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FORAGING BEHAVIOUR OF *RHAGOLETIS POMONELLA*: A PARASITE OF HAWTHORN (*CRATAEGUS*)

A Dissertation Presented

By

BERNARD DAVID ROITBERG

Submitted to the Graduate School of the
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DEDICATION

This dissertation is dedicated to my grandparents.

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Many people have contributed in many different ways to the research reported herein.

First, my committee, Drs. Elkinton, Prokopy and Sargent provided many useful suggestions that significantly improved experiments and/or reports of such.

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ABSTRACT

Foraging behaviour is a complex process that is influenced by several ecological and physiological factors. Thus, analysis of the foraging process is often difficult and rarely definitive. The principal objectives of this dissertation are two-fold. First, in Chapter 1, I define some of the crucial areas that need be addressed to critically evaluate the foraging behaviour of parasitic insects in particular, and mobile animals in general, including: (1) patch structure, (2) perceptual abilities of foragers, (3) search paths of foragers, (4) ability of foragers to process and recall resource related information, (5) emigration release mechanisms, (6) travel costs, and (7) evaluation of foraging associated risks. Second, I examine some of these parameters (2 through 5) by employing Rhagoletis pomonella (Tephritidae) and Crataegus viridis (Rosaceae) as my model parasite-host system.

My rationale (Chapter 2) for choosing the R. pomonella-C. viridis system is based on several key factors, including: (1) R. pomonella is a true parasite (Price 1977), (2) comparative ease of observing and maintaining flies, (3) comparative ease of manipulation of individual host fruit, and (4) single oviposition bouts (and subsequent pheromone marking) by R. pomonella females usually render those fruits unacceptable for oviposition by conspecifics.

A number of phytophagous parasitic insects are known to host-discriminate (i.e. avoid laying eggs on plants already occupied by conspecifics). Through an analysis of their natural histories, I show,

in Chapter 3, that these insects share a number of ecological correlates, including: (1) association with hosts that persist for several of the parasites generations, (2) comparatively narrow host range, (3) limited mobility of parent and offspring, and (4) restricted sites of parasitization within individual hosts.

Rhagoletis pomonella has been shown to display highly sensitive host-discrimination ability. However, the propensity by flies to avoid oviposition in occupied fruit may be overridden by several ecological and/or physiological factors. In Chapter 4, I show that individual females that have not had previous experience with oviposition deterring pheromone (but have had oviposition experience) do not usually host-discriminate, and in Chapter 5, I show that the tendency for flies to oviposit in occupied fruit increases over time if flies are deprived of host fruit.

The remainder of this dissertation concerns detailed observations of fruit search behaviour of individual female flies in host trees, with particular reference to factors that influence allocation of within-tree search effort. To do this I released individual lab-maintained flies (whose larvae were of wild origin) in small (ca. 2 meter) host trees enclosed within large field cages. Results show that flies behave in a manner similar to entomophagous parasites. First, upon arrival in host trees, female flies exhibit a fixed threshold rate response. If no hosts are discovered within a few minutes of arrival, emigration occurs. However, once fruit discovery occurs, several factors were shown to act upon search behaviour and subsequent timing of emigration, including:

(1) number of encounters with unparasitized, high quality host fruit, (2) number of encounters with parasitized, high quality host fruit, (3) number of encounters with low quality, host fruit, (4) sequences of encounters with different quality hosts, and (5) distance to other trees. These factors were found to interact in a complex manner, not explainable by simple behavioural models.

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INTRODUCTION

Most insects are limited, in some way, by their ability to locate and exploit particular resources which are essential to their fitness. These resources include: food, mates, oviposition sites, shelter and transportation. Because many of these resource units are patchily distributed in space and/or time, ecologists have become interested in the way in which animals locate them. A branch of ecology called foraging theory has been developed to explain how animals should behave in order to efficiently utilize their foraging time and energy. While still in its infancy, foraging theory has produced a wide range of theoretical models that provide explanations for a variety of animal behaviours. However, many of these models appear to be rather simplistic and may have limited utility in aiding our understanding of foraging processes in complex environments. In the literature review of this dissertation (Chapter 1), I define some of the crucial areas that need be addressed in order to critically evaluate foraging behaviour of parasitic insects in particular and mobile animals in general.

Fruit parasites appear to be excellent candidates for foraging studies for several reasons, including: (1) direct correlation between behaviour and reproductive output, and (2) ease with which both forager and prey can be manipulated. In Chapter 2, I outline my rationale for choosing *Rhagoletis pomonella* Walsh (Diptera: Tephritidae) and *Crataegus viridis* L. (Rosaceae) for my model parasite-host system.

In addition to *R. pomonella*, and in common with many entomophagous parasites, a wide variety of phytophagous insects has been shown to host discriminate (i.e., avoid ovipositing on hosts already occupied by conspecifics). While these insects represent a number of different taxa and parasitize different plant taxa, it is tempting to search for biological patterns that may explain the presence of host discrimination within particular insect species. In Chapter 3, I examine some ecological correlates common to host-discriminating phytophagous parasites.

Rhagoletis pomonella has been shown to display highly sensitive host-discrimination ability (Prokopy 1981a). However, the propensity by flies to avoid oviposition in occupied fruit may be overridden by several ecological and/or physiological factors, the properties of which are poorly understood. Because survival of *R. pomonella* offspring in overcrowded fruit may be very low (Averill and Prokopy, unpub. data), lack of host discrimination by ovipositing flies may be costly to fitness. In Chapters 4 and 5 I examine two factors that appear to influence host discrimination by *R. pomonella* flies. First, in Chapter 4, I examine the influence of flies' previous experience with host marking pheromone on their subsequent ability to host discriminate, and second, in Chapter 5, I compare the responses of flies to previously parasitized, pheromone marked host fruit after flies have been deprived of any host fruit for varying lengths of time.

The aforementioned laboratory studies provide information on complex behavioural phenomena that are difficult to manipulate and/or observe in nature. However, field studies provide the best opportunities for accepting or rejecting our ideas about how animals behave in nature. Thus, the remainder of my dissertation is based upon experiments conducted within trees, in nature.

In Chapter 6, I evaluate _R_. _pomonella_ foraging behaviour in response to four different ecological situations that it is likely to encounter in nature:

(1) Host trees devoid of fruit.

(2) Trees harbouring non-host (i.e. low quality) fruit.

(3) Host trees harbouring fruit previously parasitized and oviposition-deterring-pheromone marked by conspecifics (i.e. low quality fruit).

(4) Host trees harbouring varying densities of high quality host fruit.

In the literature review section, I suggest that measurement of search effort by animals within resource patches may be of limited value unless inter-patch distance is considered. In Chapter 7, I examine the effects of inter-tree distance on the intra-tree search behaviour of individual _R_. _pomonella_ flies.

A number of mechanisms have been proposed through which foraging animals 'decide' to remain in or emigrate from host-containing patches, including (1) assessment of number of encounters with hosts, (2) rate of encounters with hosts. In the final chapter, I consider, as factors potentially influencing the intra-tree foraging behaviour of individual R. pomonella flies (1) the number of encounters flies have with parasitized and unparasitized hosts, and (2) the sequence in which these encounters occur.

In this dissertation I do not attempt to develop a predictive model of R. pomonella foraging behaviour (but see Appendix 1) but rather to evaluate various aspects of the foraging process that I feel are essential to our understanding of how parasitic insects forage for their host in nature. Through careful examination of the dynamics of the search process, I hope to gain insights into how fruit parasites respond to changes in resource quality and quantity within and between host-containing resource patches.

CHAPTER I

FORAGING THEORY: A SELECTIVE REVIEW WITH SPECIAL REFERENCE TO PARASITIC INSECTS

The success with which organisms locate and exploit their resources is dependent upon their behaviour. In recent years, a branch of ecology called foraging theory has been developed to evaluate the behaviour of foraging animals. A basic tenet of this theory is that natural selection refines the foraging process (Pyke *et al*. 1977). Under this premise, those behaviours which promote greatest genetic fitness will increase in frequency within a population. Although this assumption is very simplistic, foraging theory has generated a number of theoretical models which optimize some aspect of an individual's or group's foraging behaviour - e.g. group size (Bertram 1978), movement patterns (Pyke 1979), food quality maximization (Goss-Custard 1977), food quantity maximization (Elner and Hughes 1978), time allocation (Charnov 1976). The latter has received a great deal of attention and remains steeped in controversy (reviewed in Hassell and Southwood 1978).

Mobile animals often search for prey that are clumped or patchy in distribution. From a foraging theory perspective, the parameter most likely to be optimized is efficient use of time (energy) spent within and between resource patches. Individuals that remain "too long" in resource poor areas may realize prey captures well below those possible at other sites. By contrast, individuals that leave resource patches "too quickly" may spend inordinately large amounts of time and energy moving between resource patches.

MacArthur and Pianka (1966) were the first to propose an optimal solution for exploitation of a patchy environment. Since then, optimal foraging theoreticians have independently derived similar solutions to the patch time allocation problem (Royama 1971, Charnov 1976, Parker and Stuart 1976, Cook and Hubbard 1977). Their models are similar in that the forager leaves patches when its rate of prey capture is equal to or less than the average of that of the entire environment. All of the models are mathematically derived, but are simple and deterministic, and can be easily described verbally. It is a weakness of these models that they employ deterministic approaches to a stochastic problem (Oaten 1977). However, there have been some attempts of late to reduce the deterministic nature of these models (e.g., Green 1980). In addition to the problem of determinism, these models require the forager to obtain and process information in an unrealistic manner, given the perceptual limitations of most organisms (Oaten 1977, Stanton 1980). Optimal foraging theory suffers from three other deficiencies. First, most hypotheses generated from the theory are uni-dimensional in that they ignore all parameters (e.g., risk to predation, Sih 1980) except resource accruement. Second, they suggest a directional evolution of foraging behaviour toward a single solution (but see Wright 1931) despite numerous physiological, ecological and phylogenetic constraints (Gould and Lewontin 1979). Third, Lewontin (1979) criticized the optimization approach because of its susceptibility to "progressive ad hoc optimization" i.e., plausible explanations are developed to explain why optimal behaviours are not displayed, rather than to accept the fact that the organism may not perform optimally. Despite these limitations there is considerable qualitative evidence that many foraging animals are highly efficient in their utilization of resource patches (e.g., Cowie 1977). In addition, foraging theory provides a novel perspective from which to examine behaviour.

I believe that time allocation models derived from foraging theory are highly simplistic. Of particular importance is their lack of attention devoted to search dynamics and their implicit assumption that prey density is a good indicator of prey capture rate. For this reason, it is nearly impossible to properly evaluate current foraging theory models. For example, Iwasa et al. (1981) showed that optimal solutions from Charnov's Marginal Value Theorem (1976) were highly dependent upon the dispersion parameters of the prey. For the remainder of this literature review I will concentrate on major parameters that I feel must be evaluated before the dynamics of any foraging process can be understood. While this review is biased toward Rhagoletis pomonella, in particular and parasitic animals in general, much of this review applies to the study of all foraging animals.

A. Patch Structure

I define a patch as "any discrete spatial unit that harbours resources." When encountered by an organism seeking those resources, that organism's search behaviour is altered in some characteristic manner (e.g., turning rate, antennae tapping).

Patches take many forms. Clusters of fruit or schools of fish are obvious examples. For a less obvious example, an individual mosquito larva is a resource-containing patch for a piercing-sucking predator (Cook and Cockrell 1978). In this example, Cook and Cockrell (1978) considered the nutrients within the mosquito's body to be resource units, and as parallels other foraging studies, nutrient extraction rate from individual larvae inversely correlated with time spent feeding on a larvae because first nutrients are more easily extracted. In a novel treatment of the marginal value theorem for patch time allocation (Charnov 1976), Dunstone and O'Connor (1979) considered oxygen reserves of aquatic mammalian carnivores as single patches (i.e., time rather than spatial).

An important point to consider about patches is the many levels at which they exist (Hassell and Southwood 1978). For example, _Aphidius smithii_, a hymenopteran parasite of aphids, searches first for patches of host plants, second for individual host plants, third for clumps of aphids on one plant, fourth for individual aphids, and last, for particular areas on each aphid most suitable for oviposition. Foragers define each patch level by their behaviour. However, not all patches are obvious and discrete to the human observer (Bond 1980). In addition, foragers may search at more than one level simultaneously.

Size, shape and internal structure of the resource patch are important determinants of encounter rates between foragers and prey. However, few studies have addressed the problem of internal patch variation in relation to search effort allocation by parasitic insects. Whereas some prey are randomly distributed within patches (e.g., greenhouse whitefly, _Trialeurodes vaporarium_, van Lenteren _et al_. 1976) many others are not (e.g., aphids, Hafez 1961). In addition, Prokopy et al. (1982) recently introduced the concept of "effective distribution" which I defined as "the spatial and/or temporal dispersion pattern of those resource units that are available for exploitation by foragers." For example, not all prey within a resource patch simultaneously produce the nutrients necessary to initiate feeding behaviour by their predators or parasites (e.g., Wratten 1975).

In consideration of the importance of the aforementioned intra-patch parameters one should attempt to simulate natural density and distribution of prey when conducting foraging studies. However, most investigations on parasitic insects are conducted in the laboratory where petri dishes define patch shape and size, and these bear little resemblance to those experienced by the forager in nature. More importantly though, laboratory experiments often concentrate on a single patch level and do not provide other stimuli that animals are exposed to while foraging in their natural habitat. Such approaches have been severely criticized by Labeyrie (1978) as contributing little to our knowledge of natural animal behaviour. As pointed out by Price et al. (1980) clear understanding of biological systems is often dependent upon understanding of interactions at more than one level.

Hubbard and Cook (1978) studied the foraging behaviour of a parasitic wasp, Nemeritis canescens, on flour moth larvae, Ephestia kuhniella in the laboratory. In their experiments, petri dishes defined patches, and prey density was considered an indicator of prey encounter rate. However, those glass enclosures may have effected prey distribution so that *N. canescens* would encounter prey at different rates than they would in nature. In addition, Hubbard and Cook used fixed patch size (9 cm petri dishes). However, van Lenteren and Bakker (1978) showed that search effort of another parasitic wasp, *Pseudeucoila bochei*, is greatly influenced by patch size. Thus Hubbard and Cook's results may have little relevance beyond the specific situation they studied. Further, there is little evidence from either Hubbard and Cook's (1978) or van Lenteren and Bakker's (1978) studies that inter-patch distances approximated those found in nature. And finally, neither group attempted to duplicate the physical complexity of the parasites' natural environment even though it has been shown to be of great importance to prey encounter rates (Huffaker 1958).

In regard to patch structure, fruit parasitizing animals are excellent candidates for foraging studies for the following reasons: (1) Patch levels are often observable and defineable e.g., tree, fruit cluster, individual fruit, (2) Physical complexity of the foraging environment (e.g., host plant) can often be measured and simulated (see appendix 1), (3) prey density and distribution may be more easily measured than for mobile prey.

B. Perceptual Limitations of Foragers

To date, optimal foraging models have been strongly criticized because they rely upon unrealistic assessment of perceptual and cognitive abilities of foragers (Stanton 1980, van Alphen 1980). Although behavioural studies have shown that prey recognition is dependent upon complexity of background information (i.e., noise) (e.g., Egeth *et al.*

1973) most patch utilization studies are conducted in simple laboratory situations where prey are more easily located than they would be in nature (e.g., worms on conveyor belts, Krebs et al. 1977). Recently, some attention has been devoted to prey crypsis (Erichsen et al. 1980)

Prey encounter rates are influenced also by the distance at which foragers recognize prey (reactive distance). Reactive distance may vary with the animals' experience and physiological state (Dill 1978). In addition, relative reactive distance may be dependent upon breadth of host acceptance range (Waage 1979), and ability of foragers to form search images (e.g., Rausher 1978). Thus the perceived value of a resource patch may be affected by external and internal parameters, both of which can rapidly change.

Measuring reactive distances of parasitic insects can be very difficult, particularly if the animals depend upon olfactory cues to find their prey. For animals that visually search for their prey, measurements of their reactive distance may be somewhat easier, although knowledge of the visual performance of the organisms is essential (Prokopy and Owens, MS in prep). In addition, it is almost impossible to categorically state the moment prey recognition occurs because observable behavioural responses only tell us that some form of stimulus response has occurred. Finally, it is not sufficient to state that the organism sees prey at a given distance. For example, Elkinton et al. (appendix 1) employed a fixed reactive distance of 0.3 m in their simulation model for Rhagoletis pomonella flies visually searching for clusters of hawthorn (Crataegus) fruits within host trees. Subsequently, I found that this visual reactive space around a given fruit cluster is not spherical in shape but rather pear shaped and that animals foraging above fruit cluster were far less likely to discover fruit than those searching below a cluster (Roitberg and Prokopy, unpub. data). Thus reactive distance should be considered a relative measure.

C. Search Paths

Most predatory and parasitic insects display characteristic search behaviour before and after prey encounter (Flanders 1947). For example, animals that search for clumped prey generally increase turning rates (i.e., exhibit area restricted search) following encounters with prey (Dixon 1959). Conversely, the parasite _Encarsia formosa_ does not alter its random search paths after encountering one of its randomly distributed _T. vaporarium_ prey. In addition, search paths may vary depending upon particular ecological conditions and/or physiological state of the organism. Finally, Roitberg _et al_. 1979 showed that plant parasitic pea aphids, _Acrythosiphon pisum_, displayed very different search behaviours after dropping to the ground from their host plant, depending upon their age, density of conspecifics and modality of the dropping stimulus.

In conjunction with patch structure and the forager's perceptual ability, search path mechanics determine if/which prey are encountered. At present, most patch utilization models suffer from unrealistic treatment of search mechanics (Stanton 1980). A notable exception is Zach and Fall's (1976a,b) studies of ovenbird search mechanics and patch utilization.

Search path models have been developed in which employment of movement rules provide animals with maximum benefits (e.g., Cody 1971; Pyke 1978). However, to my knowledge, search path characteristics are not employed in patch time allocation models for foraging insects, although Waage (1979) considered orthokinetic and klinotactic responses of *N. canescens* to host chemicals and patch edge in his patch utilization model.

Little is known about the search paths of host-plant seeking fruit parasitic insects. With regard to *R. pomonella* flies, Moericke *et al*. (1975) showed that flies appear to avoid large open spaces and generally fly within 2 m of the ground. Within trees, these flies display diel movements which take them from the tops of the tree in early morning to lower portions as the day progresses, then back toward the tree tops at days end (Prokopy *et al*. 1971).

D. Information Processing and Memory

Patch utilization models require foragers to acquire and process information regarding resource quality within and between patches (Cowie and Krebs 1979). For example, Ollason (1980) developed a model in which foragers acquire and lose information at some constant rate. While a number of studies suggest insects lose information, it is not known whether this is due to memory decay or interference (Minami and Dallenbach 1946, Plotkin 1979). In addition, there is still controversy on how information is processed and stored (e.g., Griffith 1979; Meldonado *et al*. 1979). Klomp *et al*. (1980) suggested that the insect egg parasite *Trichogramma embryophagum* learns and forgets how to discriminate between parasitized and unparasitized prey. However, because of the design of their experiments, it is not possible to separate forgetting from simple changes in acceptance/rejection thresholds for parasitized prey over time. In Waage's (1979) parasitioid search model, information about the timing of ovipositions, rather than the absolute number, is crucial to releasing emigration behaviour. While Waage's model provides a reasonable account of how parasitoids "decide" when to leave patches, it is simplistic in that it considers only the parameters of oviposition success and host derived kairomone concentration. Clearly, other information about resource quality and quantity (e.g.,ratio of parasitized to unparasitized hosts) is available to the parasite. How much of this information is perceived, stored, and recalled, probably varies among different species of organisms. Krebs (1978) suggests foragers possess a sliding memory window of the last "n" patches visited. There is a paucity of information available on memory dynamics of fruit parasites, save some genetic studies on *Drosophila* memory (Quinn *et al*. 1979, Dudai 1979).

Critical analysis of spatial memory may be as important to understanding the foraging process as is memory of resource assessment. For example, Pyke (1978) suggested that the memory of nectar collecting bumblebees *Bombus flavifrons* and *Bombus appositus* encompasses a knowledge of direction of arrival at present inflorescence and the change in direction at the previous inflorescence. If similar memory capacities can be shown for parasitic insects it may enhance our understanding of search path dynamics of these particular foragers.

E. Mechanisms Underlying Allotment of Search Effort Within Patches

In general, optimal foraging models such as those developed by Charnov (1976) pay little attention to the actual behaviour of the animal in question. They merely suggest what the optimal foraging strategy might be, given an animal that is fully capable of "deciding" its next move (e.g., to emigrate from the patch or continue searching within that patch) based upon an intelligent assessment of the rate of success thus far. Such assessment is undoubtedly beyond the capabilities of most animals, humans included. Instead, animals in nature probably use a series of "behavioural rules" which allow them to approach the optimal solution suggested by the theory. A different appraoch to foraging theory centers upon an attempt to elucidate these "behavioural rules." For example, Elkinton *et al*. (unpub. MS) has attempted to model the movement rules of mate-seeking gypsy moths *Lymantria dispar*. In recent years a number of hypothetical mechanisms have been proposed, through which animals allot search effort within patches.

1. Hunting by expectation (Gibb 1962). Forager enters patch with expectation of prey capture, and leaves patch when quota is reached. Krebs (1973) criticized this model as unrealistic. For example, an animal entering a patch of value X and having an expectation of X + 3 might never leave that patch.

2. Hunting by expectation - Fixed time expectation (Krebs 1973). Forager enters patch with preset fixed foraging time allocation. Animals displaying this behaviour are efficient in predictable environments and inefficient in unpredictable ones.

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). This mechanism is more sensitive to resource heterogeneity but might require complex sampling and calculations in variable environments (Oaten 1977).

4. Fixed threshold rate (Murdoch and Oaten 1975). Forager leaves patch after capture rate falls below some fixed value. This mechanism may be inefficient in variable environments.

5. Variable threshold rate (Parker and Stuart 1976). Forager exits patch after success rate falls below some threshold which is dependent upon value of other patches in the habitat and travel costs between patches. May require highly complex calculations beyond the capabilities of most animals.

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. Good predictor of *N. canescens* search behaviour. May be too simplistic to predict behaviour of many parasites in nature (see van Alphen 1980).

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. This model provided a good fit to Cowie's (1977) data on foraging tits (*Parus major*). It has not been tested on any insect.

8. Re-encounter ratio (Morrison and Lewis 1981). This mechanism

was developed for parasitic insects. In the model, the parasite emigrates from the host containing patches when the ratio of re-encounters with hosts (i.e., already parasitized) to encounters with new (unparasitized) hosts exceed some value. Appears to be an important but not exclusive component of the foraging behaviour of the egg parasite *Trichogramma pretiosum* (Morrison and Lewis 1981).

9. Giving up as a Poisson process (Bond 1981). Random emigration probability is set by the level of host deprivation (e.g., prey availability). No time criterion is employed. Comparisons between richness of patch and habitat are not made.

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: (a) number of encounters with unparasitized hosts; (b) rate of encounters with unparasitized hosts, (c) ability of parasite to recognize parasitized hosts, (d) pre-search ability (sensu Price 1970), (e) habituation to host derived arrestment chemicals, (f) experience on other patches, (g) encounters with non-hosts, (h) encounters with unsuitable hosts, (i) interference from other parasitoids. To date no study has examined all of these factors in an integrated way.

F. Travel Costs

The occurrence of emigration behaviour is often dependent upon travel distance to the nearest alternate resource (e.g., Parker and Stuart 1976). This is particularly true for insects where travel may have direct costs to fecundity (e.g., Roff 1977 for Drosophila; Roitberg et al. 1979 for aphids). Travel costs are generally ignored or held constant in most patch utilization studies even though it is generally agreed that the experimental animal usually forages in a heterogeneous habitat where inter-patch distances may be highly variable. Notable exceptions to the aforementioned trend are (1) Cowies (1977) study, where he showed that tits foraging for mealworms moved less readily between patches when travel costs were high than when low and (2) Zimmerman (1981) who showed that bees visited fewer flowers per plant as interplant distance decreased. While many theoretical studies have explored the relative costs and benefits of dispersal (e.g., Lidicker 1962; van Valen 1971) few have actually attempted to measure these parameters in nature (e.g., Roitberg and Myers 1979). In addition to the problem of measuring travel costs and benefits it is essential to evaluate how much information about alternate patches a forager can perceive and process while foraging within a given patch. For example, can the forager perceive the presence of patches beyond a specific distance? (see Chapter 5).

G. Risks Associated with Foraging

Increasing evidence suggests foragers are influenced by risk factors associated with foraging. For example, crayfish (Crustacea), reduce grazing activity in the presence of fish predators (Stein and Magnunson 1976, Bertness 1981). Risk components have been included in some models and tests of foraging theory. Rosensweig (1974) developed a model for bannertail kangaroo rats where risk to predation influences length of foraging periods. Recently, Milinski and Heller (1978) and Sih (1980) demonstrated that the foraging activities of sticklebacks *Gasterosteus* and waterboatmen *Notonecta glauca*, respectively, are altered in the presence of predators. In both cases, foragers altered their behaviour in a manner suggesting a compromise between lower risk to predation and lower foraging efficiency.

Foragers may reduce predation pressure through mimicry or crypsis. Schultz (1980) demonstrated that degree of crypsis (twig mimicking) could be correlated with foraging efficiency of tree defoliators. *R. pomonella* flies, the principal subjects of this dissertation, may cope with foraging-associated risks by mimicking jumping spiders (Salticidae) in both morphological characters (e.g.,wing and scutellum markings) and defensive postures (Gardner 1965, Roitberg unpub. MS). The protection afforded by these characters and their associated costs remain unknown.

H. Selecting a Currency and Time Frame

The basic premise behind foraging theory is that increased efficiency leads to increased fitness. To evaluate foraging efficiency, Shoener (1971) and Pyke *et al*. (1977) suggest usage of a common currency (e.g.,energy). While this approach is theoretically possible, it is difficult to convert calories to fitness, in practice. This greatly limits the usefulness of food foraging models. Foraging studies that deal directly with reproductive success provide a much better index of fitness. To date, most models and experimental studies of insect foraging that have focussed directly on reproductive success have been carried out with parasitoids (e.g., Hassell 1971; Rogers 1972; van Lenteren 1976; van Lenteren and Bakker 1978; Hubbard and Cook 1978; Waage 1978; 1979). In addition, several excellent studies on the fitness value of host plant choice for ovipositing insect herbivores have been conducted (e.g., Chew 1977; Rausher 1979). Apparently no published studies to date have examined patch time allocation tactics for phytophagous insects.

In addition to the problem of relating foraging efficiency to fitness, there is the problem of time frame. Short term "optimizers" may behave differently from long term ones (Katz 1974). For example, Kushlan (1979) showed that the robbing behaviour of foraging egrets is not energetically cost effective (but see Dunbrack 1979 and Caldwell 1980 for counter arguments). Kushlan suggested that other benefits (e.g., long term tracking of environment) may result from this apparently non-optimal behaviour. Whether this is true, or instead, another good example of "progressive ad hoc optimization," has not been conclusively demonstrated. However, this example does point to the problem of defining the variable to be optimized and its concurrent time frame. Studies that deal directly with reproductive success may be the best approach to dealing with the time frame problem.

Conclusions

The literature devoted to foraging theory is currently experiencing an exponential growth rate. Because of its basic tenet of microevolutionary development the optimization idea is intuitively appealing and therefore embraced by many theoreticians and field biologists. Unfortunately, as I have attempted to show in this review, many foraging theoreticians have chosen to ignore the fact that foraging efficiency is but one component in the evolution of animal behaviour.

I suggest that contemporary foraging models are too simplistic to be of much practical use. Conversely, I do not believe that highly detailed models that specifically describe the behaviour of a particular organism in a specific situation will greatly increase our understanding of the foraging behaviour of animals in general. However, I have attempted to point to particular areas that should receive careful consideration in any foraging study, to provide realism and generality (e.g., measurement of patch structure).

Lewontin (1979) criticized evolutionary theoreticians for frequently employing "progressive ad hoc optimization." If the optimality approach is to gain wider acceptance in the scientific community, investigators must avoid employing these tactics when their optimization models fail to accurately predict behaviour.

Finally, optimization represents one approach to the study of foraging. Alternative theories and hypotheses should be investigated concurrently. The optimization approach will probably prove most beneficial if the investigator employs the theory as a tool to increase understanding of an ecological phenomenon and not as an end in itself.

CHAPTER II

THE *RHAGOLETIS*-*CRATAEGUS* HOST-PARASITE SYSTEM

Mitchell (1980) suggests that fruit and seed parasites are ideal organisms for evaluating a variety of ecological theories because their lifestyle facilitates precise measurement of genetic fitness associated with particular behaviours. In this chapter I provide a brief description of *Rhagoletis pomonella* life history and then detail my rationale for choosing the *Rhagoletis*-*Crataegus* association as my model parasite-host system.

R. pomonella is a solitary endoparasite (sensu Price 1977) in the fruit of *Crataegus*. Adult flies locate host plants through visual (i.e.,tree size, shape and colour, Moericke *et al*. 1975) and olfactory cues (Prokopy *et al*. 1973, Fein *et al*. 1980). Flies detect individual fruits (or clusters) primarily on the basis of physical characteristics of fruit shape, size and colour contrast against background (Prokopy 1968, 1977). After arrival on a fruit, females carefully search fruit surface to determine host quality. If the host fruit is acceptable, the fly deposits a single egg under the fruit skin. Following oviposition, the fly drags its ovipositor over the fruit surface and releases a contact oviposition deterring pheromone (ODP) (Prokopy 1972, 1981, Prokopy *et al*. 1976). Conspecifics arriving on ODP marked fruit are generally deterred from ovipositing in those hosts. Oviposition deterring pehomones are commonly employed by solitary insect parasitoids (Salt 1937, van Lenteren 1981) and apparently function to elicit uniform egg distribution among limited larval resources. After hatching, R. pomonella larvae remain in single fruit hosts until they mature. Larvae may reduce the fitness of their hosts by promoting bacterial rot and premature abcission. Rotting fruit is usually less attractive to vertebrates the prime dispersal agent of Crataegus (Janzen 1977, Stiles 1980). Rhagoletis pomonella is an excellent candidate for foraging studies for the following reasons:

First, as with other parasites, foraging for oviposition sites is more closely related to genetic fitness than is the foraging of animals for food. In addition, the fate of individual eggs and larvae can be evaluated through larval rearing techniques (Prokopy and Boller 1971).

Second, R. pomonella is a relatively large, slow moving fly and can be easily observed in nature. Observers may be stationed within 0.5 m of individual flies without disturbing them. This facilitates precise measurement of foraging activity. Observational techniques have been used to evaluate mate foraging behaviour of male Rhagoletis flies in nature (Prokopy et al. 1971, 1972, Prokopy and Bush 1973, Smith and Prokopy 1980).

Third, whereas little is known about the behaviour of most parasites in nature, much is known about R. pomonella behaviour in its natural environment (Prokopy 1977 and references within). This facilitates design of experiments which incorporate natural aspects of R. pomonella's environment.

Fourth, R. pomonella visually locates host fruit (Prokopy 1968).

Visual perception is accompanied by overt orientation behaviour. This allows for precise measurement of reactive distance of flies to host fruit.

Fifth, R. pomonella searches for immobile prey (host fruit). This facilitates accurate census and manipulation of prey distribution.

Sixth, R. pomonella oviposition deterring pheromone (ODP) is an external, contact, water soluble substance. Because the pheromone trail is visible on the fruit surface it is relatively easy to observe fly contacts with the ODP trail (see Chapter 4). In addition, more is known about the ODP system of R. pomonella than any other insect (Prokopy 1981, Prokopy and Spatcher 1977, Prokopy et al. 1982, Crnjar et al. 1978, Averill and Prokopy 1980).

Seventh, collection of wild flies for laboratory and field tests is facilitated by an abundance of larval-infested hawthorn fruits in parks and recreation sites in the Amherst area. When such fruits are placed on hard ware cloth over moist vermiculite, thousands of readily collectable puparia are formed in the vermiculite. The puparia can be stored in a cooler at $5^{o}C$ up to two years and brought into the laboratory for fly emergence as needed. Flies can be maintained in laboratory or field cages at high levels of longevity and fecundity on an artificial or aphid honeydew diet (Prokopy and Boller 1971). Thus R. pomonella can be studied year round.

My choice of Crataegus viridis as the model prey was based on the following factors:

First, uninfested C. viridis can be readily collected in Massachusetts and Connecticut.

Second, *C. viridis* fruit in excellent condition for fly oviposition can be kept year round in cold storage. By hanging such fruit in trees I was able to greatly increase the length of my field season.

Third, *C. viridis* fruits are small (ca. 8mm/diam) and thus a single ODP deposition bout on such fruit is sufficient to deter oviposition by *R. pomonella* in almost 100% of observed cases.

In sum, the *R. pomonella*-*C. viridis* system is ideal for detailed investigation of parasite foraging behaviour in nature.

CHAPTER III

HOST DISCRIMINATION BY PHYTOPHAGOUS INSECTS: ECOLOGICAL CORRELATES

Introduction

Adults of many phytophagous insects choose food plants for their offspring. As pointed out by Prokopy (1981), it may often be in the female's interest to choose oviposition sites where offspring will not be restricted by competitors by food or living space. Thus, a number of insects have evolved the ability to assess resources on the basis of the presence of conspecifics, i.e., host discrimination, defined by salt (1934) as the ability to recognize and avoid laying eggs in hosts already occupied by conspecifics. Prokopy (1981) discusses twenty-six species of phytophagous insects that produce and detect spacing or epideictic pheromones (sensu Corbet 1971) that deter oviposition by conspecifics. In addition, some other phytophagous insects host discriminate by visually assessing the presence of conspecifics (e.g., Gilbert 1975; Rausher 1978; Shapiro 1981; Williams and Gilbert 1981). While these different insects represent a wide variety of lifeforms and biologies, they may share some common ecological features that confer greater genetic fitness upon individuals that discriminate against occupied hosts. In this chapter, I consider the permanence of the host plants that these insects infest.

Host plant discovery and exploitation by phytophagous insects is the product of interactions between several ecological and behavioural processes, including: (1) host plant distribution in space and time (e.g., Feeny 1976), (2) search dynamics of the insect (e.g., Roitberg *et al*. 1979), (3) vagility of the insect (e.g., Jones *et al*. 1980), (4) host defense (e.g., Berenbaum 1978) and host nutrients, including water (e.g., Scriber and Feeny 1979). Perennial plants that are discovered by insects that exploit and overwinter near them may often be reinfested the following year by the same insects or their offspring, as well as by other individuals that newly discover these plants (cf. Strong 1979). For example, I have observed *Rhagoletis pomonella* flies infesting the same hawthorn (*Crataegus* sp.) trees year after year. These readily available and predictable or permanent plants (in Feeny's (1976) and Rhoades and Cate's (1976) term 'apparent' plants) are potential hosts for large numbers of herbivore individuals, relative to the amount of resources available. This may impose nutritive, energetic, or space restrictions, as well as increase the chance of predation and or parasitism upon the insect inhabitants. This is particularly true for insects that tend to remain in the area of host discovery either because they are not highly vagile or do not engage in an obligatory dispersal phase. (For the purposes of this study I consider permanent plants to be those species whose longevity extends beyond that of two generations of their parasites).

In contrast to the situation described above, insect individuals that discover and exploit annual plants that are highly irregularly distributed in space and time may be the sole discoverers of individual hosts. Thus, the major problem facing these insects may be one of locating hosts rather than competing for exhaustible host plant nutrients and/or shelter.

I propose that phytophagous insects that parasitize (sensu Price 1977) the more permanent and readily available hosts are more likely to evolve host-discrimination systems than insects that attack annual, unpredictably distributed plants because the former are more likely to encounter and suffer from interactions with conspecifics. This may be particularly true of monophagous or oligophagous insects, especially those that exploit particular units of their permanent hosts, thereby increasing probability of intraspecific encounters. For example, oliphagous _R_. _pomonella_ larvae appear to engage in intraspecific competition within the fruit of their relatively permanent hawthorn hosts (Averill and Prokopy, unpub. data).

Methods

In Table 1, I list each of thirty-six species of insects known to discriminate against host plants infested with conspecifics. In addition, I list each insect's probable original or native host plant taxon and each plant's common lifeform i.e. woody perennial, herbaceous perennial, biennial, annual. Finally, I list the host plant range for each insect.

Results and Discussion

Results from Table 1 clearly show that most phytophagous insects known to host-discriminate are relatively oligophagous and are associated

Table 1 - Host-discriminating insects and their host plants.

INSECT	ORIGINAL (NATIVE) HOST(S)	GROWTH FORM	HOST RANGE
Azuki bean weevil *Callosobruchis chinensis*	Tropical pulse	W-HP	Grain legumes
Cowpea weevil *Callosobruchis maculatis*	Tropical pulse	W-HP	Grain legumes
Dry bean weevil *Acanthoscelides obtectus*	Tropical pulse	HP	Grain legumes
Dry bean weevil *Zabrotes subfasciatus*	Tropical pulse	HP	Grain legumes
European apple sawfly *Hoplocampa testudinea*	*Malus* spp.	WP	*Malus* spp.
Hylemya fly *Hylemya* sp.	*Polemonium* sp.	HP	*Polemonium* sp. *Ipomopsis* sp.
Ranunculus leaf mining fly[a] *Phytomyza ranunculi*	*Ranunculus* spp.	HP	*Ranunculus* spp.
Apple maggot fly *Rhagoletis pomonella*	*Crataegus* spp.	WP	Rosaceae
Walnut husk fly *Rhagoletis completa*	*Juglans* spp.	WP	*Juglans* spp.

Table 1 - continued

Black cherry fruit fly *Rhagoletis fausta*	*Prunus* spp.	WP	*Amygdalus* sp.
Eastern cherry fruit fly *Rhagoletis cingulata*	*Prunus* spp.	WP	*Prunus* spp.
Western cherry fruit fly *Rhagoletis indifferens*	*Prunus* spp.	WP	*Prunus* spp.
European cherry fruit fly *Rhagoletis cerasi*	*Prunus* spp.	WP	*Prunus* spp. *Loniceta* spp.
Blueberry maggot *Rhagoletis mendax*	*Vaccinium* spp.	WP	*Vaccinium* spp.
Dogwood berry fly *Rhagoletis cornivora*	*Cornus* spp.	WP	*Cornus* spp.
Dogwood berry fly *Rhagoletis tabellaria*	*Cornus* spp.	WP	*Cornus* spp. *Vaccinium* spp.
Rose hip fly *Rhagoletis basiola*	*Rosa* spp.	WP	*Rosa* spp.
Snowberry fly[b] *Rhagoletis zephyria*	*Symphoricarpos* spp.	WP	*Symphoricarpos* spp.
Carribean fruit fly *Anastrepha suspensa*	*Achras* spp.	WP	many different host families

Table 1 - continued

South American fruit fly[c] *Anastrepha fraterculus*	*Achras* spp.	WP	many different host families
Mediterranean fruit fly *Ceratitis capitata*	Tropical fruit trees	WP	many different host families
Paraceratitella fruit fly[d] *Paraceratitella eurycephala*	*Capparis* spp.	WP	*Capparis* spp.
Olive fly *Dacus oleae*	*Oleae* spp.	WP	*Oleae* spp.
Hadena moth *Hadena bicruris*	*Melandrum* spp.	WP	??
Pipevine swallowtail butterfly[e] *Battus philenor*	*Aristolochia* spp.	HP	*Aristolochia* spp.
Monarch butterfly *Danaus plexippus*	*Asclepius* spp.	A	*Asclepius* spp.
Heliconius butterfly[f] *Heliconius cydno*	*Passiflora* spp.	HP	*Passifloriaceae*
Cabbage butterfly *Pieris brassicae*	Perennial crucifer? (Shapiro 1981a)	HP	Crucifers
Sysymbrii pierid butterfly[g] *Pieris sisymbrii*	*Streptanthus* spp.	A	*Streptanthus* spp.

Table 1 - continued

Anthocaris pierid butterfly[h] *Anthocaris cardamines*	Crucifers	A	many different crucifers
European corn borer *Ostrinia nubialis*	??	??	many different host families
Corn ear worm *Heliothis zea*	??	??	many different host families
Cabbage looper *Trichoplusia ni*	??	??	many different host families
STORED PRODUCTS INFESTING INSECTS			
Flour beetle *Triboleum castaneum*	??	??	grains
Flour beetle *Triboleum confusum*	??	??	grains
Mediterranean flour moth *Ephestia kuehniella*	??	??	many different host families

A = Annual, HP = Herbaceous perennial, WP = Woody perennial

[a] Sugimoto 1980, [b] Averill and Prokopy 1982, [c] Prokopy *et al*. 1982, [d] Fitt 1981, [e] Rausher 1979, [f] Williams and Gilbert 1981, [g] Shapiro 1981, [h] Wicklund and Åhrberg 1978.

with perennial plants. I was unable to determine the original host plants of three polyphagous insects (*Heliothis zea*, *Trichoplusia ni* and *Ostrinia nubialis*) whose present host ranges include several annual plants.

The pierid exceptions are difficult to analyze for several reasons. First, the original hosts of some of these butterflies may have been relatively permanent plants (Shapiro 1981a) and the host assessment behaviour we presently observe may be the result of "phylogenetic inertia" (Shapiro 1981a). Second, because of their unique biochemical profile, crucifers may be relatively easy for their parasites to locate and exploit, compared to other ephemerals. Thus, individual crucifer plants may be discovered by many individuals of their highly co-evolved parasites (e.g., pierids). Such situations could lead to selection for development of host discrimination by the parasites to avoid overcrowding of exhaustible food resources. Price (pers. comm.) suggests similar ecological pressures may have selected for development of host discrimination in many entomophagous parasites that use highly sensitive kairomonal host-location systems to find their patchily distributed insect hosts.

Many of the species listed in Table 1 infest the flowers or fruit of their host plants. As I previously suggested, confinement of parasitism to limited parts of the host plant may increase levels of intraspecific competition, particularly if larvae are unable to migrate from crowded resources (e.g., dipteran larvae).

In addition to the 33 host-discriminating herbivores that feed on growing plants, at least three species of insects that infest stored products (e.g.,grains, fried fruits) refrain from ovipositing when the population density of conspecifics is high. I was unable to determine the original hosts of these insects, although both of the beetle species have been associated with stored products for hundreds of years (thousands of generations) (Evans 1975). Stored product shelters may be considered permanent hosts.

Although the data I present support my hypothesis of a relationship between host-discriminating insects and permanent host plants, several factors must be more closely examined before my argument may be applicable to the general case. First, while most host-discriminating phytophagous insects are associated with relatively permanent hosts, I do not know what proportion of non-discriminating parasites also associate with permanent hosts. Unfortunately, confirmation of non-discrimination by any given insect species is rare because such information is negative and rarely published. Also, as pointed out by van Lenteren _et_ _al_. (1978), field data may be a very poor indicator of host-discrimination ability. Second, I suggested that immature offspring of most host discriminators have limited mobility. However, in order to assign a relative value to mobility, one must know the relative distribution of resources that individuals move toward should the original resource site become unsuitable. Third, in addition to host permanence, and as previously discussed for the Pierid-Crucifer example, relative ease of host location must be considered. Thus Feeny's (1976) concept of 'bound to be found' or 'apparency' should take into consideration: (1) permanence, (2) density and distribution of conspecific hosts, (3) ability of insect to locate hosts, and (4) community structure of habitat within which hosts reside, including attractancy/ repellancy of neighbouring non-hosts (Atsatt and O'Dowd 1976). Finally, I showed that most host discriminators are largely oligophagous. It is essential that this feature be compared with feeding selectivity of non-discriminators. Published host records must be treated with caution however. As pointed out by Fox and Morrow (1981) and Wagner *et al*. (1981) field collected data on host ranges may be highly misleading.

Roitberg and Prokopy (unpub. MS) pointed to the potential dangers of anticipating ubiquitous presence of host-discrimination ability in insects living upon exhaustible resources. For example, from extensive studies I have conducted on the codling moth *Cydia pomonella*, adults and larvae, I have observed no evidence that either lifestage recognizes or avoids apple fruit occupied by conspecifics (unpub. data), even though at least two other parasites of apple, *R. pomonella* and *Hoplocampa testudinea* (Hymenoptera: Tenthredinidae), are known to host discriminate (Prokopy 1972, Roitberg and Prokopy, unpub. MS).

In conclusion, while a constellation of genetical, physiological and ecological factors may contribute to the evolution of resource assessment, host-discriminating insects appear to share several ecological features, including: (1) association with hosts that persist for several of the parasites' generations, (2) comparatively narrow host range, (3) limited mobility by parent and offspring, and (4) restricted sites of parasitization within individual hosts.

CHAPTER IV

INFLUENCE OF EXPERIENCE WITH OVIPOSITION DETERRING PHEROMONE ON HOST DISCRIMINATION ABILITY BY R. POMONELLA

Introduction

During the past 20 years, remarkable progress has been made in the identification of chemical components and receptor sites of pheromones of various insects. Yet, our understanding of physiological and ecological parameters which affect the response of individual insects to perhomones remains rather limited. In this chapter, I report that apple maggot fly females, Rhagoletis pomonella, requires experience with oviposition deterring perhomone (ODP) before they are able to discriminate between ODP-marked and unmarked host fruit. This appears to be the first conclusive evidence in an insect that pheromone recognition may depend upon prior contact with that pheromone.

Following egglaying in the fruit flesh, an R. pomonella female deposits ODP by dragging its ovipositor on the fruit surface (Prokopy 1972). One bout of dragging on a hawthorn (Crataegus sp.) fruit of about 5 mm diameter deters the same or other females from ovipositing in that fruit in the field, although the degree of deterrence is less in the laboratory. Prokopy (1972) suggested that employment of ODP is adaptive inasmuch as only a limited number of larvae can mature in a single fruit.

In our laboratory, I found that recently matured females deprived of host fruit until testing did not discriminate between ODP-marked and unmarked hosts. In contrast, females given access to ODP-marked host fruit 1 day before testing generally rejected ODP-marked fruit (Table 2, Expt. 1). To determine whether these results stemmed from a difference between females in oviposition deprivation or to a difference in prior contact with ODP, I conducted the following test.

I placed newly matured wild flies singly in cages and provided each fly with one of two treatments. In Treatment A, each fly was presented with and allowed to oviposit in one clean (no ODP), uninfested hawthorn fruit. Immediately after oviposition, the fly was transferred via a small triangular piece of clean filter paper to a clean uninfested apple, where it was allowed to deposit ODP. I directed the fly's course of dragging on this much larger fruit so that it never contacted its own pheromone trail with its pheromone receptors (tarsal D-hairs) (Prokopy and Spatchen 1977,Crnjar _et al_. 1978). I repeated this procedure twice more at 45 minute intervals on Day 1. On Day 2, I repeated the procedure twice more. Forty-five minutes after the second oviposition, I presented the fly with a five millimeter diameter hawthorn fruit marked with ODP from two dragging bouts by other females.

Treatment B flies were also allowed to oviposit in three hawthorn fruits and drag on three apples on Day 1. However, the second and third hawthorn fruits offered were marked with ODP from three prior (about 1 h earlier) dragging bouts. If the flies rejected the marked fruit, they were presented with clean fruit for oviposition. The Day 2 procedure was the same as for Treatment A flies.

Table 2 - Response of apple maggot flies to ODP-marked hawthorn fruit before and after experience with ODP

EXPERIMENT	TREATMENT	N	% REJECTION OF ODP-MARKED FRUIT*	N	% REJECTION OF CLEAN FRUIT FOLLOWING REJECTION OF AN ODP-MARKED FRUIT
1	No previous host or ODP experience	17	17.6 (p∠.001)	5	40.0 (N.S.)
	Previous fruit and ODP experience	20	60	14	14.3
2a	A (naive)	29	13.8 (p∠.001)	17	76.5 (p∠.001)
	B (experienced)	28	64.3	20	10.0
2b	A	24	41.6 (p∠.08)	17	41.2 (p∠.07)
	B	27	66.7	21	14.3
3	A	16	75.0 (N.S.)	23	47.8 (p∠.02)
	B	18	88.8	18	11.1
4	96 h ODP deprivation	16	62.5 (N.S.)	10	20.0 (N.S.)
	No ODP deprivation	16	56.3	9	22.2

*If a fly rejected the marked fruit, we presented it with a clean fruit. If the fly also rejected the clean fruit we disqualified it from this analysis.

Treatment B (experienced) flies generally rejected ODP-marked fruit and accepted clean ones. Treatment A (naive) flies readily accepted ODP-marked fruit (Table 2, 2a). In addition, significantly more treatment A than Treatment B flies rejected clean fruit presented them after their rejection of a marked fruit. This experiment was repeated, with similar though less dramatic results (Table 2, expt. 2b).

Prokopy (1981b) reported that barometric pressure may affect the level of activity and ODP discrimination ability of R. pomonella flies. In experiments 2a and 2b we found that more flies completed the experimental protocol on days with moderate or high barometric pressure (≥ 29.7 mbar). On other days, flies showed no interest in fruit and rarely oviposited. When we reexamined data for expt. 2b including only data from days in which we were able to test to completion at least four naive and four experienced flies, 71% (n = 14) of the naive flies accepted ODP-marked fruit compared with 40% (n=10) which accepted on days when we were unable to test four naive and four experienced flies.

To determine whether flies could obtain necessary pheromone experience by contacting their own ODP trail while dragging, I repeated the experimental protocol, but did not transfer the flies to apples for dragging. All flies contacted their own trail an average 4.4 times (per fruit) while dragging. In this case, Treatment A flies rejected ODP-marked fruit as readily as did Treatment B flies (Table 2, expt. 3).

In a final test, I withheld experienced flies from ODP for 96 hours (flies were allowed to oviposit and ODP drag, but not contact any ODP, three times on each of the four days) and found that they rejected ODP-marked fruit as readily as did recently experienced flies, thus demonstrating the retention of ability to recognize ODP for at least four days (Table 2, expt 4). Klomp et al. (1980) reported that Trichogramma embryophagum, a hymenopteran parasite of lepidopteran larvae, forgets and must relearn to discriminate between parasitized and non-parasitized hosts. However, they suggested that their results could also be explained by the increasing tendency of the wasps to oviposit with increasing time of deprivation from oviposition sites.

Alcock's (1979) definition of 'restricted learning' that is, 'an animal acquires a limited piece of information from the environment that changes the behaviour of the animal in a precise manner', can be applied to the ability to recognize ODP by apple maggot flies. Electrophysiological tests show that the ODP receptors on the tarsi fire the first time they contact ODP (Bowdan, Dethier and Prokopy, unpub. data). However, my results show that such a message is not translated into a rejection response in naive flies. This mechanism may provide flies with a means of reducing the cost of continually maintaining an unused information processing system, because flies may not encounter ODP-marked fruit in conditions of high fruit density, low fly population or when immature. However, once mature flies have oviposited in a single small hawthorn fruit (= native host fruit) they may gain, through tarsal contact with their own ODP trail, the pheromonal experience necessary to activate the system.

I cannot explain why naive *R. pomonella* flies reject clean fruit more often after encountering ODP than do experienced flies. However, van Lenteren (pers. comm.) found similar results with *Pseudeucoila bochei*, a hymenopteran parasite of *Drosophila* larvae.

I suggest that restricted learning of pheromone recognition may be more widespread than is believed. For example, Cammaerts-Tricot (1974) and LeMoli and Passetti (1978) suggested, but did not prove, that perception of pheromones by Myrmica and Formica ants, respectively, depends on experience, and Vinson *et al*. (1977) demonstrated associative learning of kairomonal ovipositional cues by *Bracon mellitor*, a parasitic wasp. Van Lenteren and Bakker (1975) first demonstrated that *P. bochei*, must "learn" to discriminate against parasitized hosts. Their results strongly suggest that the key component in the learning process is the marking pheromone deposited by *P. bochei* after oviposition. However, because the parasite marks its hosts internally, van Lenteren and Bakker were unable to demonstrate perhomonal contact. My study parallels their pioneering work and provides the first unequivocal evidence for pheromonal learning in insects.

CHAPTER V

INFLUENCE OF FRUIT DEPRIVATION ON THE RESPONSE OF *R. POMONELLA* FLIES TO OVIPOSITION-DETERRING-PHEROMONE MARKED FRUIT

Introduction

Records of parasitizations, obtained from field data, indicate that solitary parasites frequently superparasitize their hosts (van Lenteren *et al*. 1978). Van Lenteren (1981) lists several factors that may override female parasites' propensity to avoid oviposition in parasitized hosts, including:

(1) Female has not yet learned to discriminate (e.g., van Lenteren and Bakker 1975),

(2) Female's tendency to oviposit increases when she encounters only parasitized hosts (e.g., Salt 1934),

(3) Female lays a second egg within the period needed for some oviposition deterring factor to diffuse through the host (e.g., Rogers 1972b).

In the previous chapter, I showed that experience with oviposition deterring pheromone (ODP) is required before *R. pomonella* flies are able to host discriminate. Further, Prokopy (1972) showed that flies are not deterred from ovipositing in ODP-marked fruit if they are withheld from ovipositing for two days. However, there exists no information on changes in *R. pomonella* fly response to ODP-marked fruit when withheld from fruit for short periods of time, as may commonly occur in nature, among flies foraging for fruit in trees bearing a light crop. In this chapter, I attempt to quantify changes in fly acceptance of ODP-marked fruit in response to short-period fruit deprivation.

Materials and Methods

Methods of fly rearing are detailed in Chapter 6. All tests employed 15-day post-eclosion flies that had not previously oviposited. All tests were conducted over a three day period.

On Day 1, flies were presented with and permitted to oviposit in a single, uninfested, clean (no ODP) hawthorn fruit. Flies were permitted careful examination of the fruit following oviposition and ODP deposition to provide experience with ODP. I repeated this procedure twice more at 45 minute intervals.

On Day 2, I repeated the entire procedure of Day 1. Flies that failed to oviposit during any of the fruit presentations on either Day 1 or 2 were disqualified.

On Day 3, flies were presented and permitted oviposition in two clean fruit under the same protocol as Days 1 and 2. Following their second oviposition, flies were allowed to rest either 5, 10, 20, 40 or 80 minutes and then presented a hawthorn fruit marked with ODP from two dragging bouts by other females. Flies that rejected such fruit (i.e., left the fruit without attempting oviposition) were allowed to rest ca. one minute, then presented with a clean fruit. Flies that still rejected clean fruit were disqualified from the analysis.

Results

Results from this experiment show that R. pomonella flies display a greater tendency to oviposit in ODP-marked fruit as time since last oviposition increases (Fig. 1) ($p < 0.05$, Spearman's Rank Correlation).

Discussion

The physiological processes through which changes occur in acceptance/rejection thresholds for stimuli eliciting motor responses in insects are poorly understood, particularly for parasitic insects foraging for oviposition sites. My results suggest, in parallel with other studies on entomophagous parasites, that host acceptance spectrum increases over time if oviposition is prevented.

Most studies on changes in propensity for oviposition by deprived parasites differ from my study in that deprivation of healthy hosts is accomplished by either (1) withholding all hosts from parasites for long periods of time (i.e., days) (e.g., van Lenteren 1976) or (2) by only providing parasites with parasitized hosts (e.g., Salt 1934). Apparently, there exists only one published study involving measurement of short-term changes in behaviour of host-deprived parasites. Thus, Klomp et al. (1980) showed that Trichogramma embryophagum behaves in a manner similar to R. pomonella, in that females readily accept parasitized hosts after being deprived of any hosts for more than 100 minutes. Klomp et al. (1980) interpreted their results to mean that

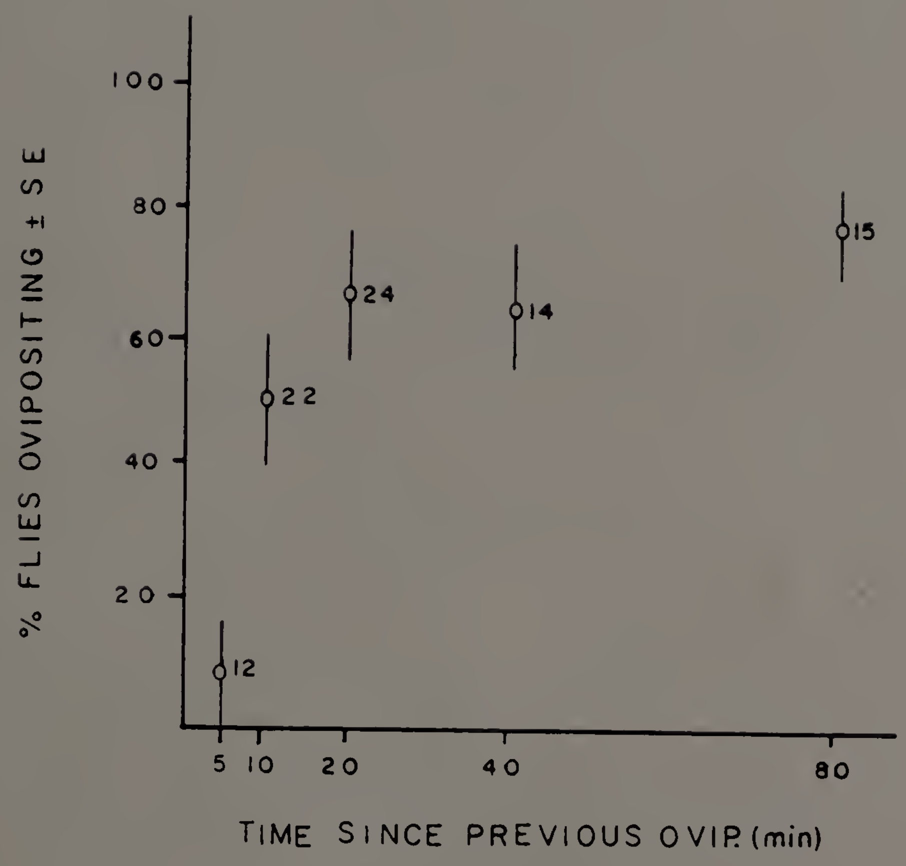
% FLIES OVIPOSITING ± SE
100
80
60
40
20
12
22
24
14
15
5
10
20
40
80
TIME SINCE PREVIOUS OVIP. (min)

Figure 1

T. embryophagum females forget how to host discriminate during host deprivation. Previously (Chapter 1), I showed that R. pomonella remembers how to discriminate for at least 96 hours. Thus, acceptance of parasitized hosts by short-term deprived flies must be due to changes in physiological state associated with host deprivation. Because Klomp et al. (1980) did not separate oviposition from host marking processes it is not possible to make a finer analysis of their data.

It is also not possible to ascertain from my data whether host deprived R. pomonella flies display a greater propensity to oviposit in ODP-marked fruit over time because they possess (1) a lower host stimulus acceptance threshold for fruit, or (2) an increased ODP-stimulus threshold for rejecting marked fruit. Parallel studies on changes in food acceptance by food-deprived insects are inconclusive. For example, Stadler and Hansen (1978) were unable to confirm whether changes in food discrimination ability of starved tobacco hornworm (Manduca sexta) larvae were due to (1) reduced responsiveness to feeding deterrents, (2) increased preference for feeding stimulants, or (3) both. Dethier (1976) discusses several analogous experiments where he obtained equally uninterpretable results with starved blowflies (Phromia sp.) offered different foodstuffs. Alcock (1979) defines "drive" as "the hypothetical physiological variable that in some way reflects the internal state and alters tendencies to employ certain behaviours." For example rats on high saline diet develop a "thirst drive" that is exemplified by (1) the amount of water they consume, (2) rate of water consumption, (3) tolerance to shock incurred when searching for water, and (4) the distance that is travelled to reach water (Alcock 1979). Whether or not we accept the premise that mature R. pomonella flies develop a "drive" for ovipositing, evidence from studies on other insects strongly suggests that deprived insects are generally more likely to respond to "positive stimuli", regardless of level, as deprivation time increases. For example, host deprived tsetse flies, Glossina morsitans, display increased response to moving objects (Brady 1972), and male deprived female field crickets, Gryllus sp., phonotactically respond to male calls 5 to 9 times more frequently than non-deprived females (Cade 1977). However, such effects are not universal. For example, host deprived leafhoppers, Oncopsis sp., die before laying any eggs if isolated on plants other than their native hosts (Claridge and Wilson 1977). Thus acceptability spectra varies between species, even under deprivation.

Finally, the relevance of these experiments to natural field events is not clear. My observations on flies foraging on trees either artificially laden or naturally bearing a low density of fruit suggest that flies may forage for comparatively long periods (e.g., 30 minutes or more) without discovering fruit before emigrating. These results may partially explain the presence of some superparasitisms in nature.

CHAPTER VI

INFLUENCE OF FRUIT QUALITY AND QUANTITY ON INTRA-TREE FORAGING BY *R. POMONELLA*

Introduction

Foraging behaviour of predatory and parasitic insects is currently receiving much attention from ecologists (e.g., Hassell and Southwood 1978). While some studies deal with natural history aspects of foraging (e.g., Klein and Horn 1976), others analyze foraging "tactics" and "strategies" from 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 by 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 and Bakker 1978). Van Lenteren and 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 and 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 their parasites. However, because of certain characteristics, plant predators and plant parasites (Price 1977) may be preferable. Herbaceous prey are sedentary and may be considerably easier to manipulate than mobile prey, whose escape strategies are often based on short term objectives, such as immediate avoidance of parasites.

I 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 my 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 chapter, I examine 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 et al. 1976) 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 their use may result in 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 abcission. Rotting fruit is usually less palatable to vertebrates (Janzen 1977), the prime dispersal agents of Crataegus (Stiles 1980).

In this study, I evaluate R. pomonella foraging behaviour in response to four different ecological situations likely to be encountered in nature:

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

Materials and Methods

I 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. I removed the puparia from the vermiculite and stored them for ca. nine months at $4^{o}C$. Following this, I placed them in a desiccator at $24^{o}C$, 90% R.H., 16L:8D until adults emerged (ca. four weeks). Adults were maintained in 25 x 25 x 25 cm Plexiglass-screen cages on a diet of sucrose, enzymatic yeast hydrolysate and water (Prokopy and Boller 1971).

Seventeen days after eclosion, I presented individual females (now mature) with an uninfested hawthorn (Crataegus viridis) 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- (Chapter 4). Each fly was then isolated in a smaller plastic-screen cage (modified 250 cc Dixie^{TM} 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^{TM} 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, I 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 3½ x 3½ x 2½ m nylon screen cage (mesh size 1.5 cm^2). 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 = ca. 1.5 millimeters diameter, and extending from ca. 0.5 - 2.0 meters above the ground). I trimmed the limbs to achieve a similar number (ca. 900) and distribution (one every five centimeters) of leaves per tree. All eight limbs per tree were number tagged.

I pre-tested and post-tested all flies. To pre-tests, we presented each cup-caged fly an uninfested hawthorn fruit. Those that oviposited were allowed to rest for 20 minutes and then were released in trees for testing. After completing the foraging test, flies were returned to their cup-cage, allowed to rest for five minutes and then were presented with an uninfested hawthorn fruit for the post-test. I discarded data for flies that failed to oviposit in the post-test, except those flies that oviposited eight times or more during the test. I 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, I assumed that they had used their complement of eggs for that day.

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

(i) Trees devoid of host fruit. In this two-part test, I compared foraging parameters of flies within empty trees (i.e., with no fruit) in situations where flies had not recently oviposited (Series A) vs. situations immediately following a single oviposition (Series B). In Series A, flies were released individually on trees (20 minutes 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, I removed the cup-cage from the tree. Flies were allowed to forage up to 120 minutes 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. I attached stems of freshly picked fruit of buckthorn (Rhamnus) which is not a known host of R. pomonella) to wires (0.2 millimeter diameter x 10 centimeter length). I assembled the fruit in clusters of 4 and hung one cluster from each of the 8 major tree limbs, in the upper third of the canopy (ca. 1.5 m above the ground). Single flies were released in trees, as in Expt. i, 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. i. 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 ($4^{o}C$) 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. I 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. ii. 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. I attached clean (no ODP), uninfested hawthorn fruit clusters to trees as in Expt. ii but at densities of 2, 4, 8, or 16 clusters. Single flies were released on trees as in Expt. i (ca. 0.5 meter 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. ii. In addition, I released some single flies within 20 centimeters of one of the fruit clusters in trees holding two clusters. I did this to increase my data base for intra and intercluster 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 Expt. iii and iv, I 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.

Results

(i) Trees devoid of host fruit - Series A flies, which had not recently oviposited had brief foraging persistence in these host trees (Table 3). Compared with Series A flies, Series B flies, which oviposited coincident with release into those trees, visited more leaves more often (15 vs 2, $p \angle 0.001$, Wilcoxon Matched Pairs test), visited more branches more often (15 vs 1, $p \angle 0.003$ Wilcoxon test), searched more tree area (61 vs 20%), and remained in trees longer (i.e. search allotment time) more often (16 vs 2, $p \angle 0.0001$ Wilcoxon test) (Table 3). In addition, search allotment times of flies in Series B covered a much broader range compared with those in Series A (Fig. 2). Figures 3 and 4 compares the search path of a typical fly in Series A vs one in Series B.

(ii) Trees harbouring non-host (*Rhamnus*) fruit - All flies migrated from the trees before laying any eggs in *Rhamnus* fruit (Table 4). The mean search allotment time for these flies was much shorter than for flies released in trees harbouring the same density of uninfested hawthorn

Table 3 - Comparison of *R. pomonella* behaviour in host tree before and after oviposition. All values are ± SE.

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 ± 0.5	9.8 ± 1.4	20 ± 3	3.8 ± 0.5
Series B	At release	9.9 ± 2.0	29.5 ± 5.1	61 ± 12	8.7 ± 1.2

Table 4 - Comparison of _R. pomonella_ behaviour on host trees harbouring different quality fruit. All values are ± SE.

Fruit Type	N	X No. Visits to Fruit Clusters/Fly	X No. Visits to Fruit/Fly	X Acceptance of Fruit Visited/Fly	X No. Ovipositions/Fly	X Total Time in Tree/Fly (min)
Hawthorn: uninfested, unmarked	14	11.4 ± 2.6	64.3 ± 15.5	0.11 ± 0.01	7.2 ± 1.4	64.3 ± 10.5
Hawthorn: 1X infested, 1X ODP marked	6	4.8 ± 2.3	23.5 ± 5.8	0.11 ± 0.03	2.7 ± 0.8	67.8 ± 10.9
Hawthorn: 2X infested, 2X ODP marked	13	3.6 ± 0.8	21.9 ± 4.6	0.03 ± 0.01	0.1 ± 0.01	21.8 ± 6.4
Rhamnus	20	1.5 ± 0.2	5.9 ± 1.2	0	0	15.7 ± 3.3

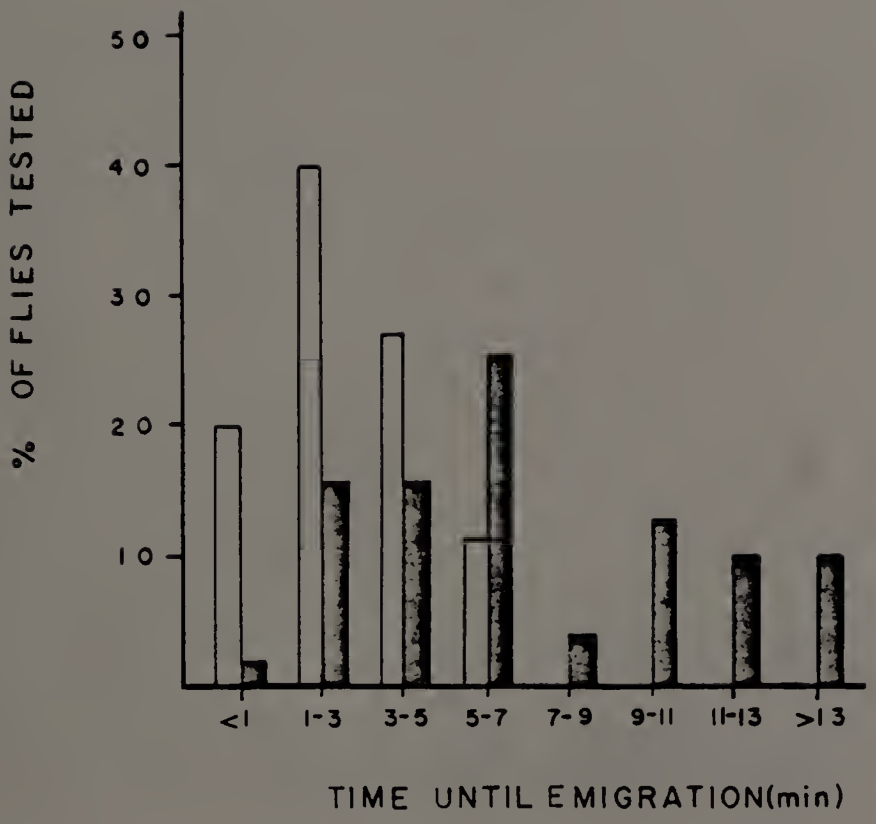
% OF FLIES TESTED
50
40
30
20
10
<1
1-3
3-5
5-7
7-9
9-11
11-13
>13
TIME UNTIL EMIGRATION(min)

Figure 2

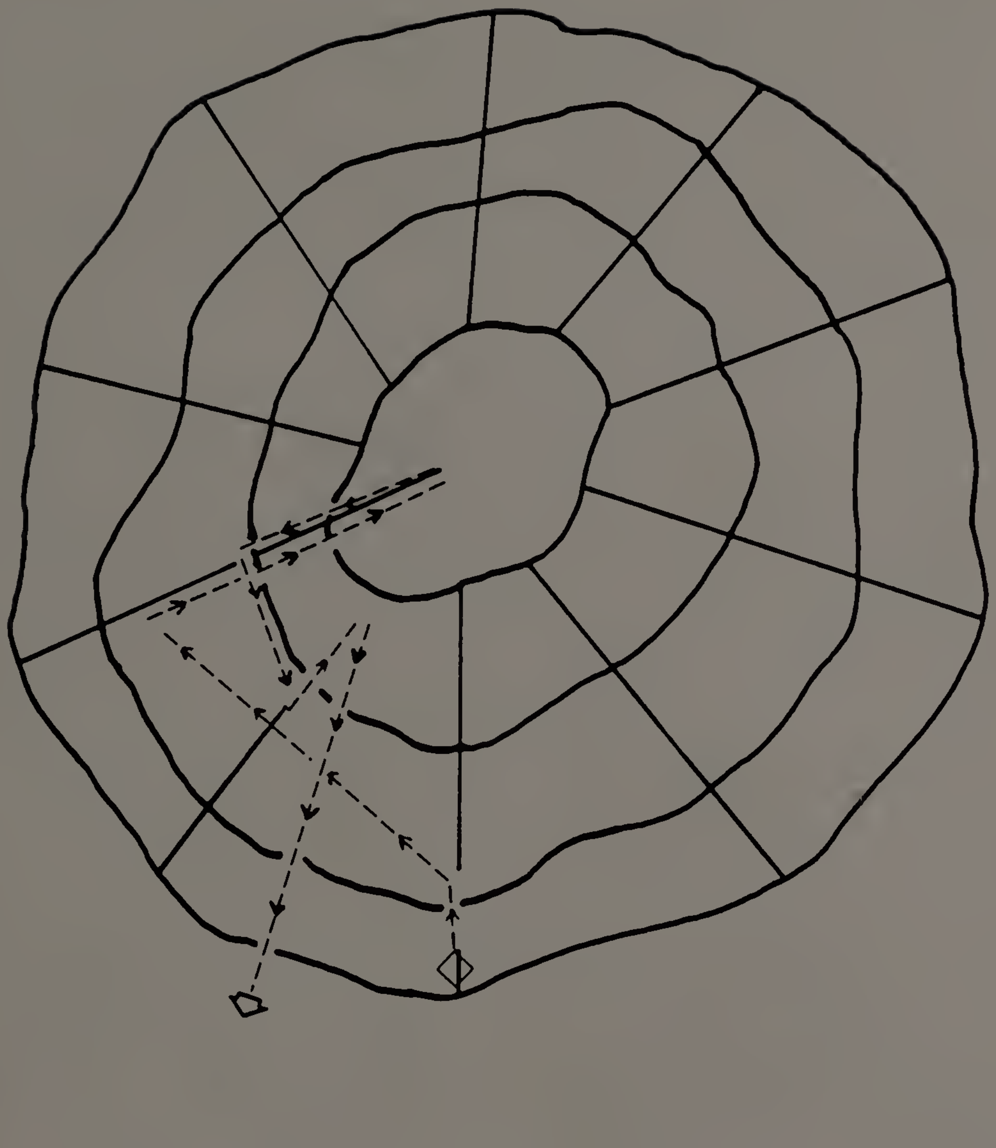

Figure 3

Figure 4

fruit (15.7 vs 64.3 minutes, $p < 0.0001$, Mann Whitney U test). Flies made fewer visits to Rhamnus clusters than to uninfested hawthorn clusters (1.5 vs 11.4 visits, $p < 0.01$, U test). They also visited fewer Rhamnus than hawthorn fruit (5.9 vs 64.3 visits, $p < 0.0001$, U test). Fig. 5 shows the path of a typical fly foraging in a tree harbouring Rhamnus fruit.

(iii) Trees harbouring infested (ODP-marked) vs 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 4). 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 minutes, 11 of 14 and 6 of 6 flies foraged for more than 30 minutes in trees with clean and once-marked fruit, respectively (2X marked vs clean, $p < 0.002$, G test; 2X marked vs 1X marked, $p < 0.004$, 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 minute 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 vs 1.9 fruit/minute, $p < 0.01$, U test). Overall, flies visited almost equal numbers of once and twice-marked fruit before emigrating from trees (Table 4). However, these means were much lower than for flies on trees with clean fruit (2X marked vs clean, $p < 0.03$, u test; 1X marked vs clean, $p < 0.01$, u test).

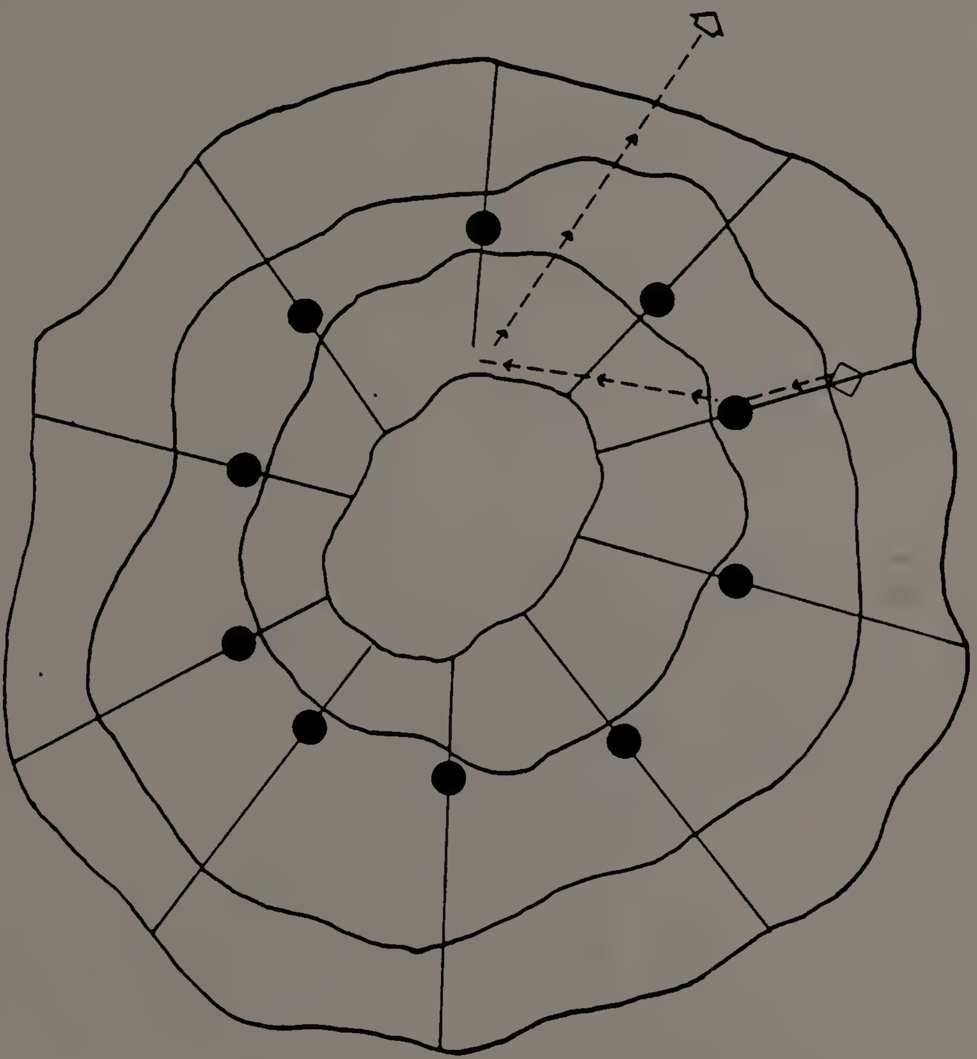

Figure 5

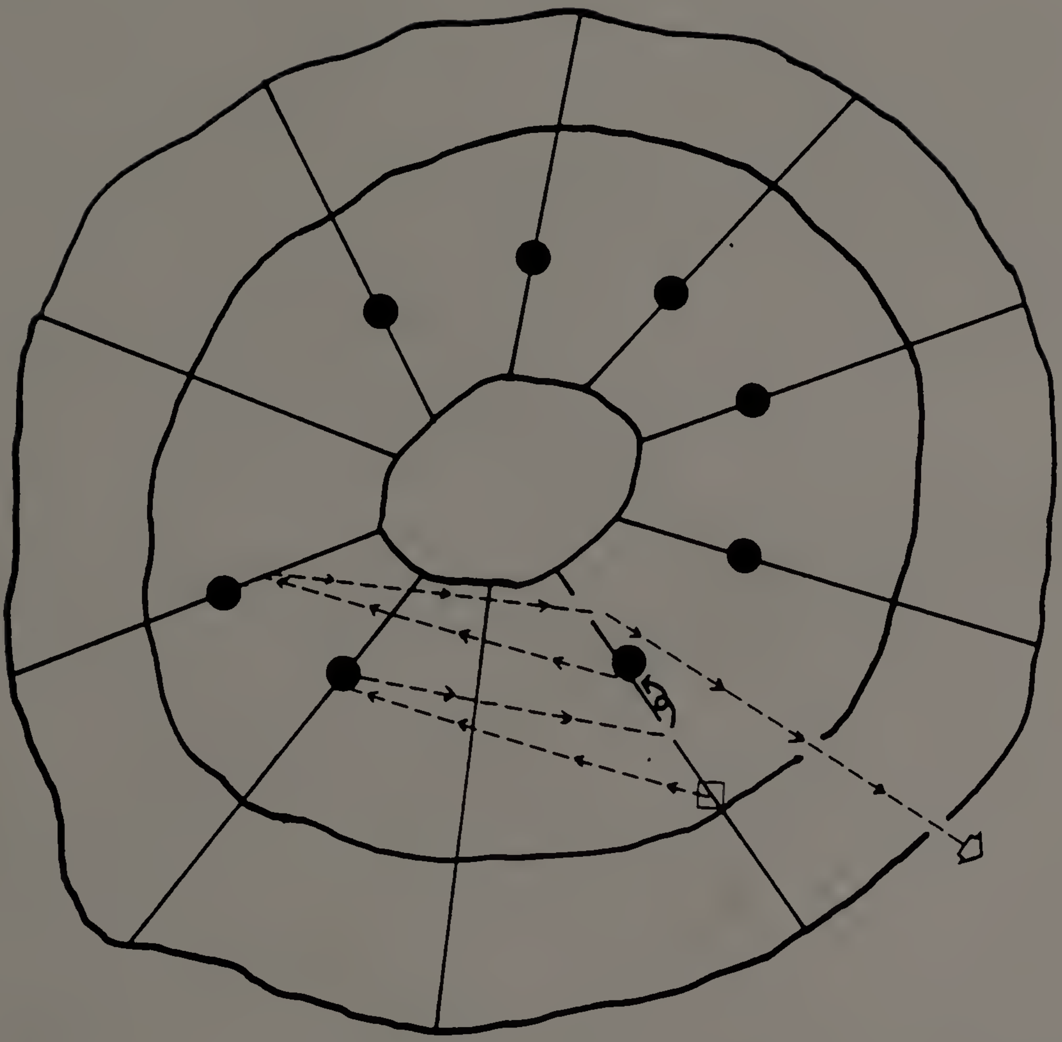

Figure 6a

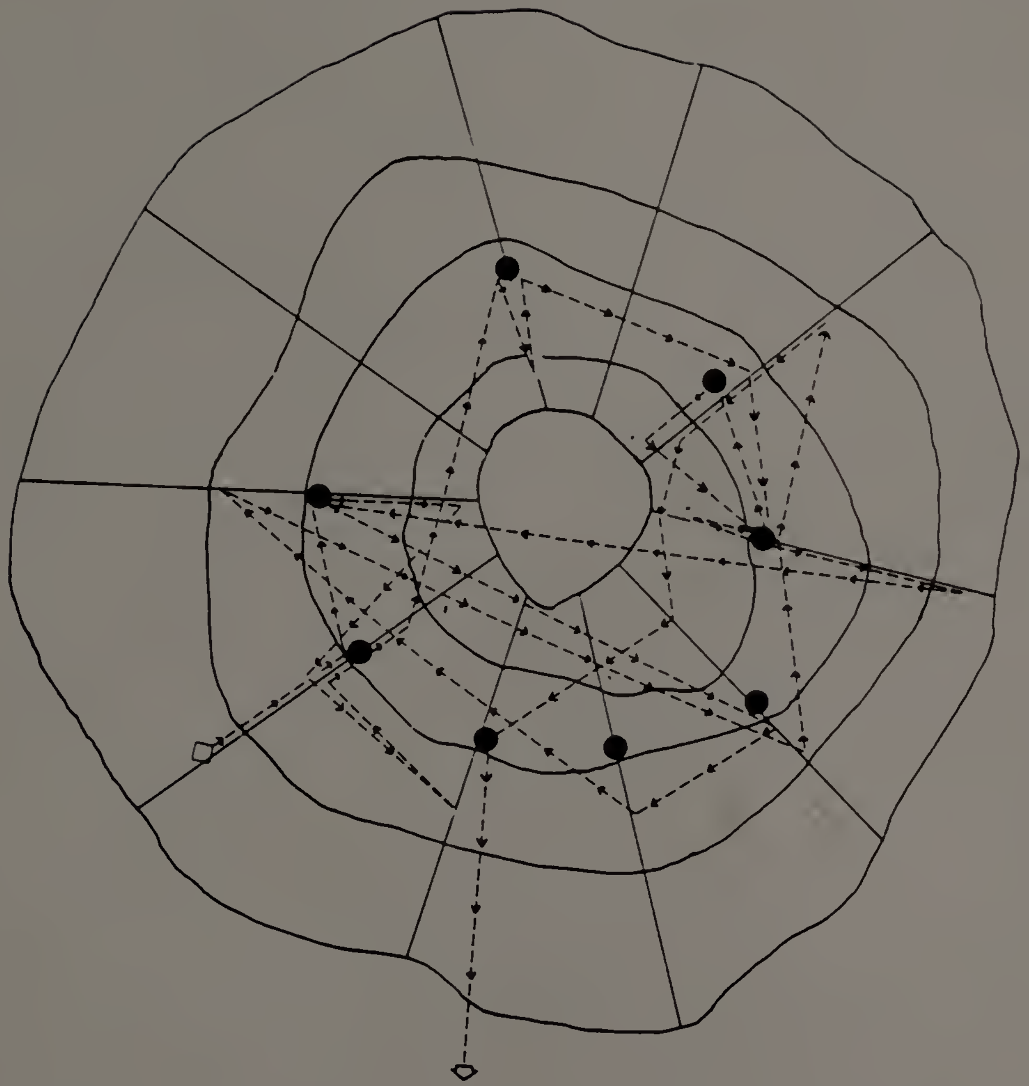

Figure 6b

Fig. 6 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 0.04, G test). Flies rejected once-marked fruit during 89% of visits to fruit (N = 141) versus 97% rejection of twice-marked fruit (N = 285) (p∠0.001), Dixon and Massey Proportions test) (rejection measured as: (1 - (no. ovipositions/no. visits to fruits) X 100)). Because flies may make frequent visits to the same fruit I also measured rejection as
(1 - (no. ovipositions/no. fruits visited) X 100)), and in this case flies rejected 90% of twice-marked (N = 89), 62% of once-marked (N = 204) (2X marked vs 1X marked, p∠0.001, Proportions test; 2X marked vs clean, p∠0.0001, Proportions test, 1X marked vs clean, N.S., Proportions test).

(iv) 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. 7) (Table 5). 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. i (density 2: 3.9 minutes ± 1.0 SE, N = 17; density 4: 3.9 minutes ± 1.1 SE, N = 22, Series A: 3.8 ± 0.5 SE, N = 18). The search allotment time was longer for unsuccessful searchers when the density was 8 clusters (9.9 minutes ± 3.1 SE, N = 7). However, 4 of the 7 flies in this category spent considerable time resting (i.e. not actively searching

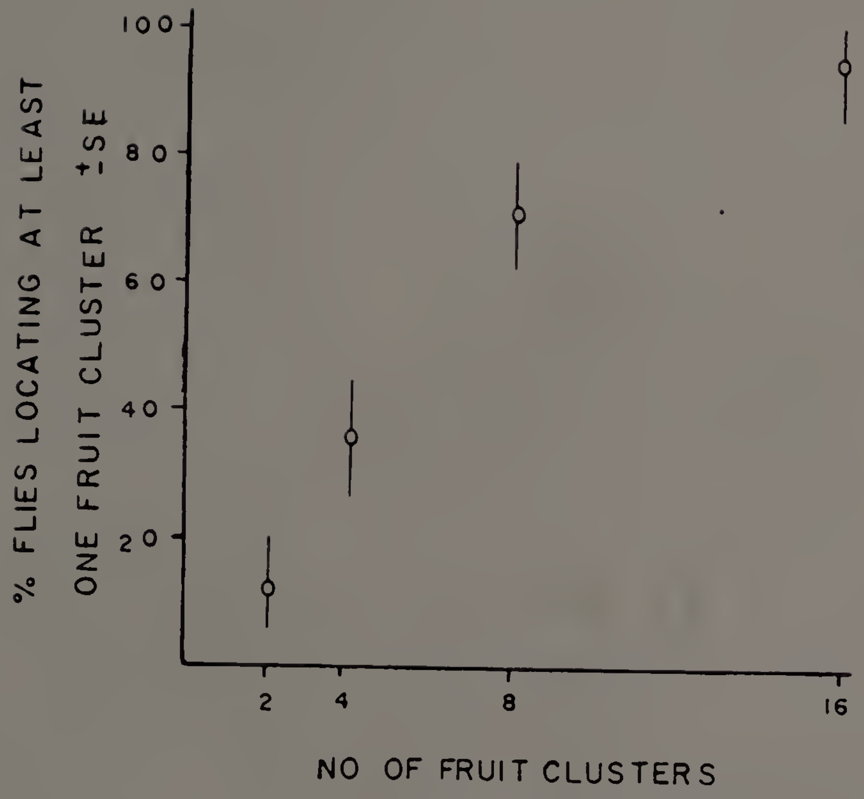
% FLIES LOCATING AT LEAST
ONE FRUIT CLUSTER ±SE
100
80
60
40
20
2
4
8
16
NO OF FRUIT CLUSTERS

Figure 7

Table 5 - Comparison of R. pomonella behaviour on host trees harbouring different densities of fruit clusters. All values are ± SE.

No. Clusters	N	% of Flies Locating Fruit	X No. Visits to Fruit Clusters/Fly	X No. Visits to Fruit/Fly	X Acceptance of Fruit Visited/Fly	X No. Ovi-positions/Fly	X Total Time in Tree/Fly (min)
2							
All Flies	26	15 ± 8	1.0 ± 0.3	8.0 ± 2.8	--	1.2 ± 0.4	10.6 ± 2.7
Finders Only	9	--	2.8 ± 0.6	23.2 ± 5.0	0.31 ± 0.05	3.6 ± 0.8	22.3 ± 4.8
4							
All Flies	34	35 ± 8	3.7 ± 1.2	22.7 ± 7.4	--	2.4 ± 0.7	24.1 ± 6.0
Finders Only	12	--	10.6 ± 2.3	64.3 ± 15.1	0.23 ± 0.02	6.8 ± 1.3	55.4 ± 10.2
8							
All Flies	22	68 ± 9	7.5 ± 2.1	42.9 ± 12.3	--	4.9 ± 1.2	46.1 ± 9.0
Finders Only	15	--	11.3 ± 2.6	65.9 ± 16.1	0.17 ± 0.02	7.3 ± 1.4	64.2 ± 10.5
16							
All Flies	13	92 ± 7	17.6 ± 3.1	120.9 ± 21.7	--	11.5 ± 2.0	71.5 ± 13.1
Finders Only	12	--	19.4 ± 2.8	133.0 ± 19.9	0.13 ± 0.01	12.6 ± 1.9	76.9 ± 13.2

for fruit). Only 1 of 13 flies did not locate fruit when the density was 16 clusters.

In most of the remaining analysis, I 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: $y = 1.15x - 1.28$, $p < 0.0001$; Finders Only: $y = 0.99x - 3.72$, $p < 0.005$) (Fig. 8). Differences in number of visits to clusters at different cluster densities were significant (All Flies: $F = 13.77$, $p < 0.0001$, 1-way ANOVA; Finders Only; $F = 5.8$, $p < 0.003$, 1-way ANOVA).

There was a positive relation between fruit cluster density and the number of visits flies made to individual fruits (All Flies: $y = 7.96x - 12.15$, $p < 0.001$; Finders Only: $y = 6.87x + 19.70$, $p < 0.0001$) (Fig. 9). Differences in number of visits to individual fruits at different cluster densities were significant (All Flies: $F = 16.13$, $p < 0.0001$, 1-way ANOVA; Finders Only: $F = 7.36$, $p < 0.0005$, 1-way ANOVA).

There was no statistically significant relation between density of fruit clusters and proportion of available fruit of 53% ± 7.4 SE ($N = 45$) 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 ($\overline{X} = 1.8$

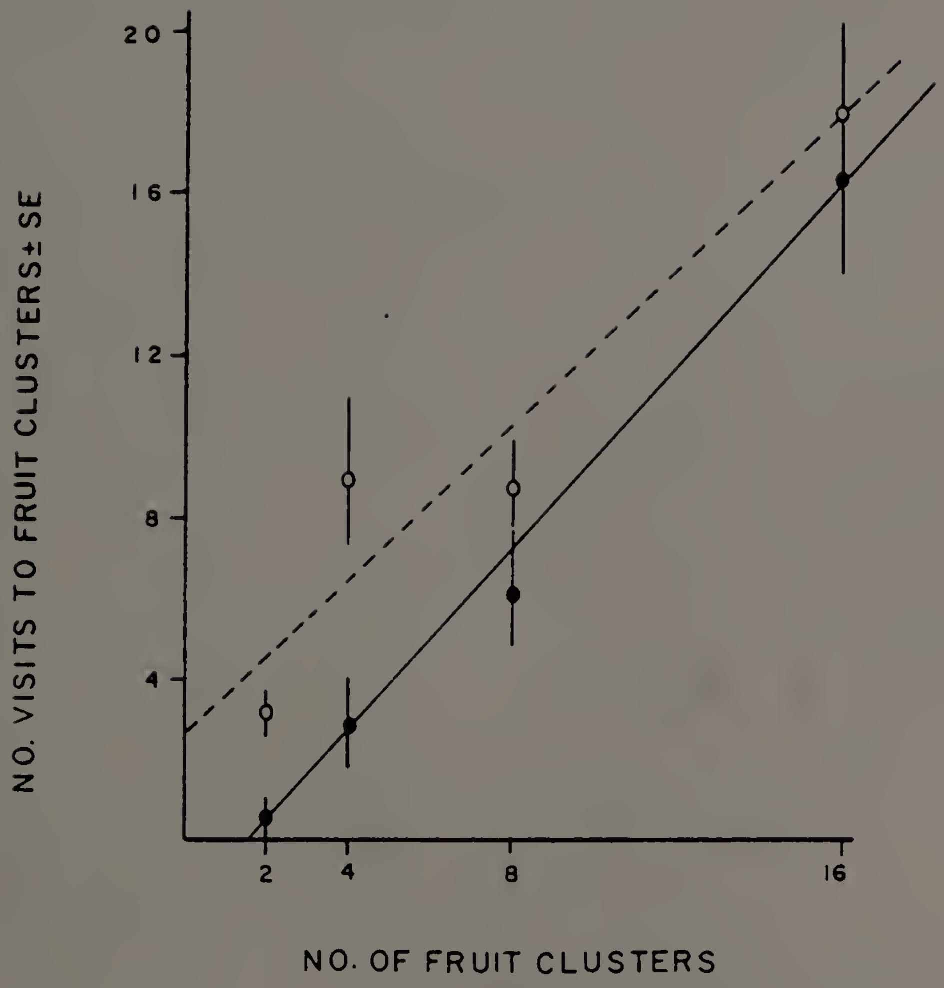
NO. VISITS TO FRUIT CLUSTERS± SE
20
16
12
8
4
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 8

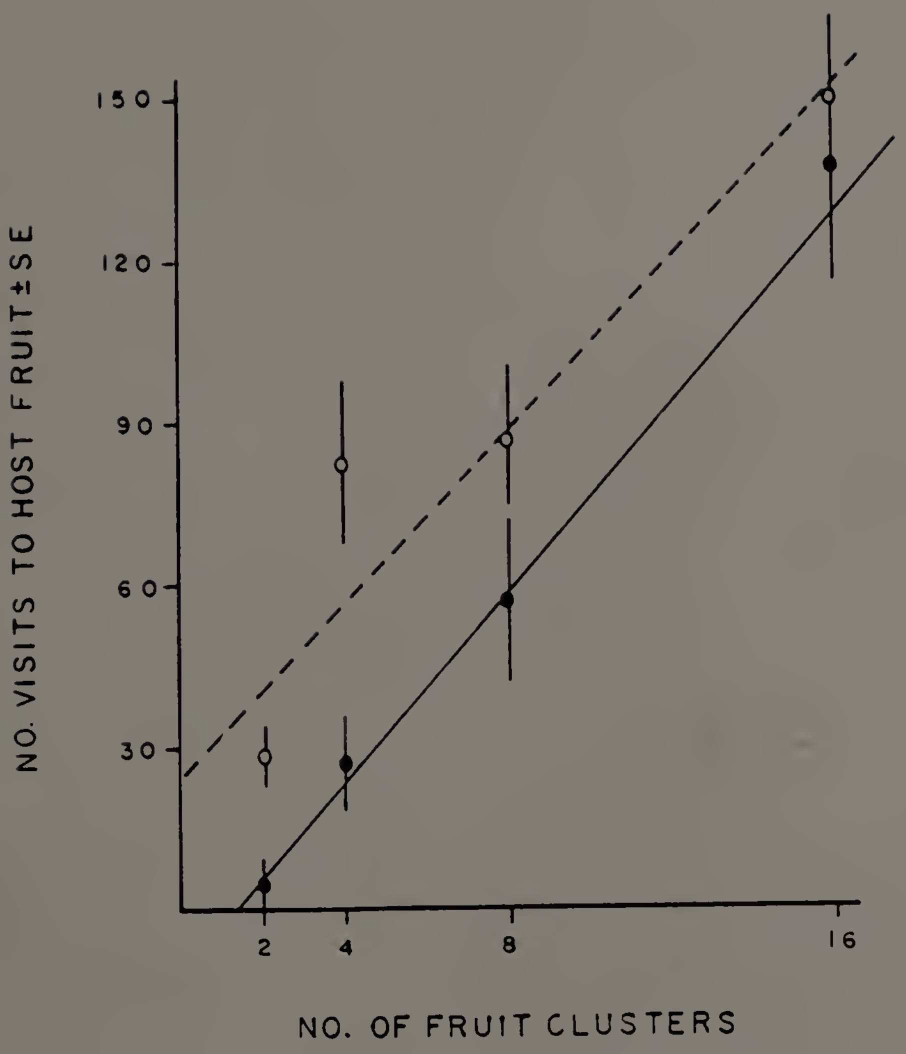
NO. VISITS TO HOST FRUIT ± SE
150
120
90
60
30
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 9

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. 10). While flies oviposited during 31% ± 4.8 SE (N = 91) of visits to fruit at the 2-cluster density, they oviposited during only 12.5% ± 1.1 SE (N = 905) of visits to fruit at the 16-cluster density ($p \angle 0.0001$, Proportions test). Flies rejected fruit during 97% ± 0.5 SE (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 ($p \angle 0.01$ and 0.0001, Proportions test) (Table 5).

Flies oviposited more often in trees with higher compared with lower densities of fruit clusters (ALL Flies, $p \angle 0.0001$; Finders Only, $p \angle 0.02$). 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. Fig. 11 shows the functional response of flies to fruit density. Among Finders Only, there was no relation between the rate of oviposition and density of fruit clusters. Fig. 12 shows the relation between the time flies spent in trees and the number of eggs laid ($y = 0.42x - 26.49$, $p \angle 0.0001$). 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. 13). Differences between these times at the different cluster densities were significant

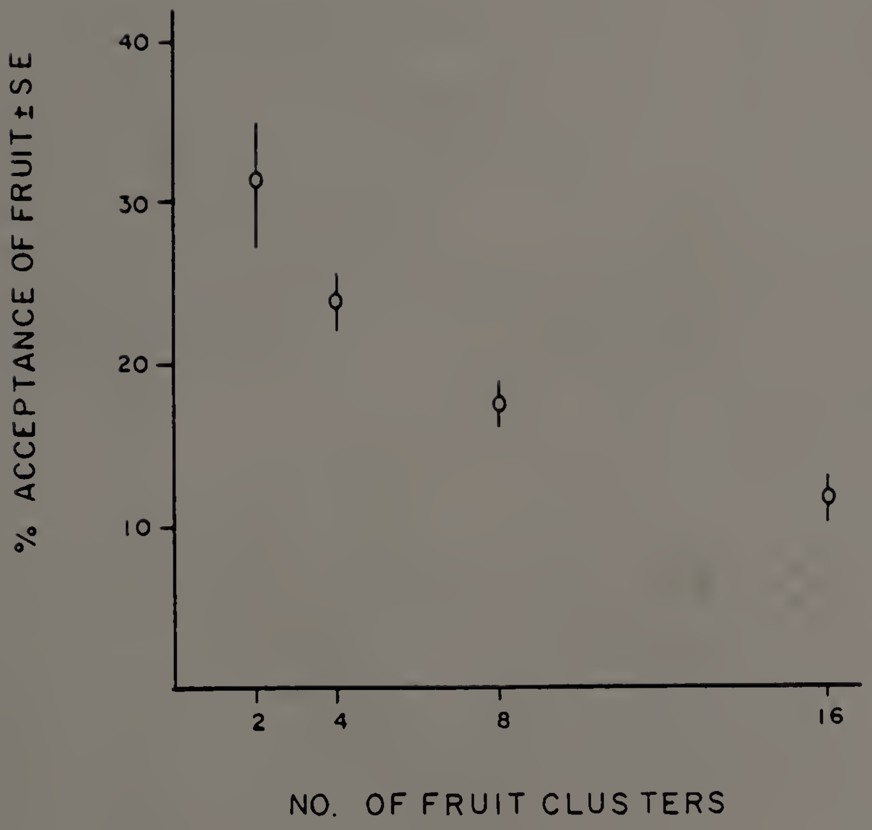

Figure 10

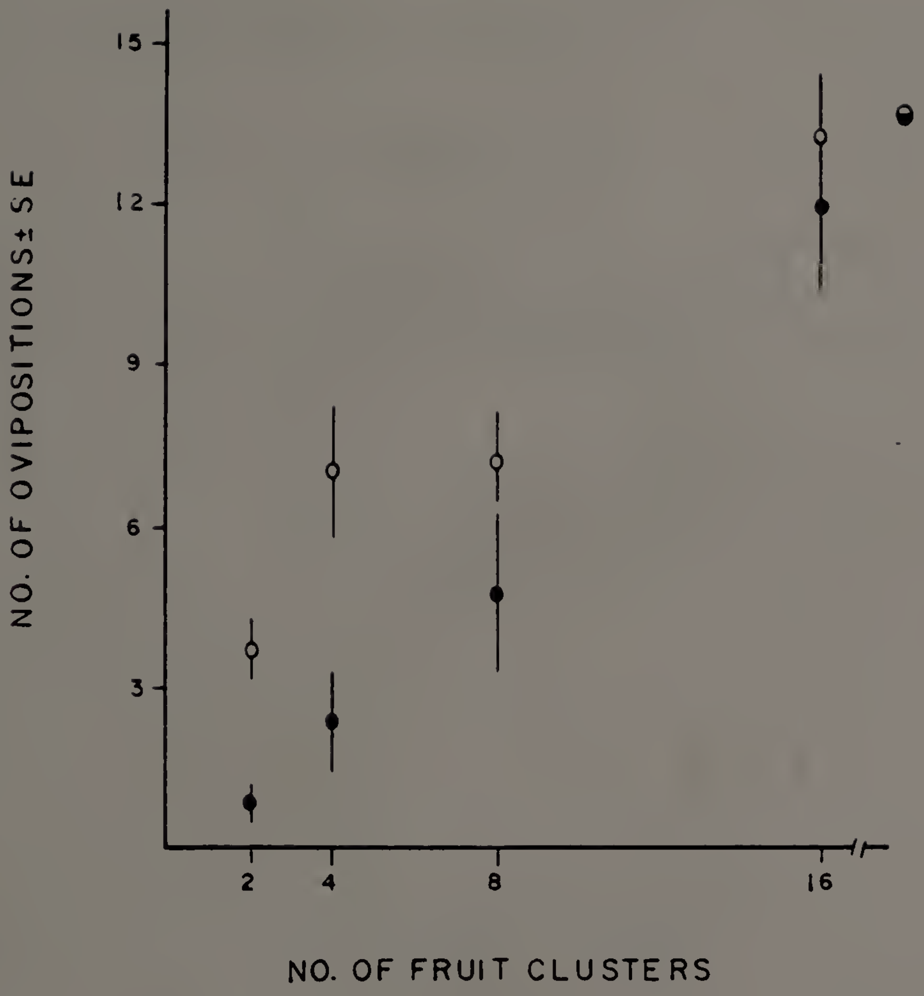

Figure 11

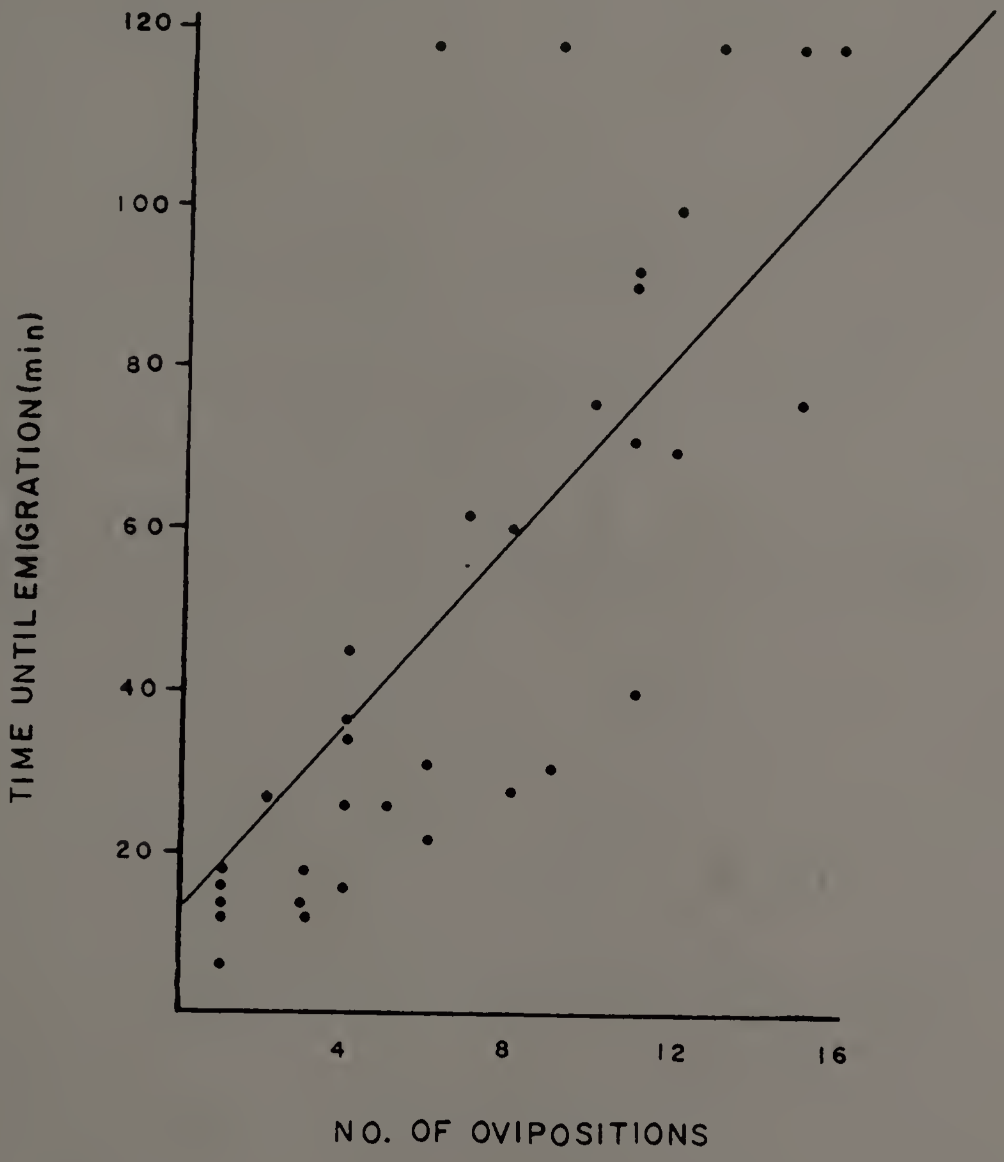
120
100
80
60
40
20
TIME UNTIL EMIGRATION(min)
4
8
12
16
NO. OF OVIPOSITIONS

Figure 12

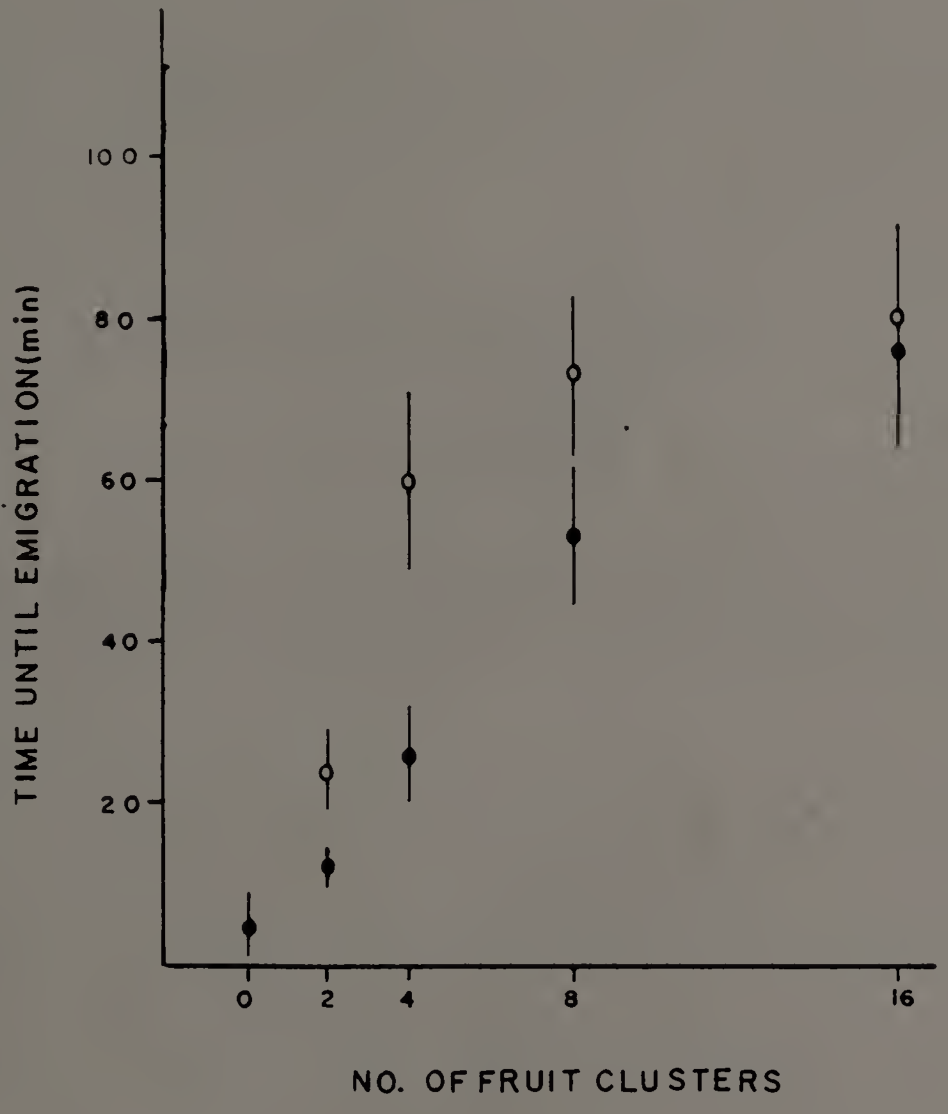
TIME UNTIL EMIGRATION(min)
100
80
60
40
20
0
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 13

(All Flies: $F = 10.8$, $p \angle 0.0001$, 1-way ANOVA; Finders Only: $F = 4.3$, $p \angle 0.02$, 1-way ANOVA). Finders Only stayed longer in trees than All Flies at densities 2, 4 and 8 clusters (2 clusters, $p \angle 0.002$; 4 clusters, $p \angle 0.002$; 8 clusters, $p \angle 0.08$; 16 clusters, no difference; t-tests).

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. 14) ($y = -0.126x - 3.70$, $p \angle 0.001$). Differences between GUT's at the different densities were significant ($F = 5.17$, $p \angle 0.005$). Similarly, flies gave up on trees sooner after their last cluster visit as cluster density increased (Fig. 15) ($y = -0.09x - 2.74$, $p \angle 0.01$). Differences between GUT's were significant ($F = 4.24$, $p \angle 0.02$, 1-way ANOVA).

Finally, flies remained longer on clusters during their initial visit than on successive visits (189 vs 50 sec, $X^2 = 130.5$, $p \angle 0.0001$). 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 vs 24 sec; $X^2 = 98.7$, $p \angle 0.0001$).

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 contribute to the functional response of *R. pomonella* to prey density.

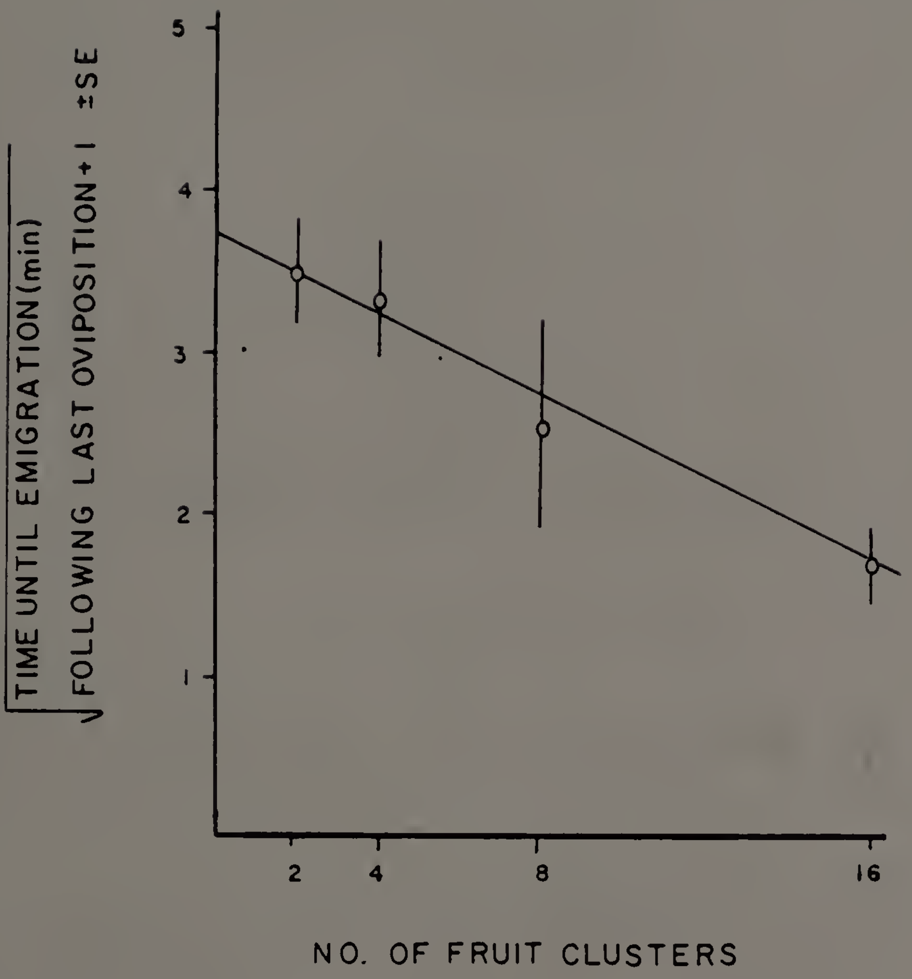
√(TIME UNTIL EMIGRATION (min) FOLLOWING LAST OVIPOSITION + 1) ±SE
5
4
3
2
1
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 14

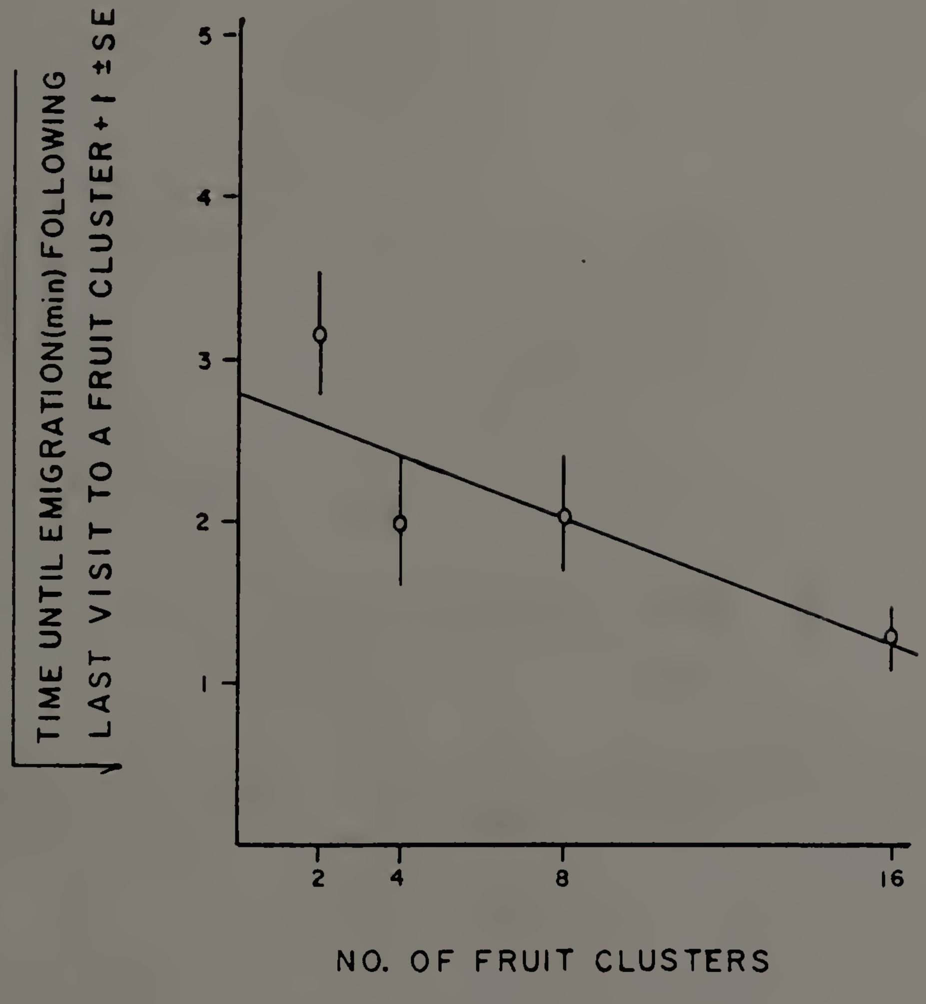
TIME UNTIL EMIGRATION(min) FOLLOWING LAST VISIT TO A FRUIT CLUSTER + 1 ±SE
5
4
3
2
1
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 15

First, *R. pomonella* increases allotment of search effort, within trees, after a single host fruit has been encountered and exploited (Table 3). Similar responses have been demonstrated for other parasites (e.g., *Pseudeucoila bochei*, van Lenteren and Bakker 1978) and have been defined as success-motivated or area restricted 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 (ca. 4 min), the same search allotment time as shown by females in trees without any fruit (Fig. 16).

Second, *R. pomonella* flies give up on and emigrate from trees after encountering only a few non-host fruit (Table 4). Such "decisions" are adaptive in that encounters with a non-host fruit indicates all fruit in that tree will be non-host (unsuitable). I do not know if flies can distinguish between leaves of host and non-host plants. In addition, I have no information about the effect of encounters with low quality (e.g., low moisture content) fruit on the allotment 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

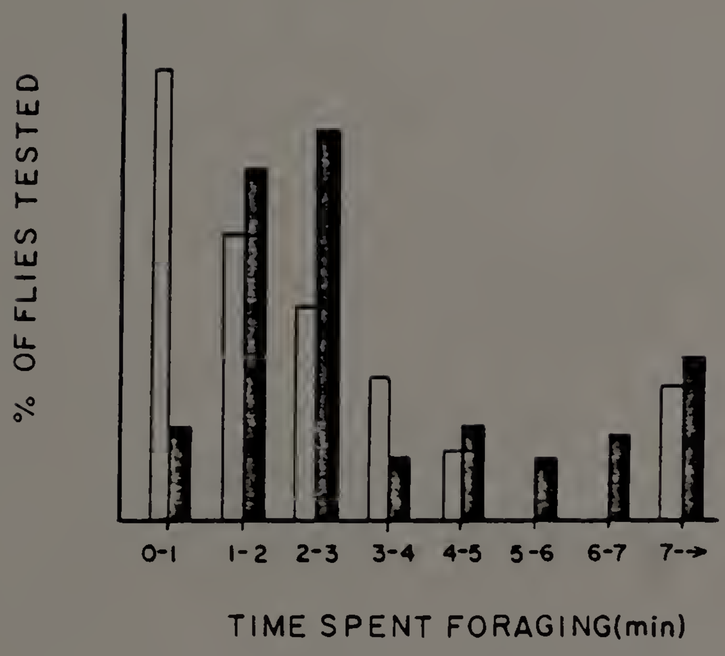

Figure 16

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 and Mukerji (1963) showed that R. pomonella ovipositions are evenly distributed among multiple infested apples within individual trees (ca. 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 versus 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 analagous to foraging theory predictions for food seeking animals that only high ranking prey items be accepted when their density is high (e.g., Mac Arthur and 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 and 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. I 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 appear 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 ($y = 0.014x - 0.49$, $4 = 0.44$, $p \angle 0.001$) (Fig. 17). At high cluster density, flies often visually located and then flew directly from one fruit cluster to another. 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) probability of locating and alighting on an already visited host is greater (68% at 2 clusters vs 54% at 16 clusters).

R. pomonella displays a Type 3 functional response to host fruit density (Fig. 11). The Type 3 curve is produced by an accelerating increase in the number of prey captured (or parasitized) as a

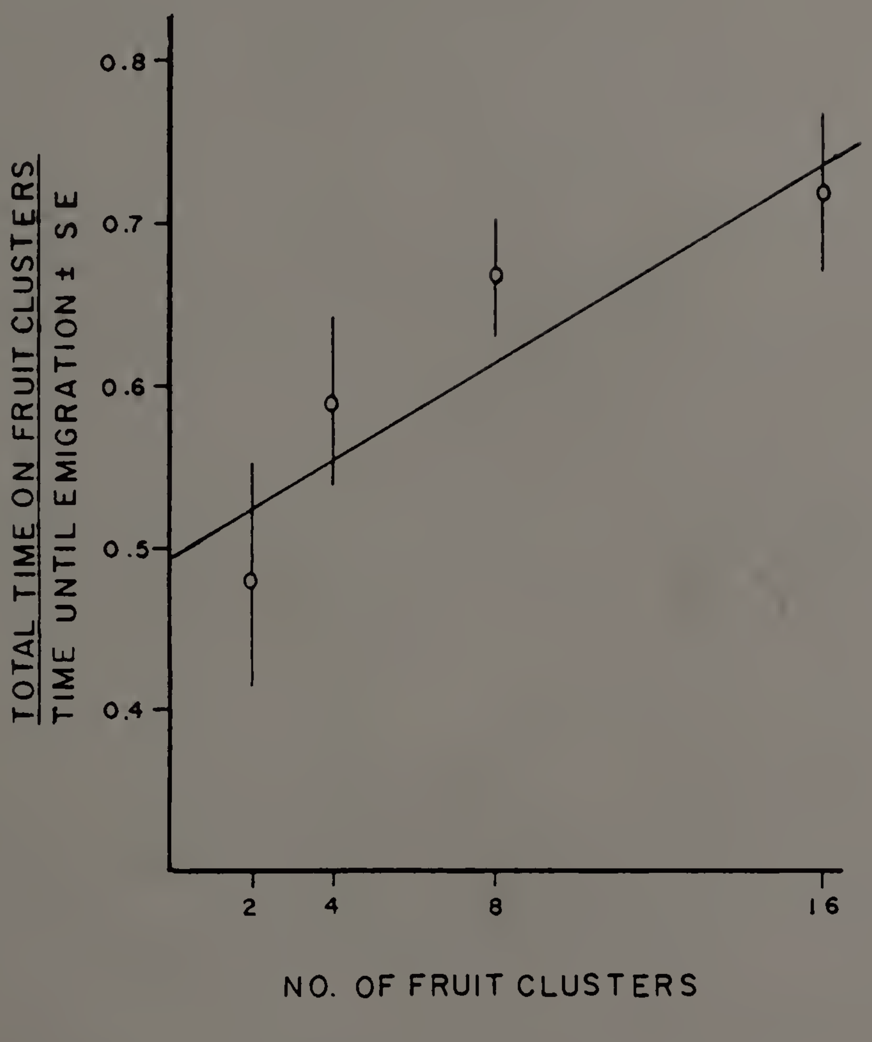
TOTAL TIME ON FRUIT CLUSTERS
TIME UNTIL EMIGRATION ± S E
0.8
0.7
0.6
0.5
0.4
2
4
8
16
NO. OF FRUIT CLUSTERS

Figure 17

function of prey density. Similar Type 3 responses have been reported for few other insects (e.g., P. bochei, van Lenteren and Bakker 1976; 1978; Notonecta glauca, Hassell et al. 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. My 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. 13).

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 to 9.6 min), although there was a trend toward shorter time until emigration at higher fruit density (Fig. 14 and 15). 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 and Oaten 1975) - Forager leaves patch after capture rate falls below some fixed value.

(5) Variable threshold rate (Parker and 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) list 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 minutes 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 my results in the varying cluster density experiments, I 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). My 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, the distance to alternate foraging sites (i.e. other trees) influences the search time allotment of R. pomonella on host trees (Chapter 7). Further, the sequence in which infested versus uninfested fruits are encountered influences search effort parameters of flies on trees with low fruit density (Chapter 8). 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 appraoches. This is probably because economic benefits may derive from emphasizing foraging success in the case of the entomophages, and foraging failure in the frugivores. I 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.

CHAPTER VII

INFLUENCE OF INTER-TREE DISTANCE ON THE INTRA-TREE FORAGING BEHAVIOUR OF *R. POMONELLA*

Introduction

The foraging behaviour of insects is currently receiving much attention from both behaviourists and ecologists (see Hassell and Southwood 1978). Of particular interest is the means through which insects "decide" to remain in or emigrate from resource patches. Several mechanisms have been proposed through which emigration decisions are made. However most of them may be too simple to explain the complex behaviour of insects foraging in nature. Many of the experimental studies from which the various hypotheses are derived are conducted in simple laboratory systems where potentially important naturally occurring stimuli are eliminated or ignored (cf. Labeyrie 1978).

Fruit parasites are excellent candidates for foraging studies. Several features render them amenable to studying foraging behaviour in nature:

(1) Their herbaceous prey are sedentary and may be considerably easier to manipulate than mobile prey.

(2) Prey density, and more importantly, distribution (Prokopy *et al*. 1982) are easily measured.

(3) Patch boundaries are discrete and quantifiable (Bond 1980).

(4) For insects that oviposit in their fruit hosts, successful

foraging for oviposition sites may be more closely related to genetic fitness than is the success of animals foraging for food.

In the previous chapter, I showed that allocation of search effort by R. pomonella flies within host trees is influenced by a constellation of factors, including: (1) density of host fruit, (2) number of encounters with high quality, non-parasitized fruit, (3) encounters with high quality parasitized fruit, (4) encounters with low quality fruit. In this chapter, I consider the influence of presence of and distance to alternate foraging sites (i.e., other trees) on the within-tree behaviour of individual R. pomonella flies searching for host fruit. Based on the contemporary foraging theory prediction that efficient foragers will alter their search behaviour in response to travel costs, I predicted that flies would emigrate sooner from host trees when alternate foraging sites were nearby (and therefore easier to move to) than when farther away.

Materials and Methods

Methods of fly rearing and pre-test conditioning are described in Chapter 5. All tests employed 17-day, mature, oviposition deterring-pheromone-experienced flies (Chapter 4).

A typical R. pomonella fly searches for host fruit in the following manner. After arrival on a host tree, the fly hops from leaf to leaf, primarily to adjacent and nearby higher leaves and occasionally to nearby limbs at the same height. A fly that arrives at the upper region of a tree limb and does not discover fruit either makes spiralling flights to lower parts of the same limb or to other nearby limbs, or flies from the tree. Occasionally, a fly will move to more distant limbs, often after encountering previously parasitized fruit. Upon locating and assessing a suitable host fruit (Prokopy 1977), an R. pomonella fly normally deposits a single egg under the fruit skin and then marks the fruit surface with a pheromonal substance which deters further oviposition in that fruit by that fly or conspecifics (Prokopy 1972). A fly that is unsuccessful at locating either any fruit, or any fruit not already parasitized and marked with oviposition deterring pheromone, eventually emigrates from the tree in a rather straight-line type of flight, although this may be preceded by several looping flights away from and then back to the tree.

I tested my prediction of differential within-tree search effort as a factor of distance to alternate foraging sites by measuring search effort of individual R. pomonella flies foraging for oviposition sites (host fruit) within small (ca. 2 meter tall) host trees enclosed within a large (ca. 8 meters diameter X 2.5 meter high) nylon mesh cage, under three different conditions:

(1) When the host tree was surrounded by four other non-fruiting host trees positioned in the four cardinal directions at a distance of 1.6 meter each.

(2) When the host tree was surrounded by four other non-fruiting host trees positioned in the four cardinal directions at a distance of 3.2 meters each.

(3) When the host tree was not surrounded by any other trees.

I measured search effort of each fly two different ways: (1) time spent actively foraging. Foraging flies often cease moving and remain motionless for periods of a few seconds to several minutes. I subtracted these passive periods from the total foraging times; (2) number of leaves visited. The latter is a highly sensitive measure of search effort (Chapter 6). I tested individual flies in two types of experiments for each of the three inter-tree-distance conditions:

i. Trees devoid of fruit - I presented flies, maintained in laboratory cages, with single Crataegus viridis fruit attached to rigid wires. As soon as the fly began ovipositing in the fruit, I placed it and the fruit on one branch of the host tree, which was devoid of other fruit. Two seconds after the fly moved to a leaf following oviposition, I removed the fruit and wire from the tree. The fly was allowed to forage until either (1) 60 minutes elapsed (including passive time), (2) the fly emigrated to one of the surrounding trees, or (3) the fly emigrated to the cage wall. Emigration was determined by direct observation of fly movements.

ii. Trees with one fruit cluster - This experiment was the same as Expt. i except that here I released flies singly onto a 4-fruit cluster which we hung from the host tree. Flies were allowed to leave and revisit the fruit cluster ad libitum. Trials were concluded as in Expt. i.

All of the trials, in both Expt. i and ii, were run between 1100 and 1500 EDT on sunny days. Temperatures ranged between 28 and 35^{o}C. I never ran the same type of trial twice in succession. Thus, over the course of the experiments, flies within each trial type experienced a range of times of day and temperatures.

Results

Results from Expt. i and ii (Table 1) showed a positive correlation between search effort by flies, measured as time spent actively foraging or number of leaf visits, and inter-tree flight distance. Correlations were highly statistically significant ($p \angle 0.008$; Kendall's Tau) for all fly search effort measurements except for the time flies spent foraging after their last visit to a fruit cluster in Expt. ii ($p \angle 0.06$; Kendall's Tau). Differences in number of leaf visits by flies among the different treatment groups within each experiment were significantly different, while differences in time until emigration between the different treatment groups in Expt. ii were not (Kruskal-Wallis Analysis of Variance) (Table 1). In addition, the proportion of flies that foraged for the full 60 minutes increased with increasing distance to neighbouring trees (1.6 meters = 0%, 3.2 meters = 7%, no trees = 33%, Expt. i; 1.6 meters = 14%, 3.2 meters = 46%, no trees = 54%, Expt. ii).

Sixteen of 22 flies that emigrated from trees surrounded by other trees at a distance of 1.6 meters flew to one of these neighbouring trees, while only 1 of 14 flies flew to neighbouring trees at a distance of 3.2 meters (Expt. i and ii combined). The other 19 flies flew to the cage wall.

Discussion

Utilization of and emigration from resource patches by foraging animals are often complex processes and are likely to be influenced by many factors (van Alphen 1980). In Chapter 6, I identified several intra-tree factors that influence *R. pomonella* flies foraging for oviposition sites in nature. The present study clearly shows that *R. pomonella* intra-tree search behaviour is also strongly influenced by the presence of and istance to neighbouring trees.

My results demonstrate that *R. pomonella* flies invest less search effort within trees when alternate foraging sites are close than when farther away. Zimmerman (1981) showed that bees visited fewer flowers per plant as interplant distance decreased, and Cowie (1977) demonstrated that great tits moved between artificial trees harbouring food resources more frequently when travel costs between trees was decreased. These two studies were conducted on animals searching for food. The present study appears to be the first of this type conducted on an animal searching for resources directly related to reproductive success.

One prediction from optimal foraging theory states that as the cost of moving between patches increases, foraging organisms should spend more time within each patch (see Pyke *et al*. 1977). In a qualitative sense, the present study supports this prediction. However, quantitatively my experiments fall short of demonstrating that *R. pomonella* flies behave optimally, for several reasons:

(1) My experimental design did not allow flies to sample from different trees (patches). Optimal emigration rates are derived from

"knowledge" of the value of other resource patches (e.g., Parker and Stuart 1976).

(2) At present, I do not know the relative energetic costs of intra and inter-tree movements by _R_. _pomonella_.

(3) It is difficult to compare rewards from optimal utilization of resource patches (i.e., oviposition success) with energy costs.

(4) Many of the flies were unable to locate trees at a distance of more than 2 meters. This cost may well exceed benefits of giving up on a tree harbouring comparatively few of difficult-to-locate host fruit.

Based on preliminary flight mill studies (unpub. data) and observations in nature, _R_. _pomonella_ flies require ca. 2 seconds to fly to trees at a distance of 1.6 meters. By comparison, flies spent an average of 16 minutes foraging for fruit before giving up on empty trees surrounded by trees at that distance. Thus, giving up time differed from inter-tree travel time by a factor of several hundred. Some of the above factors may explain these large differences. In addition, one further feature of _R_. _pomonella_ inter-tree flight behaviour may be important. Moericke _et al_. (1975) showed that _Rhagoletis_ flies alight on a variety of objects which provide a tree-shape sillouette and a tree hue reflection. Even though fruit odour plays a role in orientation to host trees (Prokopy _et al_. 1973), Moericke _et al_. (1975) concluded that flies are probably not able to judge the species of a neighbouring tree solely by its physical characteristics. Hence, fly emigration from a tree of known host fruit quality and quantity to one of unknown quality or quantity may impose further risks.

It is somewhat surprising that flies did not move directly to trees at a distance of 3.2 meters, as direct flights to trees 1.6 meters away were frequent. Several explanations are possible:

(1) Flies do not perceive trees at a distance of more than two meters. This is unlikely, because flies foraged shorter lengths of time when surrounded by trees at a distance of 3.2 meters than when not surrounded by any trees.

(2) Flies are unable to make straight line flights to trees two meters or more distant.

(3) Some unique feature of the cage wall (e.g., glare from sun) may have interfered with the flies' perceptual abilities.

(4) Flies chose a random flight direction after leaving the central tree. Because the closer trees had a larger angle of incidence. they were more likely to be intercepted. This is unlikely because we have observed flies, while foraging in the central tree, to turn, face a surrounding tree 1.6 meters distant and then fly directly to that tree.

The present study calls into question evaluation search effort of animals within resource patches unless inter-patch distance is considered. Employment, in foraging studies, of inter-patch distances comparable to those which the experimental animal encounters in its natural habitat should prove valuable to our understanding of intra and inter-patch search dynamics.

Table 6 - Comparison of within-tree search effort by *R. pomonella* flies when surrounded by other trees at varying distances.

SEARCH EFFORT PARAMETER	DISTANCE TO SURROUNDING TREES 1.6 m	3.2 m	No Other Trees Present	p*
Experiment i				
N	16	14	15	
Giving Up Time (min)	16.4± 2.2 SE	22.1± 3.4 SE	32.0± 5.3 SE	∠0.01
# Leaves Visited	59.3± 11.5 SE	89.3± 19.6 SE	103.4± 15.9 SE	∠0.01
Experiment ii				
N	14	11	13	
Giving Up Time (min) (after last oviposition)	23.0± 3.2 SE	26.5± 3.2 SE	39.0± 5.4 SE	∠0.08
# Leaves Visited (after last oviposition)	64.2± 14.5 SE	98.5± 13.7 SE	113.0± 16.9 SE	∠0.04
Giving Up Time (min) (after last visit to a fruit)	18.7± 2.5 SE	21.4± 3.6 SE	31.9± 4.2 SE	∠0.07
# Leaves Visited (after last visit to a fruit)	55.7± 10.8 SE	85.2± 15.5 SE	105.6± 17.3 SE	∠0.05

*Kruskal-Wallis Analysis of Variance

CHAPTER VIII

INFLUENCE OF SEQUENCE OF VISIT TO PARASITIZED VS. UNPARASITIZED HOSTS ON THE INTRA-TREE SEARCH BEHAVIOUR OF *R. POMONELLA* FLIES

Introduction

The means by which parasites allocate search energy within resource patches is a topic of current interest to ecologists. Hubbard and Cook (1978) suggested, though they proposed no mechanisms, how *Nemeritis canescens* might 'decide' to remain in or emigrate from host-containing patches on the basis of optimization techniques. Waage (1979) proposed a simple mechanism in which *N. canescens* displays a continuously waning arrestment response to host-derived chemicals and leaves a host patch when this response drops below some threshold. However, if a host is encountered and parasitized, then the arrestment response rises sharply. Further, Waage showed that it is the timing of parasitizations and not the number that determines the timing of emigration. Morrison and Lewis (1981) recently suggested that *Trichogramma pretiosum* giving up times on host-containing patches are determined by ratio of encounters between parasitized and unparasitized hosts. The latter two studies are important contributions to our knowledge of parasite search behaviour in that they evaluate the response of foragers to pheromonal and kairomonal cues. However, neither study and apparently no other published study, considers the sequence in which these stimuli are perceived. In this chapter, I examine the intra-tree search behaviour of individual *R.*

pomonella flies following encounters with different sequences of infested, oviposition-deterring-pheromone marked fruit and uninfested, unmarked host fruit.

Materials and Methods

Methods of fly rearing and pre-test conditioning are described in Chapter 6. All tests employed 17-day, mature, ODP-experienced flies.

I compared the search activity of flies in trees devoid of fruit under three different conditions:

(1) Following presentation of five consecutive infested, ODP-marked *C. viridis* fruits.

(2) Following presentation of and oviposition in one uninfested, unmarked fruit, followed by presentation of five consecutive infested, ODP-marked fruit.

(3) Following presentation of five consecutive ODP-marked fruit followed by presentation of and oviposition in one uninfested unmarked fruit.

I employed the following protocol:

Single flies were released in trees, allowed to forage for 30 seconds and then presented with a single *C. viridis* fruit attached to a rigid wire. Each fly was permitted careful exploration of the fruit surface. Flies that rejected marked fruit were allowed to fly to a nearby leaf and were presented with the next fruit in the sequence, 20 seconds later. Flies presented with clean fruit were permitted oviposition in and ODP marking on those fruit. These flies were also provided a 20 second rest on a leaf following their oviposition bout. Following presentation of the final fruit in the series, flies were allowed to forage until (1) 30 minutes elapsed or (2) flies emigrated to the cage wall. Flies that oviposited in marked fruit were eliminated from the tests.

All of the tests were conducted within cages described in Chapter 6, between 1100 and 1530 EDT. I never ran the same type of test twice in succession and each fly was tested only once. The ODP-marked fruits were prepared two hours prior to testing by hanging single fruits in laboratory cages with laboratory maintained, wild flies and were removed from the cage after receiving two eggs and ODP from two dragging bouts.

Results

Results from the experimental trials showed that the sequence in which flies encountered marked and unmarked host fruit influenced subsequent search behaviour, measured as time spent actively foraging or number of leaf and limb visits (Table 1). Differences between the different treatment groups were statistically significantly different (Kruskal-Wallis Analysis of Variance).

Flies spent significantly less time examining, before rejecting, ODP-marked fruit on successive visits to such fruit. Differences in time spent on the first visit versus the succeeding four visits were highly significantly different (Table 9). For statistical analysis I combined fruit search time data from flies in Treatments 1 (five consecutive marked fruit) and 3 (five consecutive marked fruit then one clean fruit). My rationale for combining these data was that flies, in each of these two treatments, faced the same protocol during their first five fruit encounters (i.e., with marked fruit).

Discussion

Several factors have been shown to influence search effort by parasitic insects, including: (1) ratio of encounters among parasitized vs. unparasitized hosts (Morrison and Lewis 1981), and (2) timing of oviposition in unparasitized hosts (Waage 1979). Results of this study suggest the sequence in which parasitized and unparasitized hosts are encountered may strongly influence timing of emigration of *R. pomonella* flies from host-containing patches.

My results indicate *R. pomonella* possesses a memory of the quality of previous hosts visited. Flies allotted more search effort in trees following presentation of one unmarked and five ODP-marked fruit than after presentation of five consecutive marked fruit. How this 'memory' functions is unknown. However, visits to marked fruit appeared to result in an increased 'nervous' appearance of flies and increased frequency of flights between rather than within limbs. By contrast, visits to and oviposition in clean fruit appeared to reduce the nervous appearance of flies and increased their within tree search effort allotment. Thus, my results suggest that *R. pomonella* search behaviour possesses elements displayed by both *N. canescens* (Waage 1979) and *T. pretiosum* (Morrison and Lewis 1981).

Weseloh (1980) showed that *Apanteles melanoscelus* females

Table 7 - Comparison of within-tree search effort by _R_. _pomonella_ flies after presentation with different sequences of ODP-marked and unmarked fruit.

SEARCH EFFORT PARAMETER	TREATMENT SEQUENCE			p*
	5 Marked Fruit	1 Clean + 5 Marked Fruit	5 Marked + 1 Clean Fruit	
N	10	12	9	
Giving Up Time (min)	5.5 + 2.0 SE	10.3 + 2.3 SE	16.4 + 2.6 SE	0.01
# Leaves Visited	19.8 + 9.1 SE	38.5 + 7.3 SE	66.2 + 11.5 SE	0.02
# Limbs Visited	6.1 + 2.2 SE	15.2 + 3.6 SE	32.9 + 8.9 SE	0.006

*Kruskall-Wallis Analysis of Variance

Table 8 - Comparison of search time of *R. pomonella* on consecutive visits to ODP-marked fruit.

TREATMENT	COMPARISON	TIME SPENT SEARCHING FRUIT Longer	 Shorter	X^2	P
5 Marked fruit (5 plus 0)	1st visit vs. all other visits	29	5	40.3	∠0.0001
5 marked then 1 clean fruit (5 plus 1)	"	32	2		
1 clean then 5 marked fruit (1 plus 5)	"	36	8	16.6	∠0.0001
5 plus 0	1st visit vs. 2nd visit	8	2	7.6	∠0.006
5 plus 1	"	8	1		
1 plus 5	"	9	1	4.9	∠0.03
5 plus 0	2nd visit vs. 3rd visit	8	1	4.5	∠0.04
5 plus 1	"	6	3		

All other comparisons not statistically significantly different habituated to host derived chemicals after constant exposure to them. My results with R. pomonella suggest that flies became more sensitive to ODP as the number of exposures to ODP increased. Flies displayed increased 'nervous' behaviour and spent less time searching fruit on successive visits to ODP-marked fruit. However, it is difficult to compare the responses of these two insects because: (1) A. melanoscelus received constant stimulation and R. pomonella received intermittant stimulation and (2) A. melanoscelus was stimulated by a contact 'arrestant' pheromone, while R. pomonella was stimulated by a contact 'dispersal' pheromone. Nonetheless, I observed no apparent habituation by R. pomonella to ODP. Further, Bowdan (unpub. data) showed no electrophysiologically detectable sensory adaptation by R. pomonella flies over more than 10 minutes continuous exposure to ODP.

In conclusion, results of this experiment suggest that the sequence in which parasites encounter parasitized and unparasitized hosts should be added to van Alphen's (1980) list of factors that influence search effort allocation by parasitic insects within host-containing patches.

Conclusions

Foraging in nature involves complex interactions at different spatial and temporal levels (Gass 1978). Because of these complexities it is often difficult to perform experiments in nature that provide definitive results. Most often, alternate hypotheses cannot be excluded.

I examined the Rhagoletis pomonella-Crataegus viridis system as a model for parasitic insects. I found that R. pomonella flies behave in a manner similar to that described for entomophagous parasites. However, a major advantage of working with R. pomonella was the relative ease with which it could be studied in nature. For example, I quantified the functional response of R. pomonella flies to host fruit density. This appears to be one of the first functional response studies conducted on an insect in nature, and lends support to van Lenteren and Bakker's (1976, 1978) theories on parasite foraging behaviour, which were derived from laboratory studies on Pseudeucoila bochei, an entomophagous parasite.

The most important feature impressed upon me during the tenure of this study was the importance of habitat structure in influencing foraging success or failure. Physical characteristics of host trees, e.g., density and distribution of leaves and limbs, dramatically affected the success with which flies located fruit clusters. Thus, results of the studies reported herein question the value of any foraging study conducted in simple, unnatural environments. A reasonable aim of foraging theoreticians should be to include as much detail of environmental parameters as possible while still retaining the structure within which answerable questions can be framed.

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APPENDIX 1

PRELIMINARY SIMULATION MODEL OF *R. POMONELLA* INTRA-TREE FORAGING BEHAVIOUR

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Preliminary Simulation Model of Foraging Behaviour of *R. pomonella* Flies *Within* a Host Tree.

Here we report our first attempt to simulate the foraging behaviour of *R. pomonella* flies for hawthorn fruits in a host tree. The model is constructed from behavioural information already accumulated on *R. pomonella* in preliminary studies (Roitberg *et al.*, unpub. data). In these studies, flies were released singly and observed for up to 2 hr each in a small host tree enclosed in a screen cage in the field.

In one series of experiments flies were permitted to forage in trees without fruit before and immediately following an oviposition.

In another series, flies were again permitted to forage in trees without fruit, but after being exposed to a series of five ODP marked fruits either immediately before or after an oviposition in an unmarked fruit.

The model incorporates information on the movement of flies in the tree, the amount of time spent foraging in the tree before dispersing, and the probability of accepting a clean or ODP marked fruit as a function of time since the most recent oviposition. The model incorporates several simple assumptions about the behavioural rules that govern the time spent foraging until dispersal from the tree. The validity of the model is checked against another series of experiments conducted in the same way, where single flies were released in host trees harbouring either two, four, eight or sixteen clusters of four fruits each.

1. *Simulation of the Host Tree*.

The host tree is represented in the model by a three dimensional matrix of numbers. Each (X, Y, Z) coordinate represents a location within the tree separated by 5 cm from the nearest adjacent locations within the tree. This distance approximates the average minimum distance between leaves in the tree. Running the simulation consists of moving the simulated flies from point to point in the simulated tree according to experimentally derived rules of movement discussed below. The number stored at each X,Y,Z coordinate within the tree conveys information concerning the proximity and identity of nearby fruit clusters. A zero indicates that there is no fruit cluster nearby. A number larger than zero indicates that the fly is near enough to a fruit cluster to respond to it visually. This "reactive distance" has not yet been determined experimentally but preliminary observations indicate that it is on the order of 20-30 cm when leaves are present on the tree (it may be up to ca. 80 cm in a cleared area). All locations within the "reactive distance" from a fruit cluster in the simulated tree are assigned numbers that identify the cluster and tell how far the fly is from the cluster. Whenever a fly enters locations within this "reactive volume" during a run of the model, we assume that it can see the cluster and will approach it. Whenever the fly enters an area where reactive volumes around two or more fruit clusters overlap, the model assumes the fly will go to the nearest cluster. Whenever a fly leaves a cluster following "inspection" and/or oviposition, the model assumes that it will not immediately return to the cluster until it has moved out of sight of the cluster at least once before re-entering the "reactive volume." The initial numbers and locations of the clusters within the simulated tree are chosen by the model-user at the start of the simulation according to the actual number and location of fruit clusters used in the field experiment being simulated.

2. Simulation of Movement of Flies in the Host Tree

The rules that determine the movement of flies from point to point in the simulated tree have been derived from preliminary observations of flies moving in trees devoid of host fruit before and immediately after an oviposition (Fig. 1). Movement of such flies has been shown to consist primarily of hops from leaf to adjacent leaf within the tree (Table 1). In addition, the flies tend to move upwards in the tree as they proceed from leaf to leaf along a limb. Periodically the flies will engage in flights either to the adjacent limb or to more distant locations within the tree. This event is similated by selecting new locations for the fly at random, with 50 cm flights for movements to adjacent limbs, or anywhere within the tree for more distant movements. The probability of such events has been calculated from preliminary observations (Table 1).

Flies periodically exhibit resting behaviour. The probability of initiating a rest period during any 5 second interval has been calculated from observation to be 0.05. The duration of rest-times of 27 flies has been shown to range from 4 to 540 seconds, with a mean of 61.7 seconds and a frequency distribution shown in Fig. 2. In the simulation, during each five second interval of time during a simulated movement of a fly in a tree, there is a 5% chance that the fly will initiate a rest period. If the fly rests, we then determine the rest duration by sampling at random from the frequency distribution in Fig. 2, This is accomplished by selecting a number at random between 1 and 100. Twenty-one percent of all rest durations are between 0 and 15 (Fig. 2). Consequently, we assign a rest duration from within that interval if the random number is less than or equal to 21. Similarly, 45% of all rest-durations are within 0 and 30 seconds. Consequently, we assign a rest-duration of between 15 and 30 seconds if the random number selected is between 21 and 45. In this manner we assign rest-durations in the simulation according to the frequency distribution derived from the preliminary experimental observations.

3. Determination of Giving Up Times.

Preliminary experiments have shown that following an oviposition, an R. pomonella fly will continue to search in a host tree devoid of host fruit for 8.7 min (± 1.3 min) before "giving up" and dispersing from the tree, compared to 3.8 min (± 0.5 min) for a fly that has not oviposited (Roitberg, unpub. data). Additional experiments have shown that exposure to five consecutive ODP marked fruits immediately following an oviposition will reduce the mean giving up time (G.U.T.) to 5.5 min (Roitberg, unpub. data). We based the current simulations upon the simplest possible model of *R. pomonella* G. U. T. that is consistent with current knowledge. We assumed that G.U.T. was determined only by whether or not the fly has recently oviposited and whether the last fruit contacted was clean or marked with ODP. In nature the actual G.U.T.'s may be influenced by additional factors including the quality of fruits visited prior to the most recent one. Nevertheless, we decided to see how this relatively simple model of G. U. T. would explain the preliminary experimental results.

In our simulation model, the G.U.T. for each fly is chosen anew following each visit to a fruit from the frequency distributions in Fig. 3 in a manner similar to that described for rest-duration. There are five possible fly conditions according to our simple G.U.T. model that determine which of the four frequency distributions (Fig. 3 and 4) we sample from. The five conditions are: (1) the fly has not oviposited and has not contacted any fruit (Fig. 4a); (2) the fly has not oviposited and the last fruit contacted was clean; (3) the fly has not oviposited and the last fruit contacted was ODP marked (Fig. 4b); (4) the fly has oviposited and the last fruit was clean (Fig. 3a); (5) the fly has oviposited and the last fruit contacted was ODP marked (Fig. 3b). At present we have no data for the second condition. For the current simulation we have assumed that such flies will exhibit a G.U.T. frequency distribution to the first condition.

Each time a fly leaves a fruit, in the simulation, we assign a G.U.T. from the appropriate frequency distribution and start a timer. The timer advances as the fly moves in the simulated tree. If the fly fails to contact a new fruit cluster before the timer exceeds the G.U.T. the fly disperses from the tree and is dropped from the simulation. If instead, the fly comes within sight of a new fruit cluster before the timer exceeds the G.U.T., the timer is reset to zero.

4. Acceptance of Fruit for Oviposition.

When *R. pomonella* flies encounter host fruit they move about on the fruit surface before either "accepting" the fruit and ovipositing or "rejecting" the fruit and moving on. Acceptance of the fruit for oviposition depends upon various factors that affect fruit quality (Prokopy 1977). In particular, the presence of ODP on the fruit greatly reduces the probability that flies will accept the fruit for oviposition. The probability of acceptance of clean fruit increases with time since the last oviposition (Fig. 5). The rate of acceptance of ODP marked fruit is so low (ca. 2%) that at present we have no information about how acceptance changes with time. The current simulation incorporates the probabilities of fruit acceptance (Fig. 5) including the hypothetical values for marked fruit.

5. Leaving the Fruit Cluster

Following oviposition or rejection of a fruit, *R. pomonella* will either leave the fruit cluster or move to a new fruit within the cluster. Preliminary observations (Roitberg *et al*., unpub. data) have shown that the probability of leaving the cluster depends at least in part on the number of fruits visited and rejected and upon whether the fruits were clean or marked (Table 10). To date we have no data on the probability of leaving the cluster when fruits consist of a mixture of clean and ODP marked fruits. In the current simulation we assume that each consecutive visit to a fruit in a cluster and rejection of that fruit reduces the probability of staying in the cluster during the next move by a certain proportion depending on whether the fruit is clear or ODP marked. If the fruits are all clean or all marked the calculated probabilities are those given in Table 10. The probability of remaining in the cluster, calculated for a mixture of clean and marked fruit, would then be intermediate to the two extremes shown in Table 10.

Results

Results of preliminary computer simulations (one sample run given in Table 11; compilation of simulation runs, in comparison with preliminary experimental data, given in Table 12) show that the preliminary model predicts reasonably well (within 30%) the probability of flies finding at least one fruit cluster and the giving up times of flies after the last visit to a fruit. The model predicts marginally well (within 60%) the total time of flies in trees, the number of fruit clusters visited and the number of ovipositions.

The experiments we propose to conduct in Objectives 1-4 will provide a much broader and more replicated data base upon which we will be able to build a refined and more highly predictable model of within-tree foraging behaviour, and will enable us to construct a model of between-tree foraging as well.

FIGURE CAPTIONS

Figure

1. Search path of one R. pomonella fly foraging in a host tree devoid of fruit. The four elevation levels of the tree are separated by contour lines. The innermost area in the map represents the highest elevation level in the tree. The numbers around the outside of the tree represent major limbs of the tree.

2. Frequency distribution of rest-time duration of R. pomonella.

3. Giving up times for R. pomonella. 3a - the fly has oviposited and the last fruit contacted was clean; 3b - the fly has oviposited and the last fruit contacted was ODP marked.

4. Giving up times for R. pomonella. 4a - the fly has not oviposited and has not contacted any fruit; 4b - the fly has not oviposited and the last fruit contacted was ODP marked.

5. Acceptance of clean and ODP marked fruit by R. pomonella as a function of time.

Table 9. Categorization of 263 observed movements of 12 *R. pomonella* flies foraging one at a time in a host tree devoid of fruit.

Movement Category	Proportion of Observed Movements
a. Horizontal move to adjacent leaf.	0.42
b. Upward move to adjacent leaf.	0.22
c. Downward move to adjacent leaf.	0.07
d. Move to adjacent limb.	0.22
e. Move to distant location within tree.	0.07

Table 10. Probability of *R. pomonella* leaving a fruit cluster following visits and rejections of *n* fruits in clusters of clean or ODP marked fruit.

Number of Fruits Visited and Rejected	Probability of Remaining in Fruit Cluster	
	Clean Fruit	ODP Marked Fruit
1	0.90	0.90
2	0.70	0.60
3	0.40	0.20
4	0.30	0.05
5	0.10	0.02
6	0.0	0.0

Table 11. Sample simulation run of *R. pomonella* foraging in a host tree with 4 fruit clusters.

```
81/01/15.  18.12.05.
  File  AMFB2

This model simulates the foraging of the apple maggot fly rhagoletis
pomonella for berries in a hawthorn tree
.....................................................................
Answer the following questions
How many minutes will the experiment run? ........
? 120
How many apple maggots shall we fly?.........
? 30
How many berry clusters are there?.........
? 4
Give X, Y, Z coordinate of cluster 1 .........
? 5, 5, 30
Give X. Y, Z coordinate of cluster 2 .........
? 15, 15, 30
Give X, Y, Z coordinate of cluster 3 .........
? 5, 15, 30
Give X. Y, Z coordinate of cluster 4 .........
? 15, 5, 30
Fly No. 1
       Gives up with 275  SEC GUT
  The time is .. 4:40  Visited 24 leaves
  0 clusters, 0 berries
    and oviposited 0 times
Fly No. 2
       Gives up with 285 Sec GUT
  The time is .. 33:0  visited 122 leaves
  4 clusters, 18 berries
    and oviposited 3 times
Fly No. 3
       Gives up with 123 SEC GUT
  The time is .. 2:10  Visited 12 leaves
    and oviposited 0 times
Fly No. 4
       Rests for 393 sec
  Gives up with 800 SEC GUT
  The time is .. 20:20  Visited 81 leaves
    1 clusters, 5 berries
    and oviposited 1 times
```

Table 12. Comparison of *R. pomonella* foraging parameters as predicted from the preliminary simulation model versus data from flies foraging in nature. M equals Model data, E equals experimental field data. In the final two categories A equals *All Flies Tested* and F equals *Only Flies That Found At Least One Fruit Cluster*.

# Clusters in tree	% Flies finding at least one cluster	GUT after last visit to fruit (min)	Total time in tree (min)	# Clusters visited		# Ovipositions	
				A	F	A	F
2-M	27	10.2	8.5	0.4	1.5	0.4	1.5
2-E	15	9.4	4.7	0.7	3.9	0.9	3.6
4-M	37	9.0	9.7	0.6	1.6	0.7	1.9
4-E	35	4.4	21.5	3.7	10.6	2.2	6.8
8-M	47	5.4	17.7	2.9	6.1	2.3	4.9
8-E	68	4.5	49.6	7.5	11.3	4.9	7.1
16-M	63	4.6	58.0	4.8	7.6	4.1	6.5
16-E	92	3.6	71.5	17.6	19.4	11.7	12.6

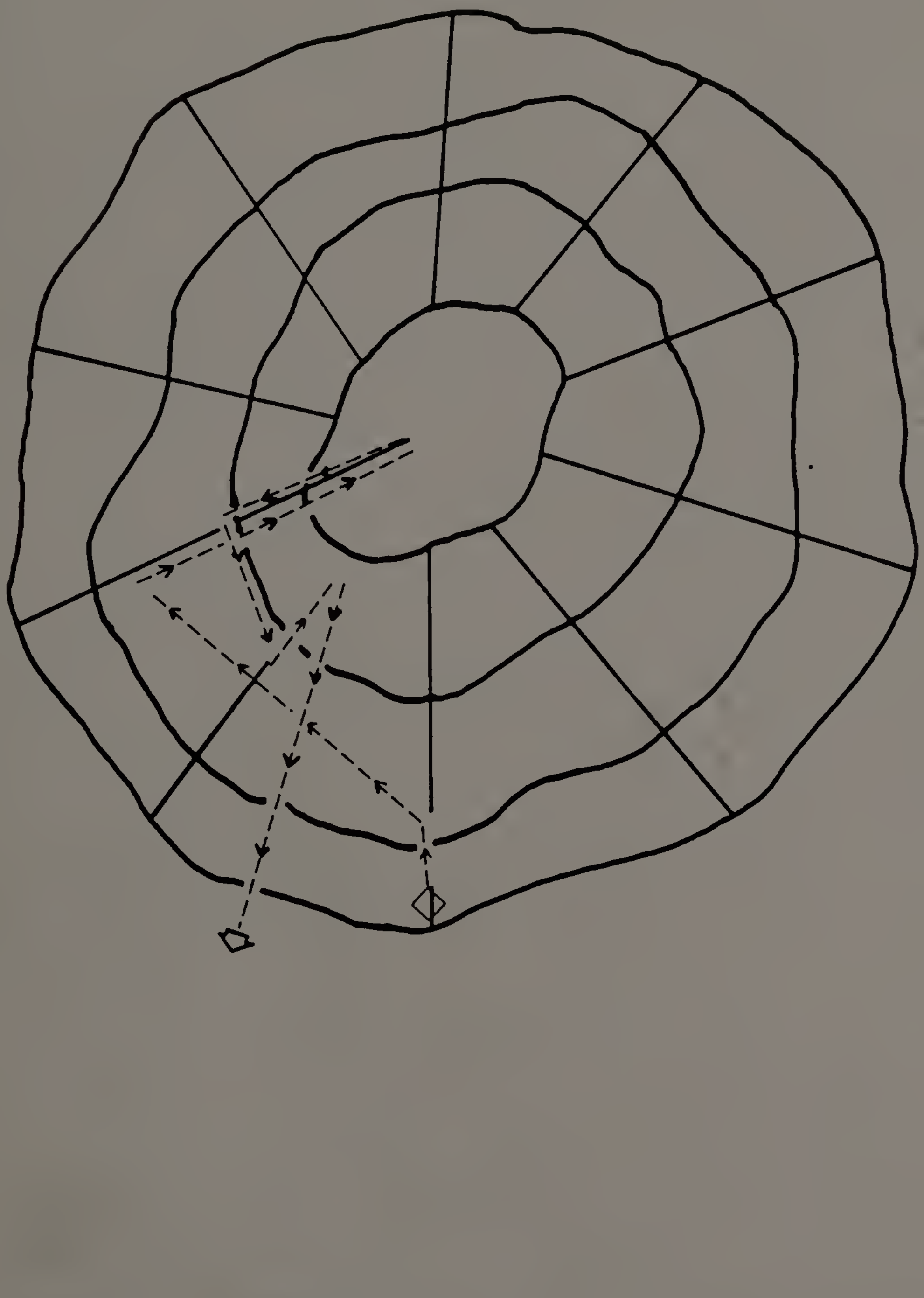

Figure 1

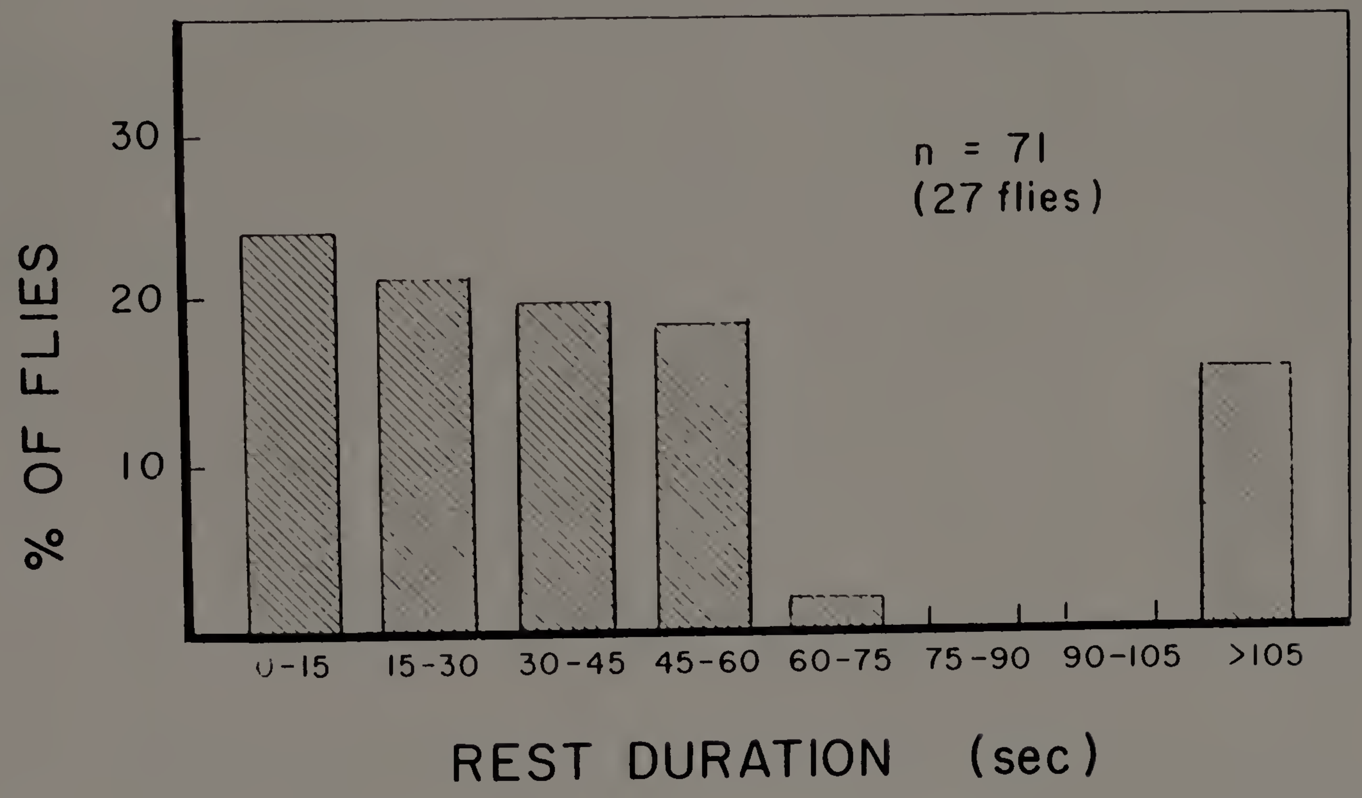
n = 71
(27 flies)
% OF FLIES
30
20
10
0-15
15-30
30-45
45-60
60-75
75-90
90-105
>105
REST DURATION (sec)

Figure 2

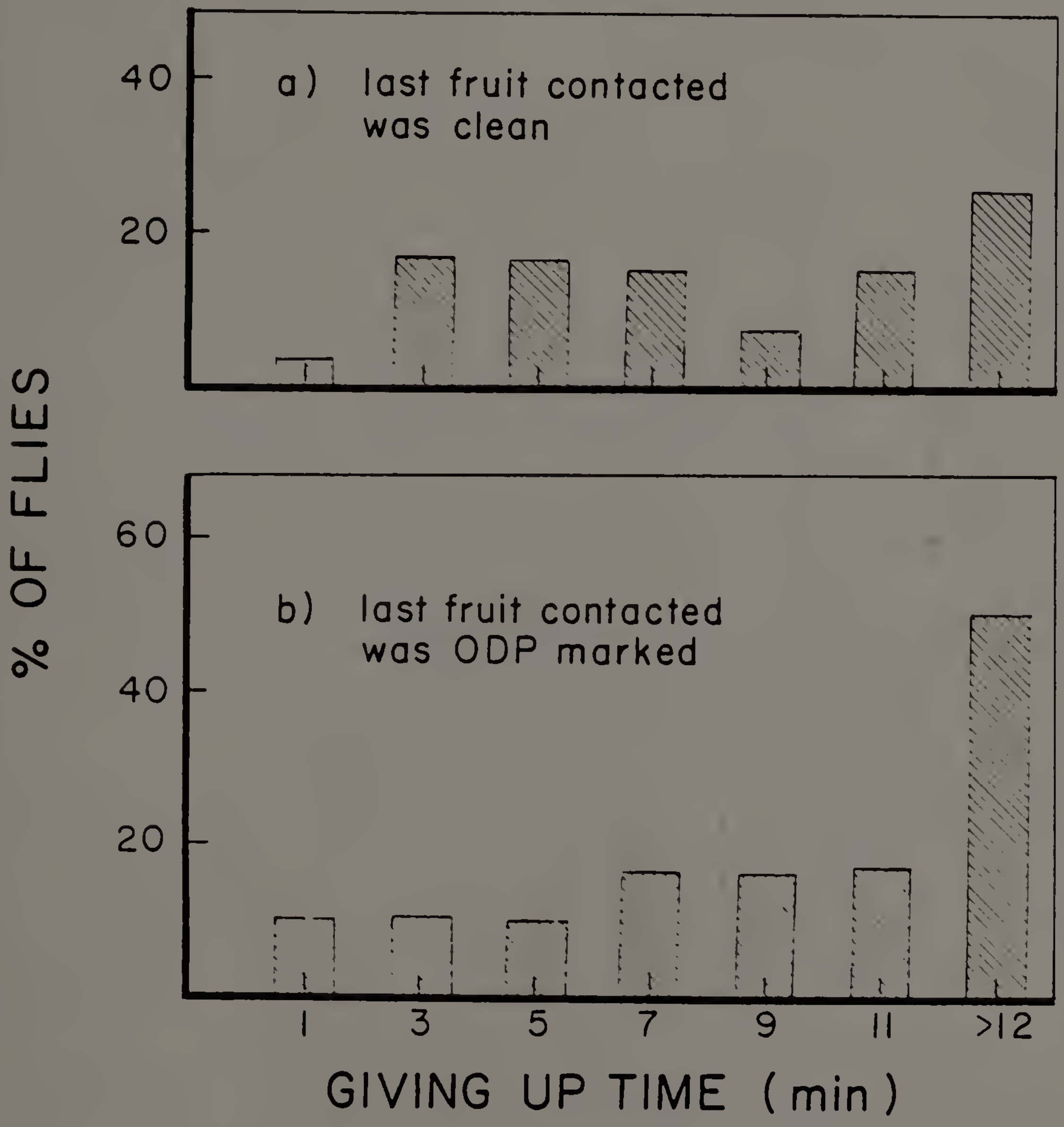
a) last fruit contacted was clean
b) last fruit contacted was ODP marked
% OF FLIES
40
20
60
40
20
1
3
5
7
9
11
>12
GIVING UP TIME (min)

Figure 3

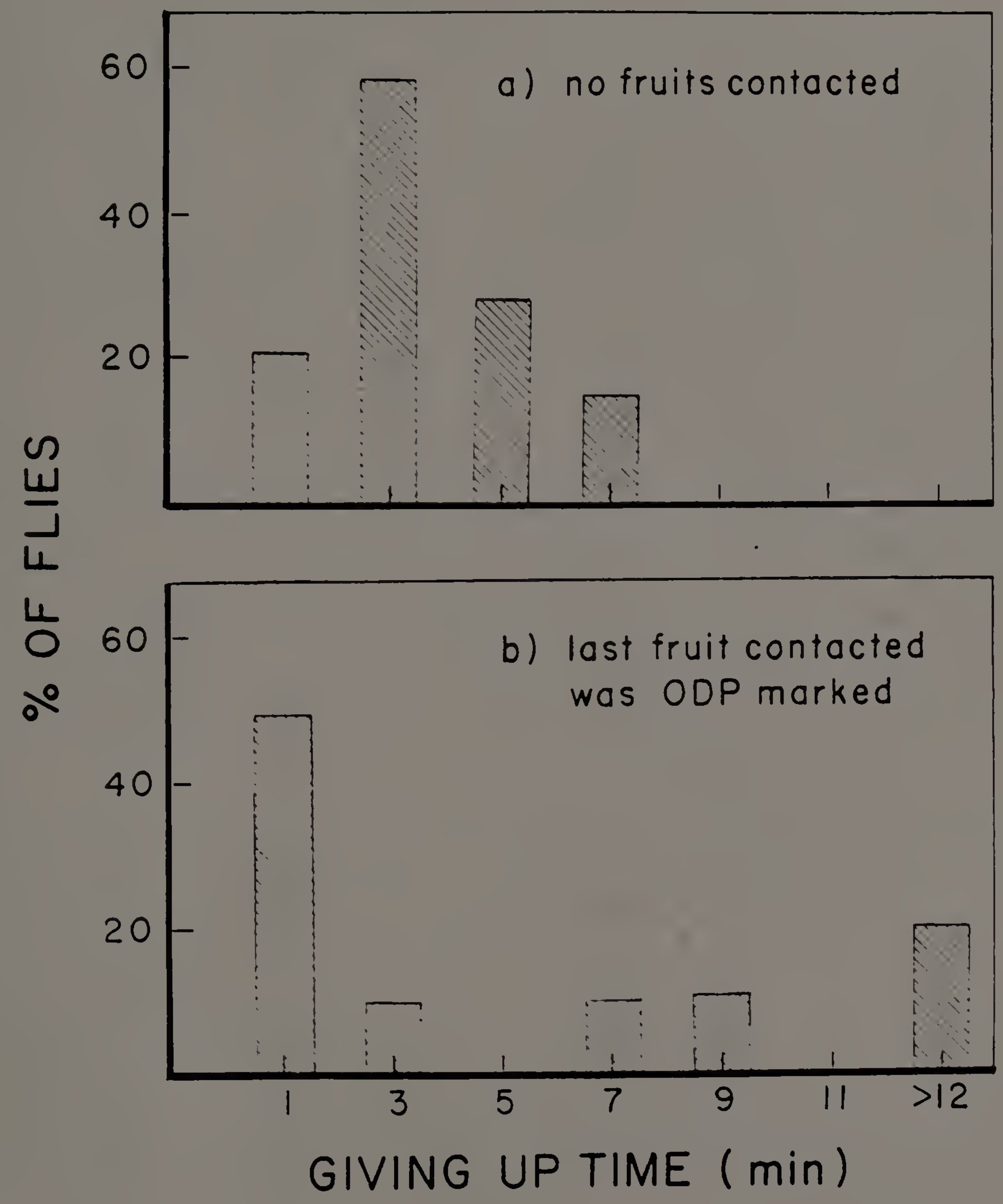
% OF FLIES
60
40
20
a) no fruits contacted
60
40
20
b) last fruit contacted was ODP marked
1
3
5
7
9
11
>12
GIVING UP TIME (min)

Figure 4

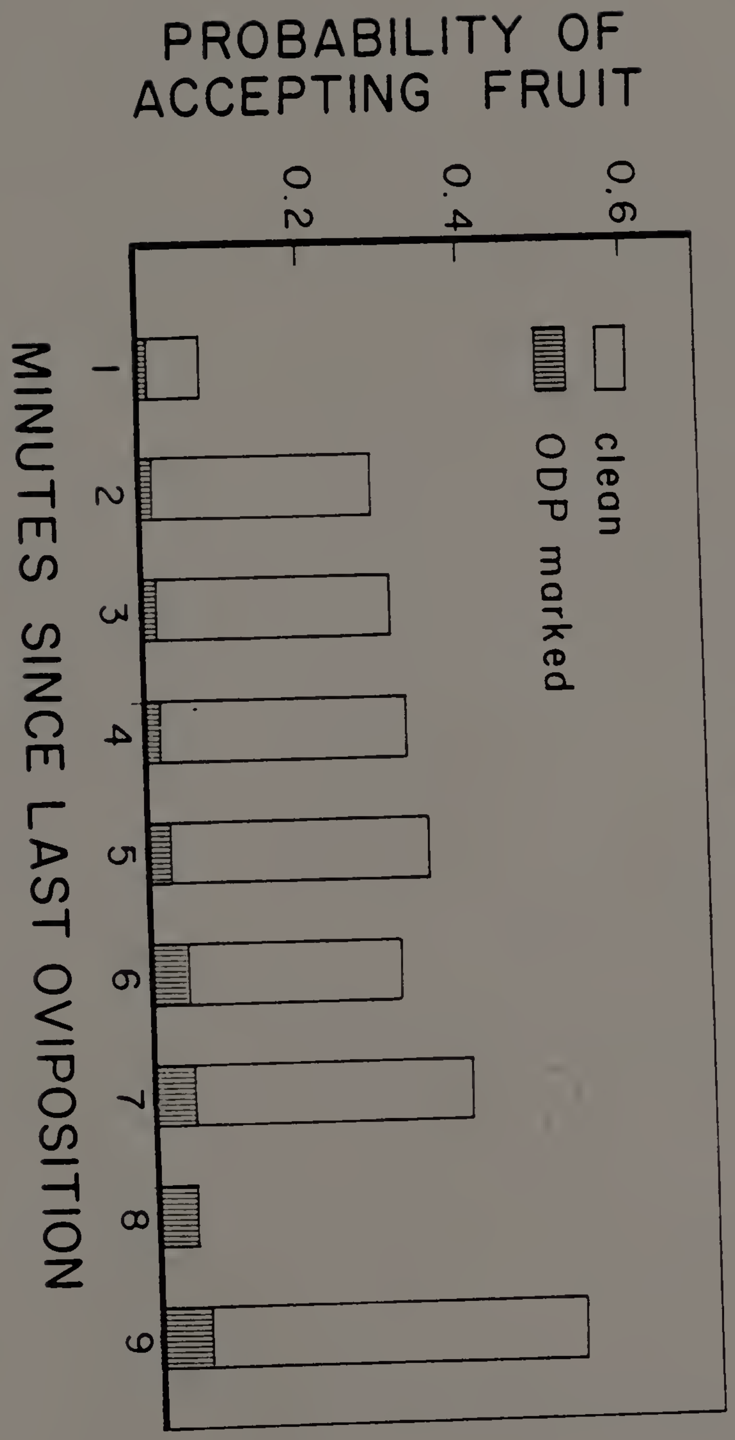
PROBABILITY OF ACCEPTING FRUIT
0.2
0.4
0.6
clean
ODP marked
1
2
3
4
5
6
7
8
9
MINUTES SINCE LAST OVIPOSITION

Figure 5