

FORAGING BEHAVIOUR OF *RHAGOLETIS POMONELLA*, A PARASITE OF HAWTHORN (*CRATAEGUS VIRIDIS*), IN NATURE

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SUMMARY

(1) We examined the influence of *Crataegus viridis* fruit quality and density on the foraging behaviour of one of its parasites, the tephritid fly, *Rhagoletis pomonella*, in nature.

(2) Individual female flies were released in trees harbouring: (a) no host fruit, (b) non-host fruit, (c) egg-infested, oviposition-detering pheromone-marked host fruit, (d) varying densities of uninfested, unmarked host fruit.

(3) Flies emigrated from trees within a narrow range of time if they did not discover fruit.

(4) Flies never or rarely oviposited in non-host and marked fruit respectively, and in both cases emigrated from trees harbouring those fruit soon after examining the fruit.

(5) Flies exhibited success-motivated search following discovery of and oviposition in uninfested, unmarked fruit.

(6) Flies visited more fruit, oviposited more often and remained longer in trees harbouring high *v.* low densities of fruit clusters.

(7) Flies emigrated sooner after the last egg they laid on trees harbouring high, *v.* low, densities of fruit clusters (Giving Up Time shorter).

(8) *Rhagoletis pomonella* foraging behaviour is discussed in relation to current foraging theory.

INTRODUCTION

Foraging behaviour of predatory and parasitic insects is currently receiving much attention from ecologists (e.g. Hassell & Southwood 1978). While some studies deal with the natural history aspects of foraging (e.g. Horner & Klein 1979), others analyse foraging 'tactics' and 'strategies' with a theoretical perspective (e.g. Charnov 1976). Regardless of approach, several basic questions emerge: (1) how efficient is the forager at locating and capturing prey; (2) when should a forager give up on one resource patch and search for another; (3) should all resources that are encountered be exploited regardless of value; and (4) what information is required to make these decisions?

Holling's (1959) classic work on the functional response of predators to prey density forms the basis for many contemporary foraging studies. Only recently have the behavioural components of this response been closely examined (e.g. van Lenteren & Bakker 1978). Van Lenteren & Bakker (1976, 1978) suggested that the functional

response data generated from simple laboratory experiments may be misleading if they do not allow for forager dispersal or alternative prey/hosts. Frazer & Gilbert (1976) demonstrated that subtle effects not readily recognizable in controlled laboratory predation experiments may have important implications for population dynamics of predators (parasites) and their prey in nature.

The principal subjects of foraging studies have been carnivorous predators and parasites. However, because of certain characteristics, plant predators and parasites (Price 1977) may be preferable. Their herbaceous prey are sedentary and may be considerably easier to manipulate than mobile prey, whose escape strategies are often based on short-term objectives.

We have initiated a study of the foraging behaviour of the tephritid fly, *Rhagoletis pomonella* Walsh, an endoparasite of the fruit of hawthorn, *Crataegus* sp. One of our aims is to understand the ecological and behavioural basis of fly response to changes in host fruit quality, density, and distribution within and between host trees. In this paper, we deal with aspects of intra-tree foraging behaviour.

In addition to hawthorn, *R. pomonella* parasitizes the fruit of apple (*Malus*), rose (*Rosa*), and cherry (*Prunus*). Adult flies emerge from puparia in mid-summer, feed on aphid honeydew, and reach maturity in 10–14 days. Flies locate host trees through olfactory (Prokopy *et al.* 1973) and visual (hue, shape, and size—Moericke, Prokopy & Bush 1975) cues. After arrival on host trees, flies detect individual fruits (or fruit clusters) primarily on the basis of physical characteristics of fruit shape, size, and colour-contrast against the background (Prokopy 1968). After arrival on host fruit, females carefully search the fruit surface to determine host quality. The sorts of fruit stimuli eliciting oviposition are reviewed by Prokopy (1977). If a fruit is acceptable, the fly deposits a single egg under the skin. Following oviposition, the fly drags its ovipositor on the fruit surface and releases a contact oviposition deterring pheromone (ODP) (Prokopy 1972). Conspecifics are highly deterred from ovipositing in ODP-marked fruit in nature, although deterrence is less pronounced in the laboratory (Prokopy 1981). Oviposition deterring pheromones are commonly employed by solitary insect parasitoids (e.g. Salt 1937; van Lenteren 1981) and may function to elicit uniform egg distribution among limited larval resources. After hatching, *R. pomonella* larvae remain in single host fruits until they mature. Larvae may reduce the fitness of their hosts by promoting bacterial rot and premature abscission. Rotting fruit is usually less palatable to vertebrates (Janzen 1977), the prime dispersal agents of *Crataegus* (Stiles 1980).

The following factors render *R. pomonella* flies particularly well-suited for foraging studies, both theoretical and natural historical: (1) the flies are relatively large, slow moving, and easy to observe in nature, (2) only the adult stage searches for hosts thus, parasite-prey models constructed to describe fly-fruit interactions need deal with only a single age class of fly (Hassell 1978), (3) successful foraging for oviposition sites is more closely related to genetic fitness than is the foraging of animals for food, and (4) foraging levels can be easily defined (Waage 1979), and patch boundaries are discrete (Bond 1980).

In this study, we evaluate *R. pomonella* foraging behaviour in response to four different ecological situations *R. pomonella* is likely to encounter in nature:

- (1) encounters with host trees devoid of fruit;
- (2) encounters with trees harbouring non-host (i.e. low quality) fruit;
- (3) encounters with host trees harbouring fruit previously parasitized and ODP-marked by conspecifics (i.e. low quality fruit);
- (4) encounters with host trees harbouring varying densities of high quality host fruits.

MATERIALS AND METHODS

We collected *R. pomonella* maggot-infested fruit from unsprayed trees at Amherst Mass. during August 1978. Fruits were held in wire baskets over plastic trays filled with moist vermiculite. Larvae completed development, dropped from the fruit into the vermiculite, and formed puparia. We removed the puparia from the vermiculite and stored them for *c.* 9 months at 4 °C. Following this, we placed them in a desiccator at 24 °C, 90% R.H., 16L:8D until adults emerged (*c.* 4 weeks). Adults were maintained in 25 × 25 × 25 cm Plexiglass-screen cages on a diet of sucrose, enzymatic yeast hydrolysate and water (Prokopy & Boller 1971).

Seventeen days after eclosion, we presented individual females (now mature) with an uninfested hawthorn (*Crataegus viridis* L.) fruit on a probe. Those flies that accepted fruit (i.e. oviposited) were permitted full movement over the fruit surface following ODP-deposition to gain contact experience with the ODP (most inexperienced flies do not recognize ODP—Roitberg & Prokopy (1981)). Each fly was then isolated in a smaller plastic-screen cage (modified 250 cc Dixie™ cup containing fly food and water) and provided with a second uninfested fruit. Following the second oviposition, flies were transferred to similar cup-cages lined with Grade 1 Whatmann™ filter paper where they remained overnight (flies remaining for extended periods in unlined cup-cages without fruit often attempt to oviposit on the smooth plastic wall and can damage the ovipositor). The following morning, we transferred the flies in the cup-cages to our study site at the Horticultural Research Center at Belchertown, Mass.

All field trials were conducted on four small non-fruiting host trees (Wealthy apple), each enclosed within a 3.5 × 3.5 × 2.5 m nylon screen cage (mesh size 1.5 cm²). The cage ceiling was covered with black cloth for two reasons: (1) to reduce glare and permit easier observation, and (2) because flies released on trees in such covered cages usually settle on trees and begin foraging in trees much more readily than flies released on trees in uncovered cages.

The four host trees were similar in shape and size (canopy = *c.* 1.5 m diameter, and extending from *c.* 0.5–2.0 m above the ground). We trimmed the limbs to achieve a similar number (*c.* 900) and distribution (one every 5 cm) of leaves per tree. All eight limbs per tree were number tagged.

We pre-tested and post-tested all flies. To pre-test, we presented each cup-caged fly an uninfested hawthorn fruit. Those that oviposited were allowed to rest for 20 min and then were released in trees for testing. After completing the foraging test, flies were returned to their cup-cage, allowed to rest for 5 min and then were presented with an uninfested hawthorn fruit for the post-test. We discarded data for flies that failed to oviposit in the post-test, except those flies that oviposited eight times or more during the test. We conducted the post-test to distinguish between individuals that migrated from the tree because either (1) they were no longer motivated to search for and oviposit in hosts, or (2) they were unable to locate any/suitable hosts for oviposition. Of those individuals that oviposited eight or more times during the test but failed to oviposit during the post-test, we assumed that they had used their complement of eggs for that day.

We examined the behaviour of individual females released in trees under four conditions

(i) Trees devoid of host fruit. In this two-part test, we compared foraging parameters of flies within empty trees (i.e. with no fruit) in situations where flies had not recently oviposited (Series A) *v.* situations immediately following a single oviposition (Series B). In Series A, flies were released individually on trees (20 min after pre-test) by placing the

inverted cup-cage (bottom removed) on a randomly chosen tree limb near the base of the canopy. In most cases, the released flies crawled or hopped to a leaf near the cup-cage. Within seconds after the fly left the cup-cage, we removed the cup-cage from the tree. Flies were allowed to forage up to 120 min within trees or until they flew to the cage wall. In Series B, flies which had foraged in Series A tests and accepted the post-test fruit were returned to the tree while ovipositing in that fruit and allowed to complete oviposition and host marking. Once the fly moved to a nearby leaf following fruit marking, the probe with the fruit was removed from the tree. Flies were allowed to forage as in Series A.

(ii) Trees harbouring non-host fruit. We attached stems of freshly picked fruit of buckthorn (*Rhamnus*) (which is not a known host of *R. pomonella*) to wires (0.2 mm diameter \times 10 cm length). We assembled the fruit in clusters of four and hung one cluster from each of the eight major tree limbs, in the upper third of the canopy (c. 1.5 m above the ground). Single flies were released in trees, as in Expt 1, within 40 cm of a cluster at a major tree limb. All flies discovered and visited at least one cluster. Trials were concluded as in Expt 1. Post-tests were conducted using hawthorn fruit.

(iii) Trees harbouring ODP-marked host fruit. Twenty hours prior to testing, we hung clean, uninfested hawthorn fruits in laboratory cages with mature *R. pomonella* flies. Each fruit that received one egg and subsequent ODP from one dragging bout was placed in the cold room (4 °C) overnight. The following morning, the fruits were returned to the laboratory and hung in front of a low speed fan until they warmed to room temperature. We did this because constant air movement reduces condensation and runoff of water from the fruit surface. Such runoff may contain large quantities of ODP, which is water soluble (Prokopy 1981). Fruits were assembled in clusters of four and trials run as in Expt 2. In a second set of trials, we repeated this procedure, except that each fruit received two eggs and ODP from two dragging bouts.

(iv) Trees harbouring varying densities of high-quality host fruit. We attached clean (no ODP), uninfested hawthorn fruit clusters to trees as in Expt 2 but at densities of 2, 4, 8, or 16 clusters. Single flies were released on trees as in Expt 1 (c. 0.5 m height). The cup-cages were not oriented in any way that might enhance the probability of a fly locating a particular fruit cluster. Trials were concluded as in Expt 2. In addition, we released some single flies within 20 cm of one of the fruit clusters in trees holding two clusters. We did this to increase our data base for intra and inter-cluster foraging behaviour of flies at the two cluster density level. In the standard protocol, most flies did not discover any fruit at this density level.

At the conclusion of each day's trials in Expts 3 and 4, we dissected all fruit hung in the trees to determine the number of eggs laid.

To determine the maximum number of eggs a female could deposit in 120 min, we placed individual 17-day, mature females in unlined cup cages with three uninfested, clean fruit. Each time a fruit received an oviposition, that fruit was replaced with a clean, uninfested one.

TABLE 1. Comparison of *R. pomonella* behaviour in host tree before and after oviposition. All values are \pm S.E.

Flies	Oviposition	\bar{X} no. branches visited/fly	\bar{X} no. leaves visited/fly	\bar{X} % of total tree area searched	\bar{X} total time in tree/fly (min)
Series A	20 min before release	3.3 \pm 0.5	9.8 \pm 1.4	20 \pm 3	3.8 \pm 0.5
Series B	at release	9.9 \pm 2.0	29.5 \pm 5.1	61 \pm 12	8.7 \pm 1.2

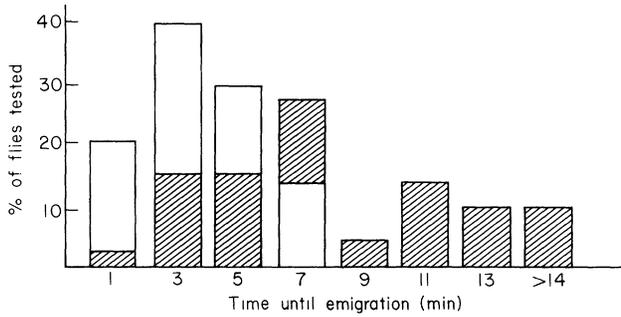


FIG. 1. Search time spent in trees devoid of fruit, by *R. pomonella* flies that did not recently oviposit (unhatched bars) (Series A) *v.* flies that oviposited coincident with release (hatched bars) (Series B).

RESULTS

Trees devoid of host fruit

Series A flies, which had not recently oviposited had brief foraging persistence in these host trees (Table 1). Compared with Series A flies, Series B flies, which oviposited coincident with release into those trees, visited more leaves more often (15 *v.* 2, $P \leq 0.001$, Wilcoxon Matched Pairs test), visited more branches more often (15 *v.* 1, $P \leq 0.003$ Wilcoxon test), searched more tree area (61 *v.* 20%), and remained in trees longer (i.e. search allotment time) more often (16 *v.* 2, $P \leq 0.001$ Wilcoxon test) (Table 1). In addition, search allotment times of flies in Series B covered a much broader range compared with those in Series A (Fig. 1). Figs 2 and 3 compares the search path of a typical fly in Series A *v.* one in Series B.

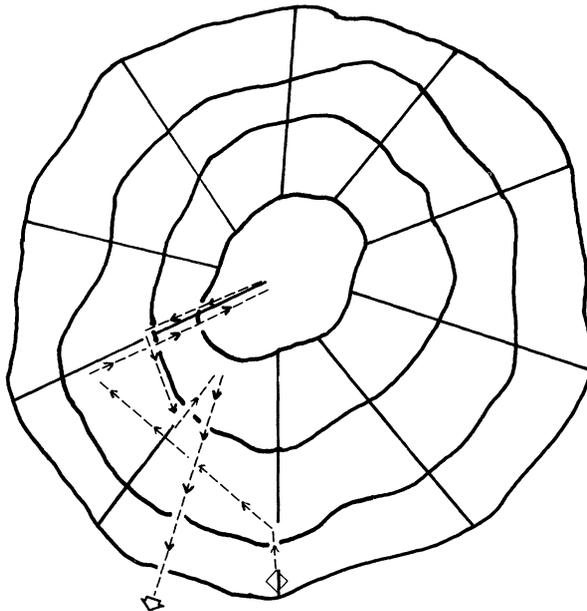


FIG. 2. Search path, in a tree devoid of fruit, by an *R. pomonella* fly that had not recently oviposited. Innermost area of the map represents the highest elevation level in the tree, while the outermost ring represents the lowest elevation level. Lines radiating from the centre ring represent the major tree limbs.

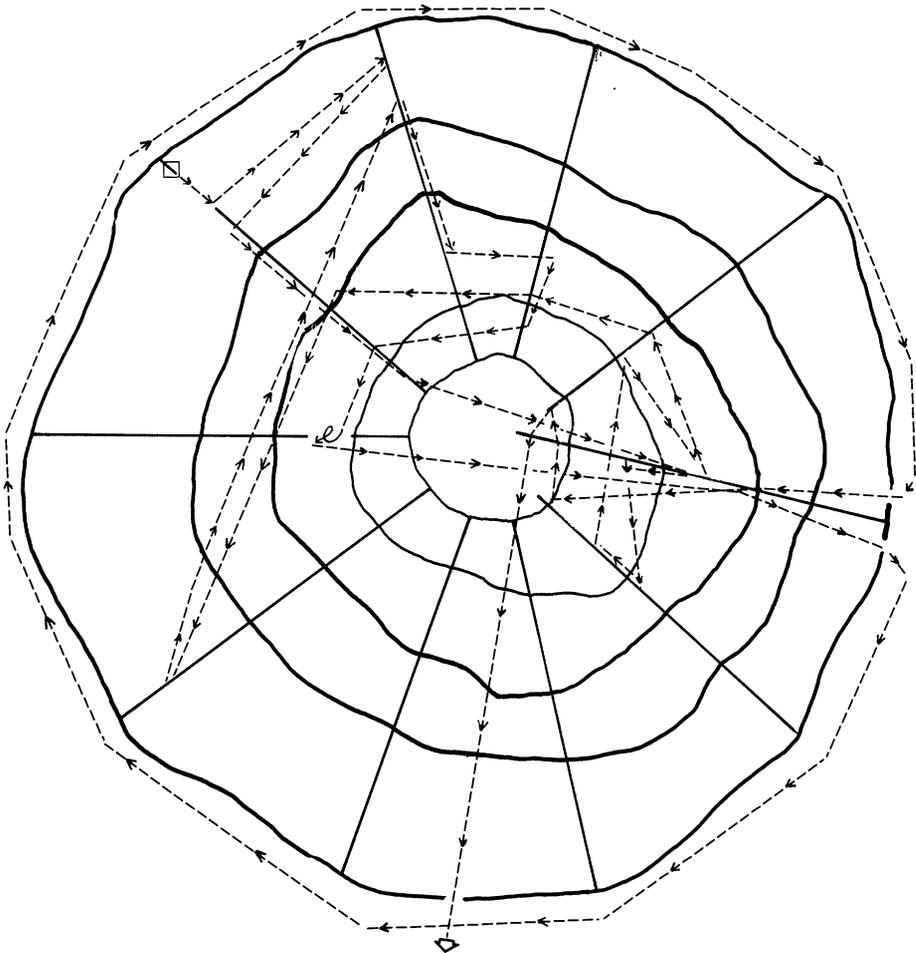


FIG. 3. Search path, in a tree devoid of fruit, of an *R. pomonella* fly which oviposited coincident with release into the tree.

TABLE 2. Comparison of *R. pomonella* behaviour on host trees harbouring different quality fruit. All values are \pm S.E.

Fruit type	<i>N</i>	\bar{X} no. visits to fruit clusters/fly	\bar{X} no. visits to fruit/fly	\bar{X} acceptance of fruit visited/fly	\bar{X} no. ovipositions/fly	\bar{X} total time in tree/fly (min)
Hawthorn: uninfested, unmarked	14	11.4 \pm 2.6	64.3 \pm 15.5	0.11 \pm 0.01	7.2 \pm 1.4	64.3 \pm 10.5
Hawthorn: 1 \times infested, 1 \times ODP marked	6	4.8 \pm 2.3	23.5 \pm 5.8	0.11 \pm 0.03	2.7 \pm 0.8	67.8 \pm 10.9
Hawthorn: 2 \times infested, 2 \times ODP marked	13	3.6 \pm 0.8	21.9 \pm 4.6	0.03 \pm 0.01	0.1 \pm 0.01	21.8 \pm 6.4
<i>Rhamnus</i>	20	1.5 \pm 0.2	5.9 \pm 1.2	0	0	15.7 \pm 3.3

Trees harbouring non-host (Rhamnus) fruit

All flies migrated from the trees before laying any eggs in *Rhamnus* fruit (Table 2). The mean search allotment time for these flies was much shorter than for flies released in trees harbouring the same density of uninfested hawthorn fruit (15.7 *v.* 64.3 min, $P \leq 0.0001$, Mann Whitney U test). Flies made fewer visits to *Rhamnus* clusters than to uninfested hawthorn clusters (1.5 *v.* 11.4 visits, $P \leq 0.01$, U test). They also visited fewer *Rhamnus* than hawthorn fruit (5.9 *v.* 64.3 visits, $P \leq 0.0001$, U test). Figure 4 shows the path of a typical fly foraging in a tree harbouring *Rhamnus* fruit.

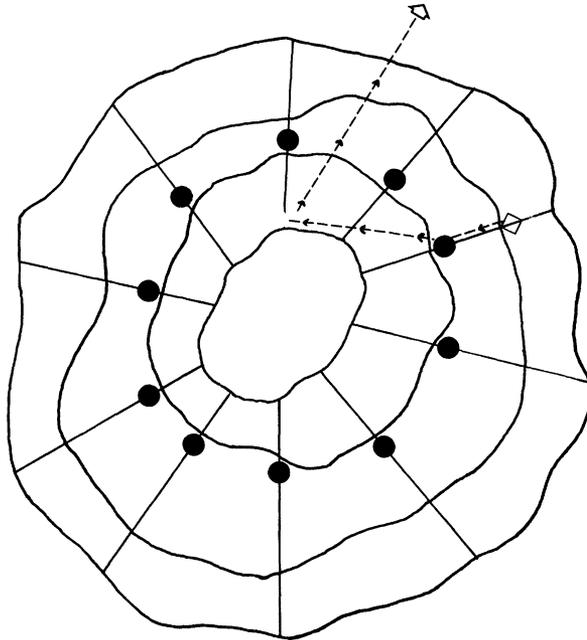


FIG. 4. Search path of an *R. pomonella* fly in a tree harbouring eight clusters of *Rhamnus* (non-host) fruit.

Trees harbouring infested (ODP-marked) v. uninfested (clean) hawthorn fruit

At the same density of fruits, flies released in trees holding egg-infested, twice-marked fruit showed differences in behaviour from flies released in trees, with either clean or infested, once-marked fruit (Table 2). Search allotment time of flies in trees with twice-marked fruit was much shorter than in trees in the other two treatments. While only 3 of 13 flies remained in the former trees for more than 30 min, 11 of 14 and 6 of 6 flies foraged for more than 30 min in trees with clean and once-marked fruit, respectively (2 \times marked *v.* clean, $P \leq 0.002$, G test; 2 \times marked *v.* 1 \times marked, $P \leq 0.004$, G test). There was no statistical difference in search allotment time of flies in the latter two treatments. The search rate (measured as: no. visits to fruit/(search allotment time minus 1 min per each oviposition)) was much lower for flies on trees with once-marked fruit compared with flies on trees with twice-marked fruit (0.4 *v.* 1.9 fruit/min, $P \leq 0.01$, U test). Overall, flies visited almost equal numbers of once and twice-marked fruit before emigrating from trees (Table 3). However, these means were much lower than for flies on trees with clean fruit

TABLE 3. Comparison of *R. pomonella* behaviour on host trees harbouring different densities of fruit clusters. All values are \pm S.E.

No. clusters	<i>N</i>	% of flies locating fruit	\bar{X} no. visits to fruit clusters/fly	\bar{X} no. visits to fruit/fly	\bar{X} acceptance of fruit visited/fly	\bar{X} no. ovipositions/fly	\bar{X} total time in tree/fly (min)
2							
All Flies	26	15 \pm 8	1.0 \pm 0.3	8.0 \pm 2.8	—	1.2 \pm 0.4	10.6 \pm 2.7
Finders Only	9	—	2.8 \pm 0.6	23.2 \pm 5.0	0.31 \pm 0.05	3.6 \pm 0.8	22.3 \pm 4.8
4							
All Flies	34	35 \pm 8	3.7 \pm 1.2	22.7 \pm 7.4	—	2.4 \pm 0.7	24.1 \pm 6.0
Finders Only	12	—	10.6 \pm 2.3	64.3 \pm 15.1	0.23 \pm 0.02	6.8 \pm 1.3	55.4 \pm 10.2
8							
All Flies	22	68 \pm 9	7.5 \pm 2.1	42.9 \pm 12.3	—	4.9 \pm 1.2	46.1 \pm 9.0
Finders Only	15	—	11.3 \pm 2.6	65.9 \pm 16.1	0.17 \pm 0.02	7.3 \pm 1.4	64.2 \pm 10.5
16							
All Flies	13	92 \pm 7	17.6 \pm 3.1	120.9 \pm 21.7	—	11.5 \pm 2.0	71.5 \pm 13.1
Finders Only	12	—	19.4 \pm 2.8	133.0 \pm 19.9	0.13 \pm 0.01	12.6 \pm 1.9	76.9 \pm 13.2

(2 \times marked *v.* clean, $P \leq 0.03$, U test; 1 \times marked *v.* clean, $P \leq 0.01$, U test). Figure 5 shows the path of a typical fly foraging in a tree with (a) twice-ODP-marked fruit, and (b) uninfested, clean fruit.

While only 4 of 13 flies oviposited in at least one twice-marked fruit before emigrating from trees, 5 of 6 flies did so in once-marked fruit ($P \leq 0.04$, G test). Flies rejected once-marked fruit during 89% of visits to fruit ($n = 141$) *v.* 97% rejection of twice-marked fruit ($n = 285$) ($P \leq 0.001$, Dixon & Massey (1969) Proportions test) (rejection measured as $[1 - (\text{no. ovipositions}/\text{no. visits to fruits}) \times 100]$). Because flies may make frequent visits to the same fruit we also measured rejection as $[1 - (\text{no. ovipositions}/\text{no. fruits visited}) \times 100]$, and in this case flies rejected 90% of twice-marked ($n = 89$), 62% of once-marked ($n = 204$) (2 \times marked *v.* 1 \times marked, $P \leq 0.001$, Proportions test; 2 \times marked *v.* clean, $P \leq 0.0001$, Proportions test; 1 \times marked *v.* clean, N.S., Proportions test).

Trees harbouring varying densities of high quality fruit clusters

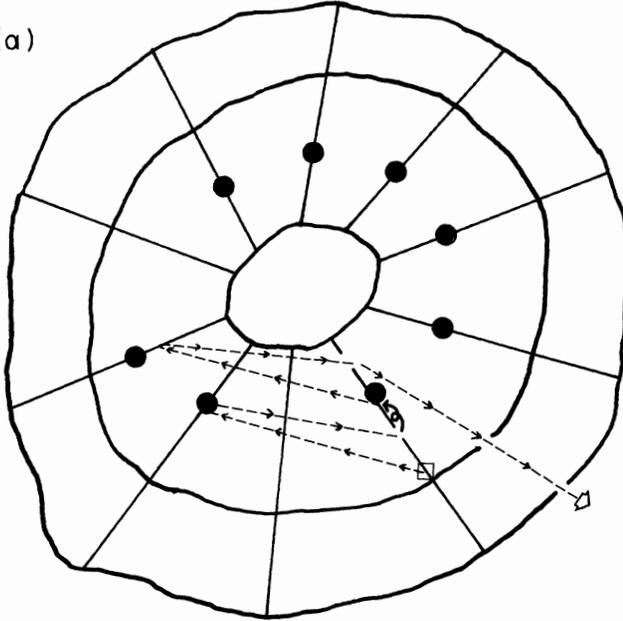
There was a positive relation between the probability of flies locating fruit and the density of fruit clusters in a tree (Fig. 6) (Table 3). The mean search allotment time of flies that failed to locate any fruit before emigrating, when fruit density was 2 or 4 clusters, was identical to the search allotment time of Series A flies in Expt 1 (density 2: 3.9 min \pm 1.0 S.E., $n = 17$; density 4: 3.9 min \pm 1.1 S.E., $n = 22$; Series A: 3.8 \pm 0.5 S.E., $n = 18$). The search allotment time was longer for unsuccessful searchers when the density was 8 clusters (9.9 min \pm 3.1 S.E., $n = 7$). However, 4 of the 7 flies in this category spent considerable time resting (i.e. not actively searching for fruit). Only 1 of 13 flies did not locate fruit when the density was 16 clusters.

In most of the remaining analysis, we examine results from treatments in two ways: (1) All Flies—we consider all flies tested (except those that failed the post-test); (2) Finders Only—we consider only those flies that arrived on at least one fruit cluster before emigrating.

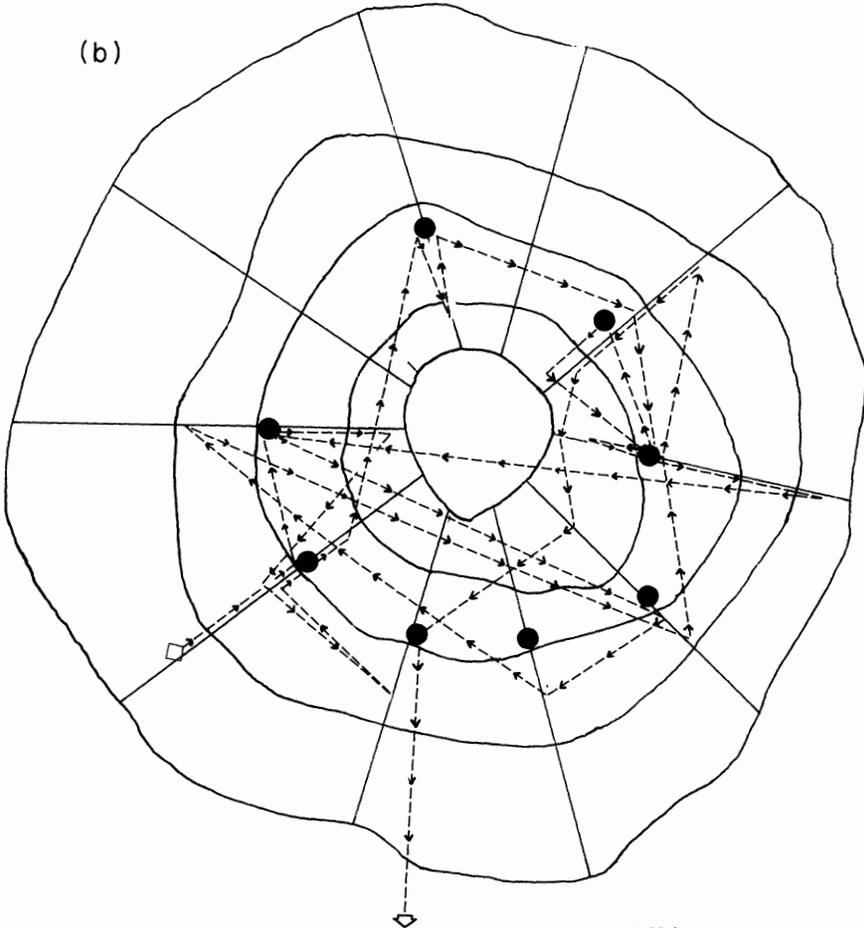
Both All Flies and Finders Only made more visits to fruit clusters as the density of clusters increased (All Flies: $y = 1.15x - 1.28$, $P \leq 0.0001$; Finders Only: $y = 0.99x -$

FIG. 5(a) Search path of an *R. pomonella* fly in a tree harbouring eight clusters of twice-ODP-marked host fruit. (b) Search path of an *R. pomonella* fly in a tree harbouring eight clusters of uninfested, unmarked host fruit.

(a)



(b)



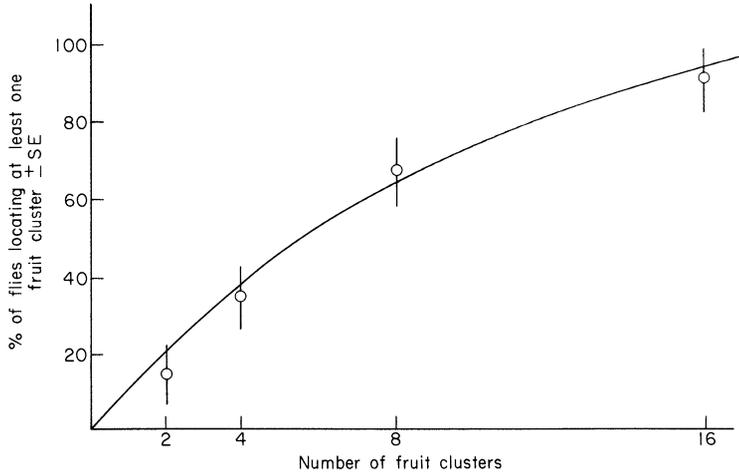


FIG. 6. Relation between *R. pomonella* flies locating at least one cluster of host fruit and density of fruit clusters. Curve drawn by eye.

3.72, $P \leq 0.005$) (Fig. 7). Differences in number of visits to clusters at different cluster densities were significant (All Flies: $F = 13.77$, $P \leq 0.0001$, 1-way ANOVA; Finders Only: $F = 5.8$, $P \leq 0.003$, 1-way ANOVA).

There was a positive relation between fruit cluster density and the number of visits flies made to individual fruits (All Flies: $y = 7.96x - 12.15$, $P \leq 0.001$; Finders Only: $y = 6.87x + 19.70$, $P \leq 0.0001$) (Fig. 8). Differences in number of visits to individual fruits at different cluster densities were significant (All Flies: $F = 16.13$, $P \leq 0.0001$, 1-way ANOVA; Finders Only: $F = 7.36$, $P \leq 0.0005$, 1-way ANOVA).

There was no statistically significant relation between density of fruit clusters and proportion of available fruit that flies visited. Flies that found fruit visited an average of

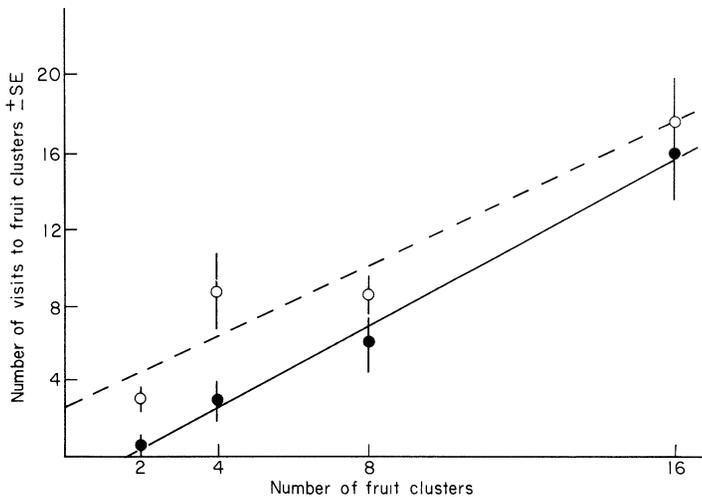


FIG. 7. Number of visits to host fruit clusters by *R. pomonella* flies at different cluster densities. All Flies are represented by filled circles and Finders Only by unfilled circles (see text for explanation). Line drawn from regression analysis.

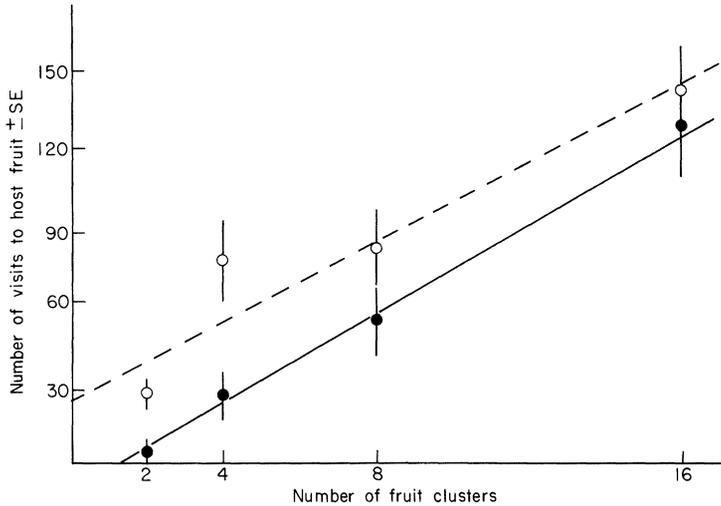


FIG. 8. Number of visits to host fruit by *R. pomonella* flies at different fruit cluster densities. All Flies, filled circles; Finders Only, unfilled circles. Lines drawn from regression analysis.

53% \pm 7.4 S.E. ($n = 45$) of available fruit before giving up and emigrating from the tree. In addition, finders made visits to fruits at an average of 1.1 visits/min (minus 1 min per each oviposition) at densities of 2, 4 and 8 clusters. Visitation rates were greater at 16 clusters ($\bar{X} = 1.8$ visits/min, $n = 10$), but none of the differences were statistically significant at the 5% level (U test).

Flies became more selective about accepting clean fruit for oviposition as cluster density increased (Fig. 9). While flies oviposited during 31% \pm 4.8 S.E. ($n = 91$) of visits to fruit at the 2-cluster density, they oviposited during only 12.5% \pm 1.1 S.E. ($n = 905$) of visits to

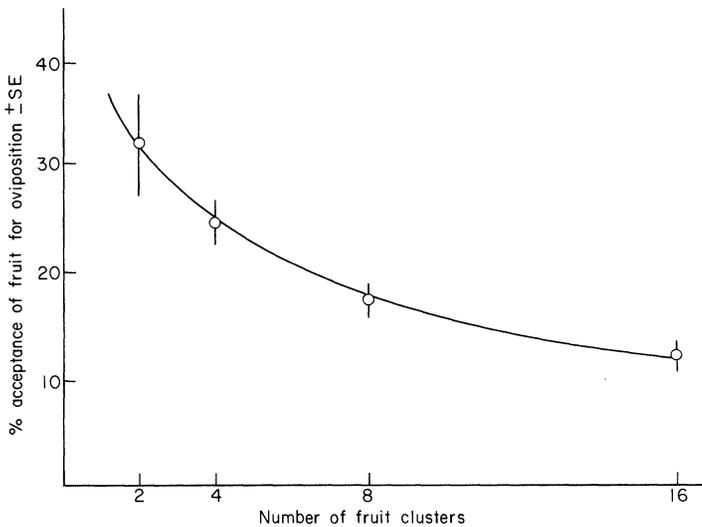


FIG. 9. Percentage acceptance of unfested (clean) host fruit for oviposition by *R. pomonella* flies at different fruit cluster densities. Line drawn by eye.

fruit at the 16-cluster density ($P \leq 0.0001$, Proportions test). Flies rejected fruit during $97\% \pm 0.5$ S.E. ($n = 1385$) of visits to fruit that they had marked with ODP during their foraging bouts. Flies oviposited in such marked fruit more frequently at density 2 and 4 clusters than at either the 8 or 16-cluster density ($P \leq 0.01$ and 0.0001 , Proportions test) (Table 3).

Flies oviposited more often in trees with higher compared with lower densities of fruit clusters (All Flies, $P \leq 0.0001$; Finders Only, $P \leq 0.02$). Both All Flies and Finders Only at the 16-cluster density, deposited nearly the same number of eggs as flies provided continuous clean fruit for 120 min in the laboratory. Figure 10 shows the functional

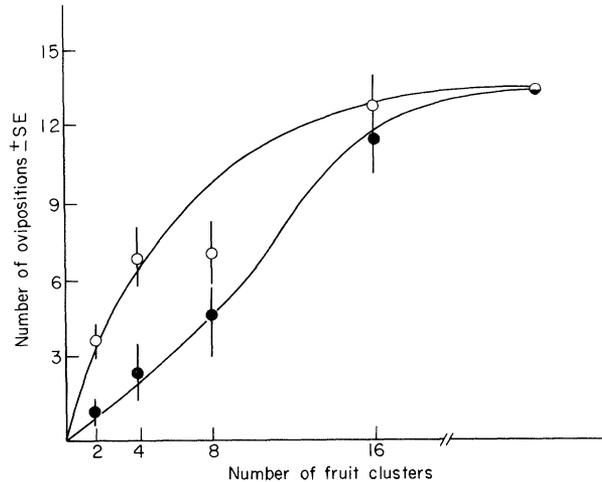


FIG. 10. Functional response of *R. pomonella* flies to different host fruit cluster densities. All Flies, filled circles; Finders Only, unfilled circles; Lab derived maximum no. of ovipositions, ●. Lines drawn by eye.

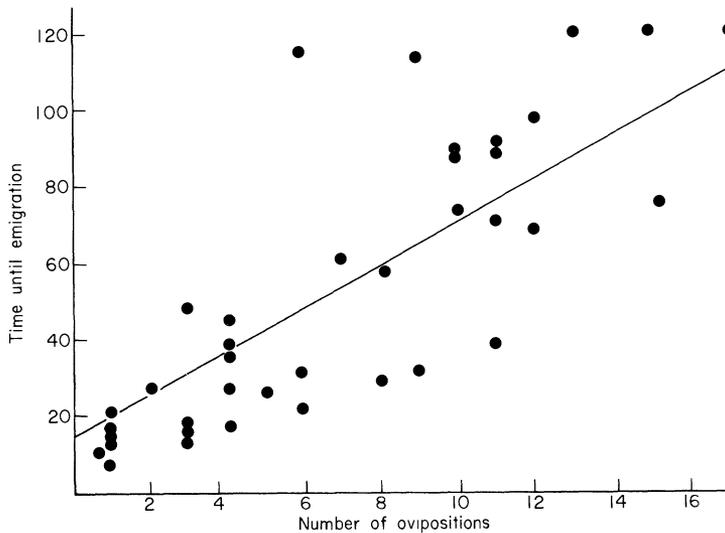


FIG. 11. Number of ovipositions by *R. pomonella* flies that spent varying periods of time in trees before emigrating. Line drawn from regression analysis.

response of flies to fruit density. Among Finders Only, there was no relation between the rate of oviposition and density of fruit clusters. Figure 11 shows the relation between the time flies spent in trees and the number of eggs laid ($y = 0.42x - 26.49$, $P \leq 0.0001$). Flies oviposited at the rate of 1 egg every 6.25 min spent foraging in the trees.

There was a positive relation between the total time flies spent foraging in trees and fruit cluster density (Fig. 12). Differences between these times at the different cluster densities were significant (All Flies: $F = 10.8$, $P \leq 0.0001$, 1-way ANOVA; Finders Only: $F = 4.3$, $P \leq 0.02$, 1-way ANOVA). Finders Only stayed longer in trees than All Flies at densities 2, 4 and 8 clusters (2 clusters, $P \leq 0.002$; 4 clusters, $P \leq 0.002$; 8 clusters, $P \leq 0.08$; 16 clusters, no difference; *t*-tests).

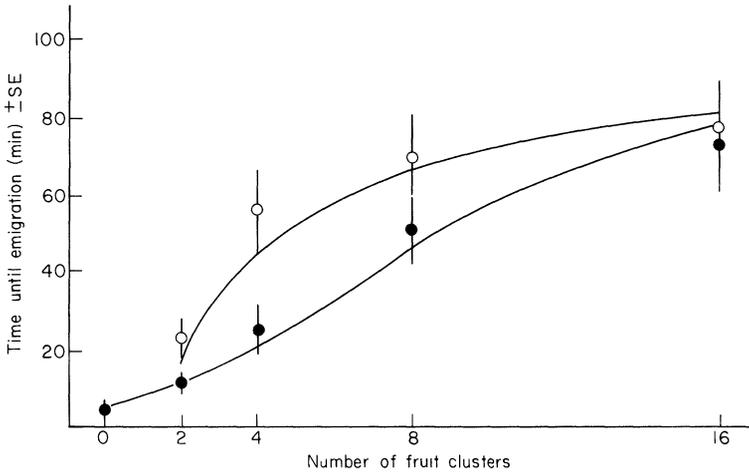


FIG. 12. Time spent foraging by *R. pomonella* flies before emigrating from trees with varying densities of fruit clusters. Lines drawn by eye.

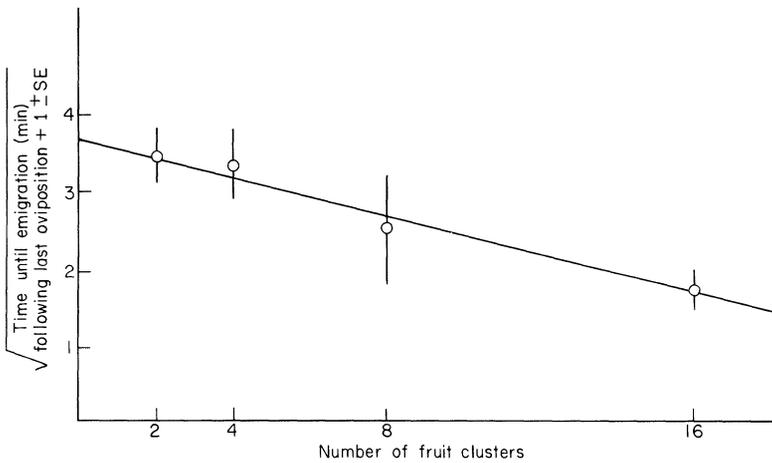


FIG. 13. Time until emigration following the last oviposition by *R. pomonella* flies in trees with varying densities of fruit clusters. Line drawn from regression analysis.

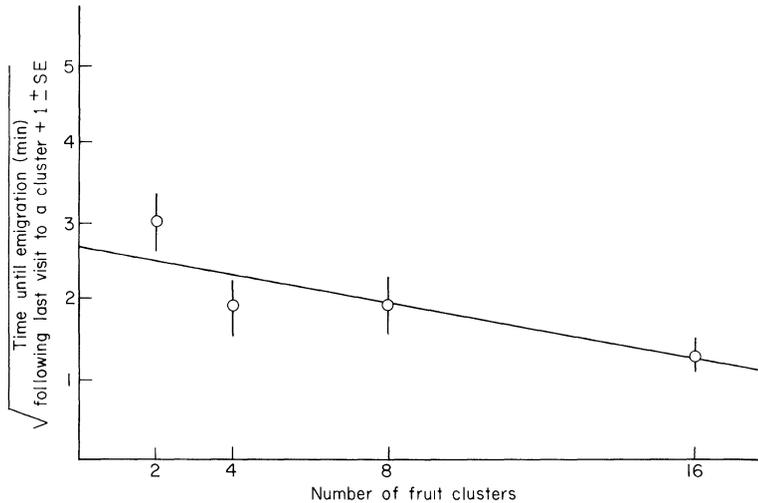


FIG. 14. Time until emigration following the last visit to a fruit cluster by *R. pomonella* flies in trees with varying densities of fruit clusters. Line drawn from regression analysis.

There was a negative relation between time until emigration of flies in trees after the last oviposition (i.e. Giving Up Time (GUT)) and fruit cluster density (Fig. 13) ($y = -0.126x - 3.70$, $P \leq 0.001$). Differences between GUTs at the different densities were significant ($F = 5.17$, $P \leq 0.005$). Similarly, flies gave up on trees sooner after their last cluster visit as cluster density increased (Fig. 14) ($y = -0.09x - 2.74$, $P \leq 0.01$). Differences between GUTs were significant ($F = 4.24$, $P \leq 0.02$, 1-way ANOVA).

Finally, flies remained longer on clusters during their initial visit than on successive visits (189 v. 50 s, $\chi^2 = 130.5$, $P \leq 0.0001$). This was particularly true when flies oviposited in and deposited ODP on at least one fruit during the first visit to a fruit cluster (158 v. 24 s, $\chi^2 = 98.7$, $P \leq 0.0001$).

DISCUSSION

Thorough understanding of the numerical interactions between parasites and their prey is often dependent upon detailed analysis of the underlying behavioural components. The present study on the *R. pomonella*–*C. viridis* system suggests a number of exogenous and endogenous factors that contribute to the functional response of *R. pomonella* to prey density.

First, *R. pomonella* increases search effort, within trees after a single host fruit has been encountered and exploited (Table 1). Similar responses have been demonstrated for other parasites (e.g. *Pseudeucoila bochei*, van Lenteren & Bakker 1978) and have been defined as success-motivated search (Vinson 1977). The response apparently functions to retain foragers in areas where host location and exploitation are most likely to occur, given the clumped or patchy distribution of many prey in nature. If, in trees with fruit clusters, females failed to locate any fruit, they left the tree after a more or less fixed searching time (c. 4 min), the same search allotment time as shown by females in trees without any fruit (Fig. 15).

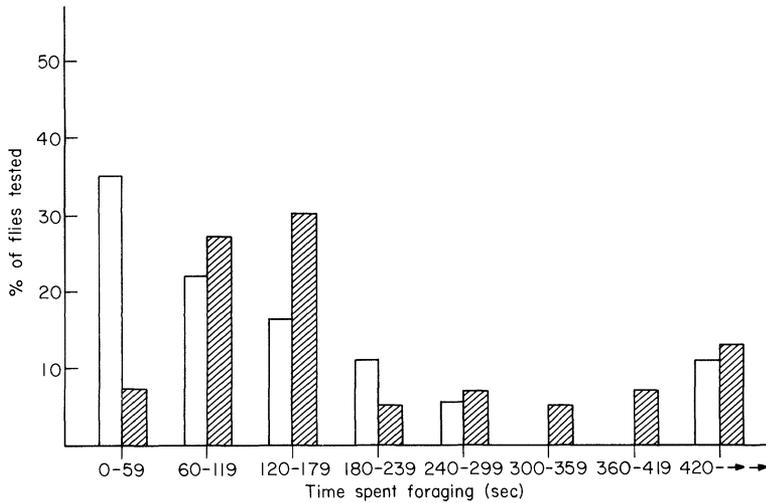


FIG. 15. Time spent foraging, in trees harbouring fruit clusters, by *R. pomonella* flies, until fruit was located (unhatched bars) or emigration (hatched bars).

Second, *R. pomonella* flies give up on and emigrate from trees after encountering only a few non-host fruit (Table 2). Such 'decisions' are functional in that encounters with a non-host fruit indicates all fruit in that tree will be non-host (unsuitable). We do not know if flies can distinguish between leaves of host and non-host plants. In addition, we have no information about the effect of encounters with low quality (e.g. low moisture content) fruit on the allocation of search effort by *R. pomonella*.

Third, *R. pomonella* generally discriminates between infested, ODP-marked fruit and uninfested, unmarked fruit. In addition, they display differential sensitivity in response to once and twice-marked fruit. This differential response may lead to a uniform distribution of eggs among host fruit, as flies lay eggs more often in fruit with lighter infestations. While *R. pomonella* flies may emigrate from hawthorn trees before superparasitizing many or any of the numerous small host fruit, the situation may be very different when they forage in apple trees harbouring large host fruit. In the latter case, several ODP dragging bouts may be required to deter further oviposition (Prokopy 1972). Sensitivity to varying levels of ODP concentration on apples apparently does occur in nature. LeRoux & Mukerji (1963) showed that *R. pomonella* ovipositions are evenly distributed among multiple infested apples within individual trees (c. 13.4/apple).

Fruit once-marked by the flies during foraging were rejected as frequently as the twice-marked laboratory treated fruit. Two possible explanations for this phenomenon are: (1) the pheromone marks applied in the laboratory were of inferior quality or their quality was affected by storage overnight in the cold room, or (2) flies can distinguish between fruit marked with their own ODP *v.* those fruit marked by other flies. We have accumulated much evidence from other experiments conducted in our laboratory that the latter is not so.

Fourth, *R. pomonella* flies are more selective in their choice of fruit for oviposition as host fruit density increases. This is analogous to foraging theory predictions for food seeking animals that only high ranking prey items be accepted when their density is high (e.g. MacArthur & Pianka 1966). Similar shifts in host acceptance thresholds have been shown for other parasites (e.g. *P. bochei*, van Lenteren 1976).

Fifth, *R. pomonella* flies spend less time searching individual fruit in clusters on successive visits to clusters. This is particularly true if one or more fruit are infested and ODP-marked. Waage (1979) reported that the entomophagous parasite *Nemeritis canescens* spends less time on patches during revisits. van Lenteren & Bakker (1978) showed the same for the parasite *P. bochei* and Price (1970) showed that some parasitic insects deposit odour trails that enable them to avoid previously searched areas. We have no evidence that *R. pomonella* produces olfactorily perceived odour trails. The ODP trails are perceived only upon contact (Prokopy 1981). Flies readily alight on previously searched clusters. In addition, flights between fruits within clusters appears to be random, with flies just as likely to alight on a previously visited fruit as on an unsearched one. Flies make proportionately more revisits to fruit clusters at low than at high cluster densities, and at low cluster densities, they spend a greater proportion of the total within-tree time searching for fruit clusters ($y = 0.014x - 0.49$, $r = 0.44$, $P \leq 0.001$) (Fig. 16). At high

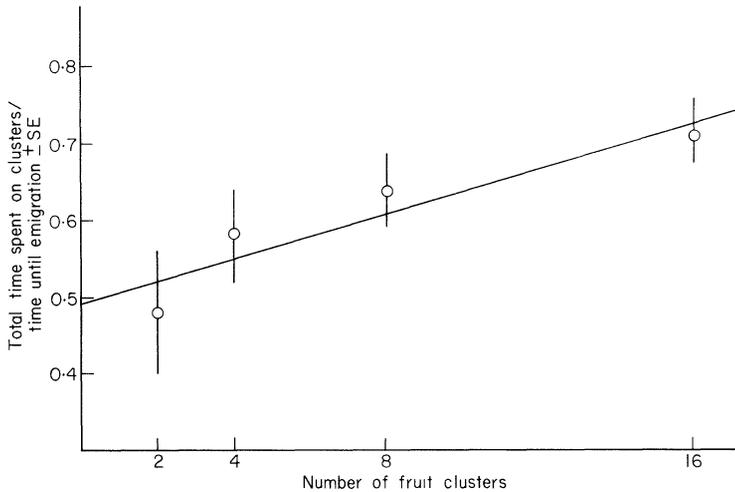


FIG. 16. Proportion of total within-tree time spent searching for fruit by *R. pomonella* flies in trees with varying densities of fruit clusters. Line drawn from regression analysis.

cluster density, flies often visually located another fruit cluster and then flew directly to it. This almost never occurred at the 2- or 4-cluster densities. Thus search time necessary for locating unsearched, unexploited fruit clusters is greater at low host densities because (1) hosts are more difficult to locate, and (2) the probability of locating and alighting on an already visited host is greater (68% at 2 clusters *v.* 54% at 16 clusters).

Rhagoletis pomonella displays a Type 3 functional response to host fruit density (Fig. 10). The Type 3 curve is produced by an accelerating increase in the number of prey captured (or parasitized) as a function of prey density. Similar Type 3 responses have been reported for few other insects (e.g. *P. bochei*, van Lenteren & Bakker 1976, 1978, *Notonecta glauca*, Hassell, Lawton & Beddington 1977). Type 3 responses may result from one or more of at least four possible changes in the foragers behaviour as influenced by changes in prey density: (1) the forager learns to find prey more readily (e.g. forms a search image) at some critical prey encounter rate, (2) forager alters rate of search at some critical prey encounter rate, (3) forager spends less time engaging in non-foraging activities at higher prey encounter rates, or (4) forager emigrates from the resource patch more readily at low host densities. Our results strongly suggest *R. pomonella*'s Type 3 response

is principally due to the fourth factor: emigration. At low host fruit density most flies leave the tree before discovering any fruit. However, if a fruit is located and 'success motivated' search initiated, chances of other fruit being encountered and exploited greatly increase. The functional response of the Finders Only is characteristically Type 2 (Fig. 10) and lends further support to our suggestion that the Type 3 response of All Flies is primarily due to emigration by a large proportion of flies before host encounter at low host fruit densities. Flies oviposited at approximately the same rate (1 ovip./6.2 min) at the four fruit densities tested, but they remained longer in trees at the higher cluster densities (Fig. 12).

The time until emigration of flies from trees was highly variable when measured as either (1) time since last oviposition (GUT) (range 0.02 to 41.8 min), or (2) time since last encounter with a host fruit (range 0.02–9.6 min), although there was a trend toward shorter time until emigration at higher fruit density (Figs 13 and 14). This trend may be explained by the fact that, at high cluster densities, most flies discover new fruit much sooner than they would at low cluster density. Therefore, most flies that leave trees before discovering fruit at high cluster densities must do so within a short period of time. By contrast, flies may display either long or short search allocation time at low fruit densities without discovery of any fruit.

A number of mechanisms have been proposed through which foraging animals 'decide' to remain in or emigrate from resource patches, the most notable being:

(1) Hunting by expectation (Gibb 1962). Forager enters patch with expectation of prey capture, and leaves patch when prey quota is realized.

(2) Hunting by expectation. Fixed time expectation (Krebs 1973). Forager remains in patch for fixed period of time.

(3) Hunting by expectation. Flexible time expectation (Breck 1978). Time expectation is fixed after forager assesses resource richness of whole environment (e.g. through intensity of olfactory cues).

(4) Fixed threshold rate (Murdoch & Oaten 1975). Forager leaves patch after capture rate falls below some fixed value.

(5) Variable threshold rate (Parker & Stuart 1976). Forager exits patch after capture rate falls below some threshold value which is dependent upon value of the habitat.

(6) Variable arrestment response (Waage 1979). Forager displays continuously waning arrestment response to host chemicals in patch. Prey captures drive arrestment response to upper threshold.

(7) Memory decay model (Ollason 1980). Prey capture information is lost from forager at some constant rate. Forager leaves patch when its rate of capture is less than it remembers.

All of the aforementioned mechanisms provide means through which animals might make 'decisions' to remain in or emigrate from patches. And while they may describe parasite behaviour in simple laboratory systems, they may not adequately describe parasite behaviour in more complex environments. Van Alphen (1980) lists nine factors that may interact to release emigration behaviour of parasitoids: (1) number of encounters with unparasitized hosts; (2) rate of encounters with unparasitized hosts, (3) ability of parasite to recognize parasitized hosts; (4) presearch ability (*sensu* Price 1970); (5) habituation to host derived arrestment chemicals; (6) experience on other patches; (7) encounters with non-hosts; (8) encounters with unsuitable hosts; (9) interference from other parasitoids. To date no study has examined all of these factors in an integrated way.

Upon arrival on host trees, *R. pomonella* flies appear to exhibit a fixed threshold rate response. In both the empty-tree and varying cluster density experiments many flies

emigrated from trees within a fairly narrow time frame if no fruit were encountered (29 of 56 flies emigrated from the tree within 2–5 min of release on the tree). However, once a single host is encountered and accepted for oviposition, the situation becomes more complex. On the basis of our results in the varying cluster density experiments, we rule out any fixed time or fixed capture rate response. Waage's (1979) model may be a more appropriate predictor of *R. pomonella* behaviour than the other aforementioned mechanisms in that his model correctly predicts that oviposition initiates 'success motivated' search (i.e. increases search effort allotment). However, Waage's model is simplistic in that it focuses on only two parameters (i.e. concentration of host derived chemicals and rate of ovipositions). Our results suggest *R. pomonella*'s search behaviour is influenced by numerous parameters. For example, search paths and search effort appear to be influenced by encounters with uninfested, unmarked as well as infested, ODP-marked fruit. In addition, we recently demonstrated that the distance to alternate foraging sites (i.e. other trees) influences the search time allotment of *R. pomonella* on host trees (B. D. Roitberg & R. J. Prokopy unpublished). Further, the sequence in which infested *v.* uninfested fruits are encountered influences search effort parameters of flies on trees with low fruit density (B. D. Roitberg & R. J. Prokopy unpublished). Thus, search effort allotment and subsequent host fruit exploitation by *R. pomonella* within individual host trees appears to be influenced by a constellation of factors in a manner more complex than current foraging models describe.

Previous studies of entomophagous and frugivorous parasites (excluding phytophagous biocontrol agents) have employed widely varying, even contrasting approaches. This is probably because economic benefits may derive from emphasizing foraging success in the case of the entomophages, and foraging failure in the frugivores. We suggest that experimental approach and design be assembled on the basis of the subject animal's behaviour and lifestyle (e.g. parasitic), regardless of ultimate goals.

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