, $F = 4.32$, $p < .05$; table 3). Thus the capture of at least one aphid in a patch increased the persistence of larvae.

While these results show that giving-up time depends on hunger, syrphid larvae may still be behaving in a way described by a simple departure model. If the departure model is a

TABLE 3

Giving-up time (minutes) of E. corollae *larvae measured by the length of time larvae spent on plants without capturing aphids. Successful larvae are ones which captured and ate at least one aphid during a visit ; unsuccessful larvae did not eat any aphids either because none were present or because they failed to capture any*

	Well-fed	24 h starved
Successful larvae	65.0 (1)	378
	53.1-79.5 (2)	130-1 094
	18 (3)	5
Unsuccessful larvae		
on plants with aphids	56.7	69.6
	36.7-87.6	1.01-4 782
	10	2
on plants without aphids	49.2	78.1
	38.9-62.1	58.5-104
	49	33

(1) Mean calculated by backtransforming and correcting for bias after analysis of log transformed data (**Sokal & Rohlf**, 1968 ; **Thoni**, 1969).
(2) 95 % confidence interval.
(3) Sample size = number of plant visits.

constant random probability with the mean of the probability function set by hunger, then the log persistence function will be linear (**Bond**, 1981). This was tested by calculating the observed and expected (i.e., linear) log persistence functions and testing for significant deviations from linearity using the distribution-free Kolmogorov-Smirnov statistic D (**Sokal & Rohlf**, 1969). Both the giving-up times and the time on plants without aphids showed significant deviations, suggesting that departure times are not simply random events.

RATE OF ENERGY GAIN

Numbers of aphids captured per unit time by syrphid larvae were transformed into rates of energy gained. Well-fed 6 day old *E. corollae* larvae from this population ingest, on average, 29.7 $\mu g \cdot min^{-1}$ of aphid dry mass and 6 day old starved larvae 11.5 $\mu g \cdot min^{-1}$ when feeding to completion on several successive aphids (**Barlow & Whittingham**, 1986). Until the 1st aphid is captured, the rate of capture is 0/min ; immediately before the 2nd aphid is caught the rate of capture is given by 1/time at which 2nd capture is made ; as the 2nd aphid is captured, the rate of capture jumps to 2/time of capture of the 2nd aphid. The average rate of energy gain by a larva during a visit to a plant is (the total number of aphids captured) × (the rate of ingestion/time on the plant). Several important results emerged. First, the average rate of energy gain of larvae that left plants by crawling from the stem was higher for well-fed larvae than for starved larvae ; i.e., starved larvae stayed on plants even when their rate of return was lower (table 4). Second, the rate of return when larvae left plants tended to be lower than at any time following the capture of the 2nd aphid. The 1st aphid was captured in less time than similar larvae spent on plants without aphids (table 3). Also, for well-fed larvae, the time between aphid captures was less than the time spent on plants without aphids. For starved larvae, the intercatch intervals were similar to the giving-up time on plants without aphids (tables 2 & 4). Third, starved larvae that had not left plants by the end of the experiment captured more aphids and had higher average rates of energy gain (at the end of the experiment) than larvae that left plants (table 4).

TABLE 4

Time (minutes) until capture of aphids and rate of energy gain (μg dry mass·min^{-1}) by 6 day old E. corollae *larvae ; n = number of plant visits*

	Well-fed			24 h starved		
Time until capture of:	mean	95 % CI (1)	n	mean	95 % CI	
aphid 1	10.2	6.6- 15.8	36	18.4	8.7- 38.9	18
2	35.2	27.4- 43.3	30	98.3	60.6-159	15
3	65.5	47.4- 90.5	19	166	99.2-276	10
4	79.0	58.9-106	16	266	190 -373	7
5	105	72.8-150	12	340	223 -518	4
Rate of energy gain:						
before 1st		0			0	
when 1st captured		2.91			0.62	
before 2nd		0.84			0.12	
when 2nd captured		1.69			0.23	
before 3rd		0.90			0.14	
when 3rd captured		1.37			0.21	
before 4th		1.13			0.13	
when 4th captured		1.50			0.17	
before 5th		1.13			0.14	
when 5th captured		1.43			0.17	
Overal energy gain:						
larvae that left plant						
$\bar{x}$ no. aphids captured		3.75 ± 0.43 (2)			2.42 ± 0.57 (2)	
total time on plant		137 (107-174 (3))			482 (219-1 060)	
$\bar{x}$ rate of energy gain		0.81			0.058	
larvae that did not leave						
$\bar{x}$ no. of aphids captured		8.29 ± 1.89			6.00 ± 1.29	
total time on plant		301 (144-631)			415 (316-543)	
$\bar{x}$ rate of energy gain		0.81			0.16	

(1) 95 % confidence interval.
(2) Mean ± standard error.
(3) 95 % confidence interval.

PERSISTENCE ON PLANTS

For well-fed larvae that visited at least 5 plants in succession without aphids there was no difference in the time spent on successive plants (ANOVA F = 1.21, p > .05). Similarly, larvae starved for 24h showed no changes on the first 4 plants visited. However, a few experiments during which larvae visited several plants without aphids before encountering any plants with aphids show the effect of increasing hunger on persistence of searching without reward.

DISCUSSION

One of the foraging problems that aphid predators face is to search a large amount of host plant environment for scattered clusters of prey. If maximizing net energy gain is important to fitness, searching behaviors should evolve that, on average, result in more prey being captured than random searching would achieve. Previous experiments conducted in 2-dimensional arenas have shown that syrphid larvae switch to area-restricted searching after they encounter prey (**Chandler**, 1969). This should keep them in a patch in which they have been successful. If, as for lacewing larvae (**Bond**, 1980), starved larvae show area-restricted searching for longer than well-fed larvae, starved larvae will spend longer in patches. This simple mechanism would produce an allocation of time among patches predicted by optimal foraging theory.

In the series of experiments reported here we investigated the behavior of *E. corollae* larvae in a 3-dimensional environment in which larvae were free to move from plant to plant. We determined that these syrphid larvae searched in a non-random manner that was likely to increase their overall net energy gain. Our results support a view that hunger induces starved larvae to stay in patches of all qualities longer than well-fed larvae because their giving-up times are longer than for well-fed larvae. In terms of foraging theory, starved larvae have lower expectations of reward than well-fed larvae so a patch of a given quality is relatively better for starved larvae. Thus they should exploit it more extensively by searching longer before leaving.

Most models of foraging behavior predict that hunger affects allocation of time among patches but not all models predict that giving-up time will vary with patch quality. The time since a prey item was last encountered is only one of several possible cues for departure that a forager might use. Other possible rules include leaving after a fixed time in a patch or leaving after a fixed number of prey have been caught. **Iwasa** *et al.* (1981) have shown that the departure rule that results in the maximum rate of energy gain depends on the distribution of prey. For a clumped distribution, leaving when the intercatch interval exceeds a fixed giving-up time is better than the other alternatives. Since aphids are often patchily distributed syrphid larvae might be expected to show a constant giving-up time. But in our experiment, the length of time *E. corollae* larvae spent searching on a plant without reward depended on whether aphids were previously captured on that particular plant (i.e. on patch quality). Neither do our results support fixed time or fixed number of captures rules. Our results are consistent with a giving-up time with a component that is preset by hunger and then updated by success in each patch. Such a mechanism fits searching behavior in other insects, for example, ovipositing tephritid flies (**Roitberg & Prokopy**, 1984).

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RÉSUMÉ

Effet de la faim sur la répartition du temps passé parmi les plants de pois, par les larves de *Eupeodes corollae* [*Dipt. : Syrphidae*]

Nous avons observé les déplacements des larves prédatrices du syrphe *Eupeodes corollae* (F.) sur des plantes de pois infestés ou non de pucerons. Les larves affamées ont passé plus de temps sur les plants que les larves bien nourries. Les 2 groupes de larves sont restés plus longtemps sur les plants avec pucerons que sur les plants qui en étaient dépourvus. Sur les plants infestés de pucerons, les larves incapables d'en capturer quittèrent le plant plus tôt que les larves qui réussirent. La capture d'au moins un puceron sur un plant, augmentait la persistance des larves prédatrices. Le taux moyen de gain énergétique était plus élevé pour les larves bien nourries parce que pour les affamées celles-ci restaient sur les plants même si leur succès de capture était peu élevé. Lorsque les larves qui avaient capturé des pucerons quittaient les plants, leur taux de gain énergétique avait tendance à être plus bas qu'après la capture d'un deuxième puceron. Le temps nécessaire à la capture du 1^er^ puceron était plus court que celui passé par ces larves sur un plant dépourvu de pucerons. Le temps écoulé entre les captures de pucerons par les larves bien nourries était plus court que celui passé par ces mêmes larves sur des plants dépourvus de pucerons. Chez les larves affamées, le temps écoulé entre les captures était semblable à celui passé sur les plants dépourvus de pucerons. Nous avons examiné la portée de ces résultats en rapport avec la théorie courante de recherche de nourriture chez les prédateurs, et avec l'efficacité de *E. corollae* en tant qu'agent de lutte biologique.

MOTS CLÉS : larves de syrphes, faim, temps de recherche sur les plantes.

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