A BEHAVIORAL-ECOLOGICAL APPROACH TO OLIVE FLY INTEGRATED PEST MANAGEMENT (IPM)

by

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Abstract

This thesis reviews the potential advantages , as well as the limitations, of using a behavioral-ecological approach to develop contemporary IPM of *Dacus oleae* (Gmel.), olive fly. In addition to an introduction to the pest status and its life history, five major relevant topics are covered: i) current and future status of IPM of the olive fly, ii) the phenomenon of learning and memory in living organisms including the insects, iii) behavioral ecology as a foundation for IPM of the olive fly, iv) foraging behavior of flies with focus on habitat structure and host-marking pheromones and their practical application, v) recent progress in moving away from mechanistic stimulus-response approaches toward an evolutionary and ecological perspective.

The major theme of this work is an attempt to connect two sorts of enterprises currently disassociated - behavioral ecology and IPM - to analyse predictions of various behavioral responses over a broad range of situations and thus facilitate development of new efficient management practices.

Dedication

To my parents, who always encouraged me to pursue higher studies.

" Nothing in biology makes sense except in the light of evolution "

TH. DOBZHANSKY, 1973

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1.0 INTRODUCTION

1.1. Pest status and host distribution

The olive fruit fly, *Dacus oleae* (Gmelin) (Diptera: Tephritidae) is a major pest of olives, *Olea europae*, in France, Spain, Portugal, Yugoslavia, Greece, Israel, Turkey, Lebanon and Oriental Asia including northern India and north-western Pakistan (Katsoyannos 1992). It has also been found in wild olives, *O. europea* sp. africana (Miller) in Africa (Munro 1984). Olive fly maggots cause heavy damage to olive crops by destroying olive pulp and reducing oil quality. On average, 30% of the olive crop in the Mediterranean is lost annually to olive flies (Fimiani 1989). However, an infestation level of 30% at harvest time in oil-producing varieties does not reduce the value of oil unless infested olives are stored for a time (Neuenschwander and Michelakis 1978).

1.2 Life history

Dacus oleae is a monophagous, multivoltine, solitary species with a life history similar to typical parasitoids. Adults are free living while the eggs and larvae are confined to host fruits. A parasitoid may be defined as "an insect that requires and eats only one animal in its life span" (Price 1975). Since *D. oleae* larvae do not kill their host fruit, these flies are not true parasitoids but may be considered "fruit parasites" (Price 1977). As a specialized exploiter of pulpy fruit, the female olive fly lays its eggs individually in the mesocarp of ripening olives. The subsequent larva bores a gallery in the mesocarp while feeding and pupates in the fruit or soil (Prophetou-Athanasiadou *et al.* 1991). The female produces a finite number of eggs on a daily and life-time basis. Maximum fecundity appears to be approximately 300 eggs per female (Fletcher 1989). Fitt (1984) reported that oviposition deterrent pheromones have not yet been found associated with egg laying in olive fruit flies. Instead of spreading a chemical marker around the fruit, after laying her eggs, the olive fly drags her proboscis across the surface of the fruit and deposits olive juice that exudes from the egg-laying puncture, as a deterrent to subsequent egg-laying (Cirio 1971). Female typically lay a single egg into each fruit and reject a previously parasitized fruit (host marked with olive juice) in favor of an unparasitized one. In the olive, a single larva survives per host, regardless of the number of eggs.

The adult olive fly is moderately mobile (up to few hundred meters), and commonly disperses over long distances (several kilometers) (Michelakis and Neuenschwander 1981). The life span of adult flies is variable. In the early season, adults may live for four weeks whereas in the mid-season, they may live for three months (Fletcher 1989). There are two to five generations per year, and wide overlap in generations is a regular occurrence.

The purpose of this thesis is to explore the developments and theories of behavioral ecology and demonstrate the applications of this discipline to the integrated pest management of the olive fly. I will demonstrate that an understanding of the development of memory and the learning process in insects is required before behavioral ecology can be an effective tool for pest management.

In this work I also plan to detail and question new understandings that have developed within behavioral ecology concepts by:

i) Introducing an evolutionary-ecological perspective on behavior that might provide an integrative multilevel framework on which to tie various and otherwise disassociated parameters.

ii) Integrating olive IPM into the mainstream of what is known in the field of behavioral ecology about fruit fly behavior and its relation to fitness.

iii) Investigating the causes of behavior and how they may have originated, so that further insights can be gained in the area of olive IPM.

iv) Providing a case study to accompany the theory.

2.0 Integrated pest management of the olive fly

2.1 Current status

The concept of Integrated Pest Management was internationalized in 1965 by the Food and Agriculture Organization of the United Nations, in Rome, Italy, as a reaction to the misuse of pesticides. Integrated Pest Management is described as an ecological, multidisciplinary approach that combines a variety of management tactics compatibly in a single pest management system (Kogan 1988). A variety of approaches are used in an attempt to manage the olive fly, including insecticides (Prota 1983), fungicides (Prophetou-Athanasiadou *et al.* 1991), color and pheromone attractants (Economopoulos 1979, Delrio *et al.* 1982), baited sprays (Brnetic 1979), various trapping methods (Neuenschwander 1982, Mazomenos *et al.* 1983, Kapatos and Fletcher 1983), sterile insect release (Boller 1983, Economopoulos 1979) and biological control (Kapatos *et al.* 1977).

Currently, control of the olive fly is achieved either by preventative, cover sprays with organophosphorous insecticides (e.g., dimethoate) or by bait sprays ('lure and kill approach') that consist of organophosphorous insecticides and protein hydrolysates. Applications are done from the ground by growers, or from the air by government or cooperative organizations. The use of dimethoate as a cover spray carries a significant environmental risk since it is a wide-spectrum insecticide. Its use can lead to an outbreak of secondary pests such as scale insects (Delrio 1987). To date, there are no selective chemicals available for management of olive flies (Prota 1983). Though, the ' lure and kill' approach is less damaging environmentally than cover treatments, the lack of specificity of the lure used can substantially disturb the ecological balance in the treated areas, since the attractant will lure both *D. oleae* and useful entomophauna (Zervas 1986). Furthermore, there is a growing consumer demand for fruit that is free of toxic residues.

With few exceptions, the focus of olive IPM programs to date has been primarily on improvement and manipulation of insecticide application. Unfortunately, insecticides are often applied with a poor knowledge of the pest concerned. Furthermore, treatments are often carried out on fixed calendar dates. These practices, based on routine treatment schedules, are only partially effective and often unjustified (Kapatos 1989). In most olive growing regions, the first treatment is initiated as soon as McPhail trap counts reach 5-6 adult olive flies per trap per week (the economic injury level). The economic injury level (EIL) is defined as " the lowest population density that will cause economic damage" (Stern *et al.* 1959). By suppressing the adult population just prior to the onset of infestation (usually the first week in July), infestation levels will likely be reduced right up to harvesting. When the level is 30% or less, the losses are considered economically acceptable. This assessment of pest status based on field capture data from traps, and its use as a guideline for management decisions, can lead to unjustified conclusions and recommendations. First, in a behavioral context, field capture data does not consider all biotic and abiotic factors. Second, (EIL) is of limited value since it is nominal and not based on comprehensive research.

Of the non-insecticidal methods, mass trapping has been utilized as an alternative means to control olive flies. Rectangular yellow sticky traps are commonly used for this purpose. These traps rely on visual (colour) attraction. To increase effectiveness and to avoid killing non-target insects, other traps have been designed that incorporate both visual and odour attraction (eg. yellow McPhail traps baited with protein hydrolysate).

2.2. The outlook

A multidisciplinary integrated approach is needed to increase our knowledge of pest behavior and lead to effective management. Although a great deal of effort has been invested in the development of curative methods involving chemicals, research dealing with causes of behavior responsible for damage have been neglected. For olive IPM to be successful, a focus on ecology is needed (Wellington 1977), even if it is expensive in the short-term. To formulate questions about the population dynamics of a pest, an understanding of evolutionary theory may be required (Luck 1990). It is insufficient to consider pest density without knowing the pest population structure. A more thorough understanding of the structure of a pest population (e.g. age) may lead to a true integration of different IPM tactics (Carey *et al.* 1993).

During the last thirty years, IPM has created an awareness of the side effects of pesticides and promoted ecological research. The use of IPM has successfully reduced damage caused by pests and ensured producer profits (Pedigo and Higley 1992). Now, applied entomologists should become 'general practitioners' grounded in several areas such as evolution, physiology, chemistry and field entomology.

Studying olive fly behavior, with the assistance of evolutionary theory from which behavioral ecology (BE) is derived, may be key to discovering environmentally sound control methods.

3.0 Memory and learning

Before proceeding to the topic of insect learning from an evolutionary perspective and its significance to the IPM, this first chapter examines learning and memory as a phenomenon in living organisms. I review information on the topic, and outline the basic concepts of how the brain works. Until recently it has been unpopular in the scientific world to suggest that intelligence of some sort might guide insect behavior. Recent advances in areas as diverse as Behavioral Ecology, Integrated Pest Management and Neurophysiology show that sophisticated learning abilities (i.e. associative learning) are present in insects.

These studies provide greater insight into the rich behavioral repertoire of insects. In this chapter, I also discuss the notion of consciousness in fruit flies. From an evolutionary perspective whether a fly is conscious of its action or not is irrelevant ; but consciousness allows her to achieve a degree of mastery over her surroundings. By my definition, this is the essence of intelligence. Drever (1952) stated : " in its lowest terms intelligence is present where the individual, animal, or human being is aware, however dimly, of the relevance of his behavior to an objective". However, no behavior of insects should be classified as " hard-wired" (species-specific response to a particular stimulus irrespective of learning) unless it is first shown by observation and experiment to occur without any contribution from learning. In general, this progression from a "hard-wired" to "soft-wired" concept of insect behavior reflects the significance of knowledge newly acquired from the studies of organisms with "simpler" nervous systems.

In the last few decades, scientists have developed elaborate theories of brain function and neuron communication (Penrose 1990, Rose 1981, Rose 1992, Morris 1990). The three prime concepts of the conventional view of how the brain works are the following: 1) information flow is linear; 2) physical and mental functions can be localized to discrete parts of the cortex; and 3) there is a hierarchy which makes the cortex supreme, dominating everything below it. Although this view is still widely accepted, a new view (LeDoux 1992) states that the flow of neural impulses is not linear, but parallel and multiplex and that there exist different levels of consciousness. The following example of visual signaling illustrates LeDoux's view. A visual signal goes first from the retina to the thalamus, where it directly and quickly passes to the amygdala. Meanwhile the message also goes to the visual cortex, where it is analyzed and assessed for its meaning. Therefore, it makes no sense to speak of the brain as linear but rather as a network.

A fruit fly (Drosophidae) can process many pieces of information simultaneously (Simmers *et al.* 1995). The advantage of parallel processing is that it greatly speeds up data processing, allowing more manipulations to be done with less equipment. Although the type of information processing demonstrated by a fruit fly is rather simple compared to processing by vertebrates, one cannot conclude that intelligence is absent in so-called lower forms of life (e.g. fruit flies, sea slugs). It appears that neurons in all animals utilize the same basic electrochemical mechanisms for conducting information, e.g., phosphorylation of potassium channels and second-messenger systems such as cyclic AMP and calcium (Kandel and Schwartz 1982). Hawkins *et al.* (1983) showed evidence that even a few milligrams of neural wiring in the invertebrate brain can accomplish impressive cognitive tasks essential to survival.

LeDoux (1994) also studied fear conditioning in various animal groups and concluded that the cortex is not necessary to establish fear conditioning, and that fear conditioning occurs in nearly every animal group, including fruit flies. He also concluded that fear conditioning happens quickly and once established, the fearful reaction is relatively permanent and that stressful experiences stored in a fly's neuronal system may have a powerful influence on its behavior.

There are several implications of LeDoux's work that are important for integrated pest management.

Insects apparently remember exposures to insecticides as aversive stimuli (Ebeling *et al.* 1966). Insects may use these memories to shape their future behavior and increase their likelihood of survival. The notion that memory is synonymous with the thinking mind (neocortex) and that memory is what can be verbally recalled (Janov 1970, Damasio 1994) is apparently not well founded LeDoux (1994).

Apparently, in the fruit fly, memory is stored at different levels of consciousness. There are discrete layers of consciousness, each with its own peculiarities and its own processing plant (Janov and Holden 1975). It has also been suggested that the properties of reactivity and sensitivity are elements of consciousness (Janov 1970). For example, a fly's memory of electric shock is not cognitive at all, but exists on a separate level. A fruit fly can remember, store and code memory and delay its reaction (i.e. primitive prerequisites for a form of consciousness) (Roitberg and Prokopy 1984). In its own way, a fly is aware of the environment and adjusts its behavior accordingly. In a discussion of the mental processes of animals, Griffin (1981) proposed that awareness involves the experiencing of interrelated mental images. Griffin argued that in strictly operational terms, “awareness” can be considered as readiness to respond to certain patterns of stimulation". Biologically speaking, memory is coded differently at each level of consciousness, making it difficult to study empirically. It may be possible, however, to develop a coherent theory of memory using the following evolutionary approach: Consciousness evolved in animals out of the most primitive cells. Prior to the evolution of the cortex, nervous systems may have operated as a primitive consciousness. Taken to this logical extreme, even plants display a form of consciousness. Jaffe (1977) showed that the pea - tendril, a primitive life form, has the capacity to store information and respond accordingly to it later.

Studies have investigated typical Pavlovian conditioning on surgically neodecorticated mammals such as rats and rabbits (Oakley 1979, Oakley 1974), and have revealed that non-human mammals exhibit Pavlovian conditioning, and in mammals, the conditioning is more efficient when the neocortex is removed than when it is present (Oakley 1983). These results suggest that perhaps one of the main functions of the neocortex is inhibition (Janov and Holden 1975).

The neocortex is the outermost, and in evolutionary terms, the most recent part of the cerebral cortex. This portion of the mammalian brain can reason and analyze. For many decades the prevailing view was that it is the site of anticipation and planning for future action. What usually gets overlooked is the fact that in evolutionary terms, it is only recently that the neocortex has been raised to such a pinnacle of importance (Janov 1992). In evolutionary terms, the survival value of having a primitive, minor brain would have been great, allowing a quick, non-analytical response option in time of danger.

Traditionally, learning theory has concentrated on a principle labeled the general principle of learning (Skinner 1953, Bitterman 1975, Macphail 1985) or the principle of equipotentiality (Roper 1983). The principle of equipotentiality (i.e. all stimuli are equally capable of becoming Pavlovian conditioned stimuli) argued that there are general principles of learning that transcend both species and learning tasks. Within this approach, both observable behaviors of animals and the responses of the animals that the stimuli evoked were quantified in terms of measurable stimuli. Most scientists now agree that the "general principle of learning" approach has failed since observed anomalies in animal behavior were not the result of procedural differences or deficiencies in experimental design and control (Bolles 1970, Seligman 1970, Garcia 1981).

Nevertheless, it must be stressed that classic-conditioning learning in invertebrates is largely specific to certain types of stimuli which are integral to their experiences associated with their ecology. For example, bees learn to associate certain kinds of colors and scents with food more readily than other colors or scents (Menzel *et al.* 1974, Heinrich *et al.* 1977). As Garcia and Koelling (1966) pointed out, some stimuli are more associable than others. For example, an earth worm can readily associate a taste with a hot, dry place, but cannot associate a tactile stimulus with electric shock (Mayr 1974, Eisenstein 1967).

Insect learning involves both physiological and ecological factors. Kamil and Yoèrg (1982) and Legg (1983) stressed the importance of ecological factors in the design of learning experiments. Attempts have also been made to use evolutionary approaches to understand learning specializations in mammals (Shettleworth 1984).

However, to provide a deeper understanding of learning, a new theoretical framework should be introduced in which learning is viewed as a more general phenomenon of phenotypic plasticity (Stephens 1993). Learning is one of the possible proximate explanations of behavioral variability within and among individuals (Rosenheim 1993). Similarly, Krebs and Inman (1994) noted that animal learning plays a crucial role in tracking spatial and temporal changes. The contemporary view of the relationship between a traditional and an ecological approach to learning theory is that they are not mutually exclusive from each other (Stephens 1993). The former approach can pinpoint some general principles of learning that may have evolved as a result of selection pressures. The latter can help to determine the functional aspects of learning (i.e. predicting the kind of adaptive behavior the animal will perform in the learning situation). There is a growing trend to integrate behavioral ecology with ideas from animal psychology (Fantino and Abarca 1985).

It is also important to understand learning and learning potential from a physiological perspective. Over the past two decade, researchers (Carew *et al.* 1983, Kandel *et al.* 1981, Hawkins *et. al.* 1983) have studied the nervous system of the marine snail, *Aplysia california*. Their studies illustrate that invertebrates can both learn from experience and establish short and long term memory. Their work contributes to the understanding of the chemical and molecular basis of memory. There appears to be no fundamental differences in structure, chemistry, or function between the neurons and synapses in man and those of a squid, a snail, or a leech (Kandel *et al.* 1981). Nelson (1971) showed that the blowfly, *Phormia regina*, can be classically conditioned. Quinn *et al.* (1974) demonstrated that conditioning can occur in a fruit fly, *Drosophila melanogaster*. Tully (1984) reviewed behavioral and biochemical information on the mechanisms of learning and memory in species of *Drosophila*. In animals as small as the snail or the fruit fly, long term memory is related to the growth of new neural connections. At the microscopic level, memory causes growth in the nervous system of *Drosophila* (Zhong *et al.* 1992, Kater *et al.* 1988). Similar results were obtained from work on the marine snail, *Aplysia* (Bailey and Chen 1983). Harris (1981) investigated the memory traces in animals and found that with repeated stimulation, certain nerve cells link with others. As nerve pathways continue to link, transmission across the synapses are facilitated, inducing memory. Hubel *et al.* (1988) presented evidence that visual experience can shape synaptic patterns of the visual cortex in invertebrates. Increasing evidence suggests that chronic stimulation of certain motor neurons induces changes in the number and shape of synapses formed at the motor terminals (Lnenicka *et al.* 1986). Atwood and Govind (1990) reached a similar conclusion in their study on crustacean neurons.

Insect behavior is not entirely fixed, but can depend on prior experiences (Heinrich 1985, Menzel *et al.* 1974, Papaj and Prokopy 1988) that may have an impact on individual behaviors such as locating habitats (Papaj and Vet 1990) and accepting hosts (Kaiser *et al.* 1989). For example, the ability to associate the color, size and shape of a habitat in the polyphagous Ichneumonid, *Itoplectis conquisitor* (Say) has been demonstrated by Arthur (1967; 1971) and Vinson *et al.* (1977). Vet (1983) suggested that associative learning plays a role in the location of host habitats by *Leptopilina claviceps* (Hartig), a larval parasitoid of fungivorous *Drosophila.* Increased response to stimuli through conditioning has also been observed (Vet and van OpZeeeland 1984) in the larval endoparasitoids of Drosophilidae viz., *Asobara tabida* (Nees) and *A. rufescens* (Foerster).

Research on phytophagous insects shows that associative learning plays an important role in their life history (Raubenheimer and Blackshaw 1994, Simpson and White 1990). *Batus* and *Colias* butterflies learned to associate plant stimuli with suitable host species (Stanton 1984, Papaj 1986). Prokopy and Papaj (1988) reported on the role of prior experiences with egg-laying sites in the ovipositional behavior of fruit flies. Jaenike (1982, 1983) showed that the prior experiences of adult fruit flies during oviposition can modify their oviposition site preference. Similar evidence has been produced for some tephritid flies (Prokopy and Fletcher 1987). Future rejection or acceptance of fruit hosts for egg-laying in females of *Rhagoletis pomonella* (Walsh) (Prokopy *et al.* 1982, Prokopy and Papaj 1988) and in *Dacus tryoni* (Froggatt) (Prokopy and Fletcher 1987) can be significantly altered by prior ovipositional experiences with particular host fruit types.

The above studies demonstrated that adult insects can change their behavior as a result of learning. Although the adaptive nature of such changes is now widely accepted (Alcock 1989, Papaj and Prokopy 1989), an unambiguous definition of learning has not yet been formed. For example, learning can be defined loosely as "any change in behavior with experience" (Thorpe 1963), "a reversible change in a behavior with experience" (Papaj and Prokopy 1986), or " a more or less permanent change as a result of practice " (Kimble 1961). Throughout this thesis my definitions of learning and memory, have been that learning is the modification of behavior by experience , and memory is the retention of such modification.

Habituation (a waning of response to stimuli with repeated exposure to the stimulus) and associative learning (establishment through experience of an association between two stimuli or between a stimulus and a response) including aversion learning, are two major types of learning that have been identified in insects (Papaj and Prokopy 1989). Another type of learning, sensitization, is defined as "a gradual increase in response to a stimulus with repeated exposure to that stimuli even when it is not paired with any other stimulus" (Papaj and Prokopy 1989).

Knowledge is increasing on how insects (especially entomophagous parasitoids) can learn odors (Visser and Thiery 1986), colors (Swihart and Swihart 1970), shapes (Rausher 1978) and other cues. Currently, the role this knowledge can play in IPM tactics is speculative but should be pursued (Katsoyannos and Boller 1976, 1980).

Through behaviorally flexible systems they already possess, including learning and instinct, flies may be able to solve problems associated with novel stimuli that have been introduced into their habitats (Jaenike and Papaj 1992). For instance, if a *Drosophila* is shocked whenever it extends one of its legs, it quickly learns to maintain that leg in a flexed position (Booker and Quinn 1981). Though electric shocks do not exist in a fly's natural environment, this shows a behavioral capacity to react appropriately to stress. Since fruit flies may frequently encounter stressful stimuli (e.g. natural toxins; heat) during their lifetime, they may successfully negotiate new contingencies primarily through use of Pavlovian-associated mechanisms. For example, in new contingencies (e.g. introduction of novel plants into the habitats) it seems that preexisting abilities acquired in ancestral habitats (habituation and Pavlovian associations) may be sufficient for olive flies to adapt to current olive ecosystems.

A strong case can be made that the cellular processes underlying learning and memory involve modulation of synaptic efficacy by 'fine tuning' of the functional architecture of neural circuits. Something besides the motor programs and programmed learning may be at work. Synaptic plasticity is a fundamental means by which environmental cues alter the function of the nervous system in both development and learning (Elliot *et al.* 1994) in invertebrates and vertebrates. Currently, research is on the verge of a new era in understanding memory and learning-based behavior which should provide us with a new model that can predict behavior with more precision. These predictions can be tested and used to develop new pest management strategies.

4.0 Proposal for the integration of behavioral ecology and the IPM of the olive fly

4.1 Proximate and ultimate causation

One of the major thrusts of current behavioral ecology is the testing of the hypothesis that specific behaviors, including those which depend on learning, are employed to optimize particular factors (e.g., caloric input and energetic costs in foraging). There is a tendency in biological research to emphasize one of two levels of causation (Gould 1982, Real 1994). 'Proximate causation - 'how' questions- deals with the ontogeny and dynamics of an individual, i.e., characteristics of the organism that one can see (Mayr 1982, Francis 1995). Proximate causation may be understood through developmental and physiological mechanisms and external stimuli induced by the current environment. Intrinsic properties and external stimuli can be counted to elicit the behavioral phenotype. 'Ultimate causation' - 'why' questions- is the province of the evolutionary biologist and is concerned with the causes of the historical origins of genotypes. Explanations from this point of view emphasize the concept of adaptation of an organism to its environment as well as evolutionary lineages based on studies of different kinds of organisms. Behavioral ecology modes of analysis combine both 'how' and 'why' questions, stressing the ultimate causes of behavioral phenotypes. Behavioral Ecology adopts the position that the present environment indicates the conditions under which behavioral phenotypes evolved and provide stimuli, which from an evolutionary perspective may be closely linked to constitutional causes of phenotypic plasticity (Boake 1994, Francis 1995). The prime consideration is how the complex behavior of insects depends on the interactions of environmental and internal factors, and the relation this concept has to IPM (Roitberg *et al.* 1994). Behavioral ecology can be of value to pest management by providing an understanding of the variables which determine the decisions that animal makes in varying sets of circumstances. Manipulation of fruit flies decisions can be used more extensively in managing the behavior of pests . Furthermore, behavioral ecology proponents stress that evolutionary explanations of 'why' should be, an ingredient of pest management and that evolutionary framework provides the most useful 'why' and 'how' questions regarding pest problems (Prokopy and Roitberg 1984). Proximate and ultimate causes are not competing means of understanding behavior, but rather complimentary modes of analysis that involve different aspects of pest biology (e.g. physiology, foraging behavior, vision etc.). Although the 'why' is an essential part of the approach, it does not in itself constitute a framework. One of the fundamental differences between behavioral ecology and other approaches of IPM is that behavioral ecology is the understanding of the dynamics of ecological, evolutionary, and behavioral aspects of particular phenomena. It is the nexus for the why's and how's of behavior, since it addresses how ultimate causes produce a behavioral genotype that interacts with proximate causes of behavior to yield a behavioral phenotype (e.g. host marking behavior).

The value of the dual approach (Charnov and Skinner 1985) to understanding behavior is it that can provide insight into factors that may have been important in shaping the evolution of a species. It may also help to develop appropriate questions regarding an animal and its environment. For example: what are the sensory cues and the neural cognitive processes involved in decision making? How will the memories of past experiences influence future decision making?

4.2 How animals might solve problems

To maximize its contribution to the gene pool, an animal is faced with a challenge of optimization (MacArthur and Pianka 1966). Because the problems are often very complex , it is likely that animals which can solve problems optimally (e.g. give up foraging in one olive grove and travel to find others) are doing so by sampling and memory processes (McNamara and Houston 1985). An optimization theory that addresses ultimate causes of behavior can provide insight into factors that have shaped the evolution of the olive fly.

The ecological approach (i.e., an animal's behavior cannot be described in isolation from its environment) to investigating learning is essential to understanding and predicting how learning is translated into a particular behavior such as, how animals spend time foraging in the most resource-rich (richest) patches (Smith and Sweatman 1974, Zach and Falls 1976, Davies 1977, Waddington and Holden 1979, Goss-Custard 1981). Since this tendency may translate to pest damage , residence time may be an important variable for pest managers to understand. Thus, it is important to know how an animal goes about determining that one patch is richer than another (Roitberg 1985).

In addition to the richness of individual patches, travel between patches may also affect patch exploitation tactics, because it also requires time and energy (Kamil and Roitblat 1985). For example, the olive fly is not only choosing which patch to exploit during its foraging activities but it is also handling the more difficult task of deciding when to leave the current patch in order to explore others. Although a particular olive grove may had abundant unexploited olives, when the fly chose to exploit it, at some point the patch will become depleted of hosts and the fly may decide to move elsewhere.

According to the Marginal Value Theorem (Charnov 1976), the olive fly should exploit a particular patch only "as long as the expected rate of return in that patch is higher than the rate of return that can be expected by leaving and exploiting another patch." Charnov (1976) predicted that first, foragers should spend more time exploiting richer patches; and second, the greater amount of time and energy required to travel between patches, the longer the forager should spend exploiting a particular patch (his assumption is that an animal has knowledge of inter-patch distance and patch quality). These predictions have been upheld in experimental studies on fruit fly *Rhagolletis pomonella*, and evidence that fruit flies can obtain and process information (e.g. the amount of time spent in a particular patch is a function of inter-tree distance traveling time between patches) that is involved in decision making (Roitberg and Prokopy 1982, Roitberg and Prokopy 1983). Other studies have yielded similar findings in the wasp, *Nemeritis canescens*, searching for hosts distributed in patches (Cook and Hubbard 1977, Hubbard and Cook 1978); and in chickadees foraging for food in an indoor aviary (Krebs *et al.* 1974). Even though these studies suggest a high degree of consistency with the Marginal Value Theorem, there may be other abiotic and biotic factors involved. For instance, an olive fly may decrease its traveling speed because of lower temperature and as a result, spends longer foraging in the poorest patches than would be predicted by the theorem.

Waage (1979) investigated the behavior of the parasite wasp *Nemeretis canescens*. This insect searched for hosts distributed in patches in a manner known as 'area-restricted search'. Waage discovered that wasps exhibit two basic responses when they encounter a patch of prey. First, the wasps start walking more slowly after entering a patch, and second, they tend to make sharp turns back into the patch whenever its edge is encountered. The edge response is important because it will gradually diminish and wasps will eventually abandon the patch. After an insect encounters healthy hosts, it will make sharp turns and remain in the area where it has been successful and will tend to search intensively. In the case of encounters with infested hosts, the pattern of movement is much broader circles and the insect will eventually leave the patch. The richer a patch is in hosts, the slower the habituation, and the longer an insect will remain in the patch (Tourigny 1985). Basic forms of learning such as habituation and dishabituation can serve to help phylogenetically 'lower forms' of life approach an optimal solution to patch-time investments problems.

Krebs *et al.* (1974) suggested that one useful strategy for an animal to adopt when attempting to forage optimally is to use the time intervals between successive captures as a measure of capture rate, i.e. giving-up time (GUT) hypothesis. Thus, the richer the habitat as a whole, the shorter the GUT would be in each patch (Hassell and May 1974, Murdoch and Oaten 1975). Roitberg *et al.* (1982) and Roitberg and Prokopy (1984) described how *R. pomonella* flies set and reset their internal clock based on host (un)availability. If no host is located within a particular allotted time, a female fly would leave a patch. If a female locates an uninfested host, she will not give-up immediately. After each oviposition, she resets her GUT clock to a lower value if her encounter was with a pheromone marked fruit and to a higher value if her encounter was with a healthy uninfested host. The GUT hypothesis and subsequent experiments clearly show that previous experience influences a fly's foraging behavior in that a fly will likely remain for a longer period of time in 'rich' patches by repeatedly resetting its GUT clock. Cowie (1977) showed that the GUT theory is not precise enough because it predicts how long a fly will remain in a particular patch but not what the fly's behavior will be while in the patch.

Knowledge of fruit density and distribution can help predict olive fly behavior. By analogy with the foraging behavior of other fruit flies (Roitberg 1985), it is likely that olive flies can assess, from a distance, host properties such as density by assessing odour concentration. In chapter five I will deal with different modality of search. Olive flies are probably primarily visual searchers and may not use odors of individual olives to locate them. Moreover, they might not perceive the ratio of marked to unmarked fruit until they actually land on host. Thus, the fly has no alternative but to sample the tree (i.e. visit individual fruits) to determine such ratios. Knowing the ratios of marked vs. unmarked hosts is important because patch value depends on density of “good” hosts and “ bad” hosts and because considerable time will be spent encountering and assessing bad hosts when they are common.

There are studies which have failed to find a relationship between GUT and overall prey density (Zach and Falls 1976, Lima 1984). Therefore, there is good reason to suggest that fly behavior is best explained by models more complex than that envisioned in the early GUT hypothesis (Mangel and Clark 1986, Mangel and Clark 1988). For example, a fly's perception of olive availability could depend on its recent history of encounters with hosts.

Cowie (1977) hypothesized that in the order to forage optimally, an animal uses information from the last few patches visited to estimate its likely net gain in a new patch (memory-window hypothesis). The memory window hypothesis suggests that it is reasonable to postulate that flies base future expectations on the sequences of past events and this is a framework that will predict fly behavior. The hypothesis helps explain certain fly behavior such as its response to encounters with marked and unmarked hosts and, the decisions that follow such encounters. These behavioral responses may employ more sophisticated forms of learning. The principal value of change is that the memory state is a very important variable in the fly's behavior and should be considered in information-dependent theories of behavior. Experimental observations show that as flies pass through life, old information falls out and the new information is gathered (Mangel and Roitberg 1989). Thus, memory updating depends on the sequence of the events (encounters with uninfested vs. infested host) that change a fly's information state. Dynamic State Variable Models that explicitly consider physiological/informational states (Mangel and Clark 1986) are useful in the study of behavioral adaptations. Such models consider the basic trade-offs that organisms face with respect to their fecundity and mortality (i.e. life history theory) (Stearns 1992). For example, an insect that forages in patch resources must make many important decisions (e.g. when to leave a certain patch) that do not fit in the unconstrained life history theory (LHT) approach, but have an effect on survival and reproduction. Bellman (1957) formulated Stochastic Dynamic Programming (i.e. a state variable approach) as a tool that allows scientists to determine the optimal control strategy for a dynamic system. The starting point of Bellman's approach is that dynamic systems are characterized by their states, and each state may consist of one or many components (e.g. body mass, crop volume). Moreover, an organism might be subjected to changes in its state variables over time which then has an effect on its behavior. Thus, the payoffs for different individual responses might be related to various ecological and physiological constraining parameters. The significance of the state-variable approach in dynamic decision models has been outlined by Clark (1993). His central five theses about the advantages of unifying LHT and BE are as follows: 1) model parameters have direct biological meaning and can be measured experimentally; 2) model predictions are often both quantitative and qualitative; they predict behavioral variation rather than unique behaviors; 3) constraints on behavior are a natural part of the model; 4) the implications of environmental fluctuations between and within generations can be analyzed; 5) a single model allows for investigating situations comprised of multiple behavioral choices and the associated tradeoffs.

Combining LHT and behavioral ecology (BE) can yield both quantitative and qualitative predictions about specific behavioral phenomena, such as payoffs for learning, and should be examined as one of the theoretical foundations for the study of adaptation (see egg-laying behavior below).

As noted above, foraging theory should consider variation in resource availability. Caraco *et al.* (1980) introduced and tested the 'risk prone hypothesis' which holds that if food or host are scarce, an animal becomes risk prone.

When an animal is threatened with starvation, rejecting current low food resources in search of potentially richer resources is clearly an advisable strategy. Experimental data are generally consistent with this thesis (Caraco 1983, Kamil and Roitblat 1985). If, however, there is a possibility that the animal will meet its current minimum requirements in current resources its behavior should become risk-averse, i.e. it is not worth "taking a gamble" and searching for new resources. If risk-proneness applies to tephritid flies then there are important implications that can be derived. First, over the course of the season, the availability of food or hosts (or both) can change drastically from bountiful to depleted resources. Second, learning might have important implications on fly behavior. If learning can lead to risk-prone behavior, it might be possible to generate risk-prone or averse tendencies in foragers.

However, it is difficult to elucidate the strategies that flies adopt to maximize fitness. The important point is that flies adopt different strategies in order to achieve their optimal solution. In some situations, habituation may be the underlying mechanism in achieving optimality. In other situations, optimality is achieved through associative learning. Insects approximate the optimal solution to a number of problems (e.g. which host patch to exploit; when to leave a certain patch). According to this general approach to optimality, learning may be a central contributor in achieving optimal solutions such as discriminating rich patches from poor patches or recognizing marked hosts from unmarked ones.

4.3 Host specificity vs. host ranking

The olive fly is practically monophagous on olives. However, under some conditions, olive flies may use alternate hosts. Host preferences are not necessarily fixed and can vary due to changes in a fly's internal physiological state caused by a shortage of the preferred host (Singer 1982, Roitberg and Prokopy 1983). There is a lack of data concerning the correlation between physiological processes and changes in acceptance or rejection of oviposition sites. There is evidence, however, that an olive fly can stop maturing oocytes and foraging for fruit when environmental conditions become unfavorable (Fletcher *et al.* 1978).

There is no evidence that the olive fly will accept other potential hosts when deprived of olives. Evidence shows that the olive fly will engage in both short and long-distance flights depending primarily on the availability of suitable hosts. In the absence of olives, olive flies behave in a risk prone way by increasing frequency movement between trees (Michelakis and Neuenschwander 1981, Katsoyannos 1983). The amount of the variation in the physiological states among individual flies is of great importance for orchard management. Flies deprived of oviposition sites are likely to exhibit changes in their behavior and energetic investment (Carey *et al.*1986, Roitberg 1989).

It is important to determine how an olive fly responds when deprived of its normal host. It is also important to examine if highly specialized fruit flies lower their threshold level of host quality for oviposition and become less discriminating (Singer 1982).

There is a difference between host specificity and host ranking according to Singer. When olive flies rank olives, black "supersize" olives are the most attractive hosts, irrespective of the season and competing hosts. Such attractiveness influences fly performance in a highly predictable manner. Ranking of hosts by flies, should be unchanged throughout the season. Depending on the circumstances, variations in the phenotypic responses of flies, with respect to host specificity (i.e. level of discrimination), are determined by the olive fruiting phenology and availability of host fruit. The willingness to accept hosts other than "supersize" black spheres as oviposition sites would occur in response to local changes in host composition at the orchard level. Such phenotypic variations in host acceptance might allow flies to utilize alternative olive hosts when the most attractive ones are not available. Whether an individual switches to a lower ranking host (e.g. small size, green variety fruits) or not will depend on the physiological/motivational state of the fly. Acceptance of a low-ranking host (strongly rejected initially) may be due to changes in physiological state of the insect (Papaj and Rausher 1983, Singer 1986). Since there is variation in phenotypic quality (e.g. age) between females, one of the critical questions to answer is how the choice is determined by previous experience with the alternatives. Prokopy *et al.* (1986) demonstrated the importance of learning on host acceptance. In experiments with apple maggot flies, females with experience show a greater tendency than naive females to reject a novel host. In insects, learning has a profound influence on the readiness to accept a familiar resource (Jaenike 1983, Papaj and Prokopy 1988). According to Jaenike and Papaj (1992) and Carriere *et al.* (1995), an increase in host acceptance is facilitated in monocultures (i.e. continuous encounter with identical resource items leads to high acceptance of those items). It may be that the positive correlation between monoculture olive systems and large-size fruit cultivars may lead to a concentration of flies in these groves. Subsequently, these systems might account for the eventual tendency to a higher infestation. There is no reason to expect that host-ranking function will be the same for all individuals of the same species; and it is unlikely that there is any single phenotype to fit patterns of environmental heterogeneity (Via *et al.* 1995). Ranking individual fruits in absolute, fixed terms of 'good' or 'bad', in their ability to influence the readiness of flies to accept a particular host, masks an understanding of the dynamic nature of memory and the dynamics of an environment which fluctuates throughout the season.

5.0 Foraging Behavior Of Fruit Flies

5.1 Introduction

Krebs and Davies (1984) and Kamil and Sargent (1981) proposed that the fundamental issue in foraging behavior is how an animal adjusts its activities in response to its environmental resources. The behavioral response of an individual to changes in the spatial and temporal distribution of resources affects the efficiency of its foraging behavior and, ultimately, its reproductive success.

The rules which govern foraging behavior can be understood by combining ecological and evolutionary approaches that emphasize the adaptive significance of behavior with mechanistic approaches that emphasize the immediate causation of behavior (Prokopy and Roitberg 1984). Contemporary foraging behaviorists focus on questions such as: What is the process by which a forager samples resources to arrive at an estimated value for a locale? How does a forager, in an attempt to satisfy all its resource requirements, go about resolving related tradeoffs? (Prokopy and Roitberg 1984).

To ensure meaningful answers to these questions, sufficient background information is needed on the physiology, ecology, and behavior of the species in question. Historically, research focused on identifying different proximate factors such as host plant distribution (Roitberg and Prokopy 1982), host fruit density, and host fruit quality (Prokopy *et al.* 1987) that influence movement patterns of flies. Though manipulation of one factor that influences foraging behavior is useful because the experimenter can manipulate a wide variety of single factors that might be important for a forager's movement patterns, such an approach may not be realistic when the combined effects are not additive (Roitberg *et al.* 1990).

Mangel and Clark (1986) and Mangel and Roitberg (1989) proposed a more unified theory-dynamic, state-variable approach to closing the gap between the 'how' and 'why' causation of behavior. The unified foraging theory is particularly useful because it recognizes that the cost and benefit for different responses during foraging might be subject to various constraining physiological and ecological factors. Such a theory could explain, for example, why a three-week-old female *C. capitata* with fully developed eggs is far less inclined to search for food than a female with undeveloped eggs, regardless of the availability of high quality food (Prokopy *et al.* 1994).

Prokopy (1993) proposed a new framework for investigating patterns of foraging behavior in fruit flies. The scheme consists of four categories: i) the current physiological state of the animal (e.g. age); ii) the current informational state of the animal (e.g. memory of previous biotic conditions); iii) the state of the current environment with respect to the distribution of essential resources (e.g. food availability); iv) the genetic state of the forager.

The ultimate aim of this approach is to investigate the foraging behavior of fruit flies in situations comprised of multiple types of resources wherein multiple factors might influence the foraging behavior. For example, Turelli and Hoffmann (1988) studied the joint effects of starvation and experience on the response of *Drosophila* flies to alternate resources. When unparasitized hosts are abundant, flies may forage similarly to one another regardless of differences in egg-load (Courtney *et al.* 1989). However, when females experience a fluctuating ratio of good vs. bad hosts, they might forage differently from one another depending upon physiological state. If there is a temporal delay of good hosts, flies might take advantage of fluctuating environment by increasing searching time for good hosts and decreasing egg production. Variation in egg-load (e.g. egg accumulation; oocyte absorption) may be due to different flies' experiences with different hosts. Research has focused on behavioral decisions of insects (e.g. host acceptance) with respect to changes in their egg-load (Rosenheim and Rosen 1991, Minkenberg *et al.* 1992). The significant interaction of egg-load and experience on the oviposition behavior of *Brachymeria intermidia*, a parasitoid of gypsy moth, was investigated by Drost and Carde (1991). Likewise, theoretical work done by Iwasa *et al.* (1984), Mangel (1987), Charnov and Skinner (1988) predict egg load as a major source of variability in insect foraging and ovipositional behavior. In fruit flies, van Randen and Roitberg (1996) showed that egg load affects tendency to superparasitize fruits.

5.4 Learning host-finding cues as a contribution to the foraging success of tephritidae

When foraging, insects may perceive host-containing environments at several hierarchical levels (Hassel and Southwood 1978). For *R. pomonella,* the overall hierarchical search levels (Roitberg 1985) are defined as: Level 1-habitat; Level 2-host tree; Level 3-tree limb (within tree location); Level 4-fruit cluster; Level 5-individual fruit.

In a hierarchical system of this sort, information obtained at one level may be used to make a decision at another level. For example, after locating an individual fruit (using information gained at level 4) a fly might engage in inter-habitat flight (using information gained at level 5).

Level 1: habitat

Entomophagous parasitoids such as *Cotesia marginiventris* (Cresson) (Turlings *et al.* 1989, Turlings *et al.* 1991a) can learn to select the habitat with which their larval hosts are associated. Such learning has not yet been demonstrated in phytophagous parasites (Papaj and Prokopy 1989).

Boller *et al.* (1971) reported that visual perception of a silhouette image may be a major long-distance cue for *R. cerasi.* Experiments with tree models indicate the importance of size, color, shape, and orientation for increased attention in Tephritidae (Meats 1983). This is also true for *R. pomonella* (Moericke *et al.*

1975). It was shown that fruit flies are generally attracted to large, colored surfaces. Wehner (1975) studied possible mechanisms underlying this attraction. Apparently, flies are not attracted to the color and hue of checker-board traps but they are attracted to silhouette images (i.e. spatial and temporal contrast) that indicate trees.

Visual landmark learning (van Iersel 1975, Gould and Towne 1988) may be influenced by an insect's orientation to the moon and sun. One possible benefit of landmark learning is being able to avoid previously visited habitats. Sheehan *et al.* (1993) demonstrated this phenomenon in *Microplitis croceipes.*

It might benefit a fly to discriminate profitable locations from exploited ones by searching efficiently and systematically at the habitat level. More information is needed on the role of visual learning at this level.

Level 2: host tree

Once in a habitat, searching by *R. pomonella* depends primarily on visual characteristics of the host plants (Prokopy *et al.* 1973, Moericke *et al.* 1975, Prokopy 1977). There are several reports on the role that visual cues, such as the shape and size of the host trees, play in tephritid foraging behavior (Prokopy and Haniotakis 1976, Meats 1983). Though visual stimuli play significant role in host tree location, it appears that they are non-specific to the host (Prokopy and Haniotakis 1976). They are attracted to the general tree shapes.

Besides visual stimuli, chemical cues emanating from the host tree might be important in attracting flies to the trees (Prokopy *et al.* 1973). Volatile components of ripening olives might be important long-range cues for guiding olive flies to host plants (Guerin *et al.*1983, Girolami *et al.*1983). The odor of host fruits has elicited a positive response in a number of tephritids: *C. capitata* (Guerin *et al.* 1983); *D. dorsalis* (Tanaka 1965); *D. cucurbitae* (Tanaka 1965). Reliance during foraging on volatile cues emitted by host plants is reported also in the larval parasitoids *Cotesia marginiventris* (Cresson) (Turlings *et al.* 1989, 1991a) and *Microplitis croceipes* (Cresson) (Drost *et al.* 1986, 1988, Zanen and Carde 1991). Turlings *et al.* (1991b) reported the importance of prior experience in wasp responses to host plants. *M. croceipes* females with more experience showed increased foraging efficiency (Lewis and Martin 1990).

It appears that, at this level, to enhance searching efficacy, flies might learn both olfactory and visual cues. Experience associated with both visual information about the olive tree and specific odor plumes of ripening olives might induce a stronger response than experience with either alone.

Level 3: tree limb (within tree location)

There is growing evidence that once in the trees, flies locate plant structures almost exclusively through visual cues (Prokopy and Roitberg 1984). According to Drummond *et al.* (1984), however, flies have to be within 1 m of the plant structures in order to locate them. Size, shape, color and hue and intensity of leaves and individual fruit is important for host location (Owens 1982, Owens and

Prokopy 1986).

Several behavioral studies of attraction by color or shape or both in Tephritidae have shown that they are attracted to shapes resembling host fruit and colors resembling host plants (Bateman *et al.* 1976, Prokopy and Boller 1971, Prokopy *et al.* 1975, Prokopy and Economopoulos 1976). Aluja and Prokopy (1993) and Prokopy *et al.* (1994) found that visual stimuli such as size, and, fruit surface chemistry, but not fruit odor, are used by *R. pomonella* as cues for finding individual fruit. Those cues also have an effect on whether a fly subsequently select a fruit for oviposition. Prior experience with fruits of the same cultivar that differ in color has no effect on the ovipositional tendencies in *R. pomonella* females (Prokopy and Papaj 1988). Learning the size and/or surface chemistry of fruits is sufficient. Similar ovipositional properties are found in other tephritid species, including *Ceratitis capitata* (Cooley *et al.* 1986, Papaj *et al.* 1988), *Dacus dorsalis* (Prokopy *et al.* 1990) and *Rhagoletis mendax* and *R. suavis* (Prokopy *et al.* 1993). In the case of *Dacus tryoni*, both visual and odor stimuli are necessary for finding individual fruit (Prokopy *et al.* 1991).

The important practical implication of these ovipositional properties is that inanimate objects mimicking visual characteristics, such as the size and color of individual fruits, are attractive to flies and can elicit ovipositional behavior in them. Prokopy and Haniotakis (1976) reported that flies can not distinguish real fruit from a mimic before actually landing on it.

A spherical shape may be the most attractive for most tephritid flies, since it can be seen by the flies from all directions (Nakagawa *et al.* 1978, Roitberg 1985). A black sphere, 7.5 cm in diameter, is the most attractive to olive flies (Prokopy and Haniotakis 1976). This preference for a size larger than the real fruit of most varieties was confirmed by Katsoyannos and Pittara (1983). *R. pomonella* flies are known to find large 8 cm, red spheres the most attractive (Owens and Prokopy 1986).

Olive flies might be capable of finding black "supersize" olives more easily irrespective of whether they had previously laid eggs in those mimics or in other types of mimics or fruits. By understanding the dynamics of host finding we may be able to provide flies with an appropriate level of experience that would subsequently lead to more predictable and desirable behavior of flies with low variability of response patterns. "Supersize" olive mimics around the perimeter of commercial plantings could be used as interception traps to prevent entry of females into the interior of the groves. A sufficient rate of fly encounters with fruit mimics would reduce encounters with regular fruit sizes. This scenario is based on the assumption that prior fruit experience of foraging flies arriving at perimeter trees has no effect on the flies targeting for supersize host (i.e. top-ranked fruit should not decline in value). Predictability of fly behavior is determined by the informational state of flies. The availability of supersize host could result in the rejection of all other cultivars when such cultivars are perceived as less valuable hosts.

There is evidence that female flies will attempt to oviposit into a fruit mimic similar in characteristics (e.g. size) to a fruit they have experienced (Papaj *et al.* 1988) and that there are seasonal differences in flies' responses to fruit mimics of different sizes (Prokopy 1977). Under certain circumstances, the memory state of immigrating flies (e.g. prior experience with black fruits approximately 3 cm in diameter) arriving on a perimeter tree containing fruit mimics would differ from the input patterns (e.g. perimeter trees of green varieties containing black fruit mimics, approximately 3 cm in diameter). If the current situation (encounter with perimeter trees of black mimics) is not similar to a previously encountered situation (oviposition experience with black varieties of olives), it is possible that the previous memory might not be recalled and the flies might bypass black mimics completely. The probability of success from this approach is based on three major assumptions. First, that the fly's short-term memory is retained intact at the time of arrival on the trap trees and that the fly would reject an unfamiliar fruit of a different size and/or color. Second, that comparatively few flies will penetrate the ring of interception traps. Third, that of all dropped fruits within the orchard are removed to prevent competition from resident flies within the planting. This is important in groves consisting of early maturing olive varieties. It is likely that early-flowering cultivars with large black fruit sizes will be preferentially attacked by this pest in early summer. In regions characterized by cold winters and hot, dry summers where *D. oleae* development is interrupted mass trapping with " supersize" fruit mimics may be economical. Therefore, it would be useful to plant cultivars with black 'supersize' fruits (or mimics) that would assume the role of interception 'trap trees'. In orchards containing olive trees of different cultivars (e.g. perimeter trees bearing green cultivars) searching females, after encountering “supersize fruits”, might base their behavior on information stored as a long-term memory (=reference memory), (or which may be largely innate) rather than on a short-term memory. Flies would then accept 'supersize' hosts irrespective of their prior ovipositional experience or subsequent encounters with novel cultivars. In the presence of “supersize” hosts, switching preference to any other type of fruit may not occur. Thus, long-term memory may be triggered and the flies would concentrate their search at those trees containing “supersize” hosts.. Presumably, flies could be eliminated there before oviposition.

In the absence of “supersize” hosts, interactions between old and new short-term memories (prior ovipositional experience vs. encounters with novel stimuli) might happen. For example, a fly may concentrate its search effort on the cultivars of the greatest local abundance if the most familiar hosts are not found (the most recent ovipositional experience on particular cultivar). When immigrating females are deprived of such fruit, it seems fair to assume that “fall outs” of the prior ovipositional memories are expected to happen after a few days (Prokopy 1993) likely due to limited capacity and duration of short-term memories in insects. However, a fly's recently remembered ovipositional experience might contribute negatively to the outcome of employment of interception traps. Though learning might be a major component of behavioral variation in foragers, other factors, such as a fly's egg-load status, may play a significant role (e.g. egg-load could override any experiential effect).

Level 4: fruit cluster

At this level, flies hop from leaf to leaf in search of fruit. The foragers search systematically until they see fruit clusters. Roitberg (1981) demonstrated that the search paths of flies can be easily and precisely mapped. His conclusion is that female movement patterns within the tree are not random. For example, if oviposition occurs, the fly will continue the search nearest to the position where she last found a cluster and oviposited.

Level 5: individual fruit

After arrival on individual fruits, foragers evaluate a variety of host characteristics through chemosensory means. Schoonhoven (1982) showed that most phytophagous dipterans do not take test-bites of hosts because of the structure of their mouths. Despite this anatomical constraint, for a fly, it is essential to obtain information on fruit ripeness, and presence of conspecific immatures in order to assess whether or not the fruit is acceptable for egg-laying (Seo *et al.* 1983, Roitberg 1985). A fly's assessment of the presence of conspecific immatures is often referred to as host discrimination (van Lenteren 1981), a phenomenon observed in many parasitic insects (Price 1977, Prokopy 1981). Thus, given this ability to discriminate between good and bad hosts foraging insets must decide either to accept or to reject a certain host. When a female *R. pomonella* accepts a host and lays an egg in it, she generally deposits a host-marking pheromone (HMP) by dragging her extended ovipositor over the surface of the fruit (Prokopy 1981, Roitberg and Prokopy 1987). According to van Alphen and Visser (1990), most parasitoids can recognize hosts which have been parasitized either by a conspecific or by themselves. In general, given a choice, a female would reject such a host due to preference to oviposit in a healthy, unparasitized host (Visser *et al.* 1992). However, often a female will lay more than one egg in an already parasitized host, an act known as superparasitism (Salt 1961). Oviposition in an already parasitized host was once considered maladaptive, and avoidance of superparasitism adaptive under all circumstances (van Lenteren 1981, Huffaker and Matsumoto 1982). Superparasitism by solitary parasitoids may however, be advantageous under certain conditions (Bakker *et al.* 1985, Visser *et al.* 1992, Visser 1993). It is of great importance to IPM to understand the conditions under which superparasitism of fruit, or its avoidance might be of adaptive value for foragers. For example, in circumstances when probability of rejection of a bad host by searching flies is high (i.e. when good hosts are abundant) application of synthetic equivalents of HMP in an orchard would be advantageous. The rationale for using HMP is based on the assumption that encounters with a bad host would have little impact on a fly's fidelity toward unparasitized hosts. The adaptive significance of avoiding infested hosts, as ovipositional sites, is in the increased fitness of a female's progeny by minimizing larval competition. On the other hand, management tactics that promote avoidance of superparasitism (deterrent effect) would probably be less effective when flies readily accept bad hosts. When the probability of finding a good host is minimal (low value habitat) and the number of conspecific females foraging in the same area is high, it is likely that foragers will lay at least two eggs in the same host. Self-superparasitism could be advantageous if it serves to increase the rate of survival of one of the female's own progeny compared with conspecific superparasitism where her progeny have to compete with eggs of other females.

Deposition of a marking pheromone is commonly observed in parasitic insects. *Opius lectus*, a parasitic wasp, employs marking pheromones after oviposition in *R. pomonella* eggs (Prokopy and Webster 1978). Van Alphen *et al.* (1987) found that host discrimination by insect parasitoids does not have to be learned, but that previous ovipositional experience with parasitized hosts might influence the inclination to superparasitize. Roitberg and Prokopy (1981) demonstrated that responses to HMP improve with experience. Furthermore, host deprivation influences a fly's response to HMP (Roitberg and Prokopy 1983).

Refraining from ovipositing is negatively correlated to the elapsed time since prior oviposition and contact experience with host markers. Active search time of fruit flies foraging in trees can vary between individuals in response to previous experiences with either HMP marked fruit or unmarked fruit. Naive *R. pomonella* females exposed to unmarked fruit had significantly longer search time within a tree canopy than experienced females exposed to HMP marked fruits. They emigrated faster from the tree and had an increased rate of trivial movement (Roitberg *et al.* 1982, Roitberg and Prokopy 1984). Work with *R. cerasi* has shown similar results (Aluja and Boller 1992). My previous discussion of insect learning stressed the importance of considering the relationship between the degree of resources variability and the value of learning within the context of decision making. However, foraging females face a patchy distribution of host and must decide to either accept or reject a certain host. A crucial way of dealing with such phenomena would be , as was discussed before, to posit the assumption that fly behavior cannot be described in isolation from its environment. Under such conditions, efficiently "sampling" these variable resources could be a primary determinant of reproductive success. Another significant fact is that when flies are continuously deprived of good hosts they eventually oviposit in marked fruits despite the presence of marking pheromone (Roitberg and Prokopy 1983). Similarly, Aluja and Boller (1992) provided evidence that when flies were continuously exposed to an HMP-saturated environment (e.g. tree completely covered with synthetic HMP) they resumed egg laying in marked fruits, probably due to habituation. For management purposes, it would be useful to exploit the ability of flies to discriminate between good and bad hosts and the propensity of HMP to elicit certain behavioral responses.

The results of field application of HMP and its potential use as a large-scale management tool to reduce infestation of cherries (Katsoyannos and Boller 1976, 1980) (they reported up to 90% reduction of fruit infestation by wild *R. cerasi*) and practical application techniques under field conditions (Boller *et al.* 1987, Aluja and Boller 1992, Boller and Aluja 1992) are promising enough to justify the continuation of research.

Direct behavioral observation of flies in the field (Prokopy *et al.* 1987) and computer simulation (Roitberg and Angerilli 1986) yielded valuable information about the patterns by which flies locate and select their ovipositional resources in the presence of HMP.

6.0 Evolutionarily valuable signals

Evolutionarily valuable signals (EVS) such as marking pheromones, or host shapes, play an integral role in insect pest management (e.g. synthetic host mimics-SHM). Evolutionarily valuable signals are highly reliable host-derived cues formed as a result of a long evolutionary history of a species. Currently, the traditional stimulus-response model of trapping (both for monitoring and mass-trapping) is used for almost all insect life stages and in all seasons (Delrio 1987). As a result, many decisions in olive fly IPM are based on the premise that all flies caught in the traps are in uniform, narrow, physiological states, and are nearly ready to lay eggs. The assumption that all flies are uniform leads to the incorrect conclusion that individual flies have the same experiences and that different responses to the same trap are rare. However, individuals in the population are likely to have different histories and thus belong to various sub groups. Therefore, one might expect a myriad of different responses to the same stimuli (Robertson *et al.* 1995) .

It is difficult to understand variations in insect responses to identical chemical signals under various environmental conditions (e.g. response to host marking pheromone in early summer vs. autumn). Insect-pheromone related studies have investigated the changes in stimulus-response patterns that may be brought about by manipulating trap variables such as size. However, traps are often used without a firm understanding of the basic behavior of the olive fly. Research on mass trapping is primarily concerned with how many individuals are caught in a trap that is set for some period of time and what type of lure is best. Research should concentrate on how and why flies respond to particular cues. A pest manager should have a working model that includes a general theory that behavior changes as a consequence of prior experiences with certain types of stimuli (e.g. size) associated with EVS (e.g. shape). This might provide a better understanding of inexplicable variations in mass-trap trials. Every variation in response within a certain population is due to higher or lower sensitivity of the insects towards EVS, which may vary greatly throughout the season. This implies that the same methods of control cannot be applied to all individual flies. On the other hand, relatively uniform physiological states may prevail for a short time at the beginning of the season, when most individuals will be more "choosy" as a result of ample healthy hosts. For two reasons, observations on how individual flies with different physiological profiles behave toward EVS in certain situations, are not sufficient to conclude how many flies would actually land on a trap or how many of them would avoid it completely. First, descriptions of the insect behavior are still merely descriptions and do not speak of origins. Second, the descriptions are of behaviors and not inner states (e. g. egg-load status, informational state). Refinement of descriptions does not lead to a better understanding of behavior. Consider only behavior, I suggest that the field of study is overwhelming since the possibilities of fruit flies to produce different behavioral phenotypes throughout the season are endless. For a better understanding of a pest's behavior, it is useful to distinguish between the correlation and causation of it. Correlation is not the proof for causation of a particular behavior. For example, two individual flies can behave exactly alike. They both may be efficient at a particular task (e. g. finding and ovipositing in a healthy host). In doing the same task, one may be a seven day old, recently-fed female, while the other one may be an unfed mature female near the end of her life. In each case a predictable outcome follows (egg laying); but the causes for it may differ radically. In either case, those different causes may affect various pest management methods. In the case of a seven day old, recently-fed female, I hypothesize that young age and the high physiological condition may lead to increased host selectivity (she is egg rather than time limited). As a result, this female would therefore be a candidate for the employment of HMP (promoting immigration from host trees). For her, it is more profitable to spend more time searching for a healthy host. The behavior of the unfed mature female near the end of her life would be governed largely by her low expectation of life. It is therefore possible that increased acceptance of an unhealthy host would translate into a significant effect on employment of synthetic host mimics. None the less, this female would likely be more receptive to this kind of behavioral manipulation than the former one, since she is time rather than egg limited. The concept of intercepting flies before they enter an orchard and oviposit and taking advantage of a fly's "choosiness" by employment of HMP will be discussed later . Fly behavior is complex. If one concentrates only on the correlation phenomenon (acceptance of a host within the context of the descriptions of an overt activity) in the foregoing example without probing the causes that constitute this behavior (acceptance of host within the context of hunger level vs. age of the animal) all explanations, or management decisions, would be of unpredictable value. Egg-laying behavior is not just an overt behavior, it is part of an organismic behavior which includes the state of hunger, age of the flies, mating status, season patterns, etc.. To study egg- laying behavior alone is but one more fragmentation of the flies behavior. Conceptually, the important point for implementing management strategies in IPM should be prediction. No prediction can exist without trying to determine both the evolutionary origins of certain behavior and the possible constrains (e.g. physiological) on the evolution of this behavioral response.

Research on insect ovipositional behavior (Courtney and Kibota 1990, Singer *et al.* 1992, Barton Browne 1993) has shown that a large number of variables affect the egg-laying process in insects. Egg laying is a complex, non- linear process thus, it is difficult to predict the dynamics of insect behavior by using a simple, one-parameter approach (e.g. egg-load, host availability).

Instead, one might employ a multivariate evolutionary theory from the perspective of a female's future reproductive success. The unifying assumption is that there must be a strong evolutionary relatedness between response profiles of individual flies and their fitness. When attempting to develop IPM practices that are semiochemically and ecologically based, an overemphasis on an insect's capability to respond to semiochemicals sometimes excludes ecological and evolutionary aspects.

The unpredictability of behavior presents problems for applying behavior-based tools in pest management, and some of the difficulties stem from the absence of an evolutionary approach (Brady 1985).

6.1 Response profiles and the concept of beyond-ethology

Insect behavior should be described in terms of response profiles rather than by traditional stimulus-response patterns (Roitberg 1992). The model employed here is only partially derived from ethology and largely from ecology and evolution. The concept of 'beyond ethology' gives as much attention to understanding chemical signals from an evolutionary perspective as to the practical implications of the range of responses to the same chemical signals under various environmental conditions (Alcock 1982, Roitberg 1992, Roitberg *et al.* 1994). Roitberg (1985) utilizes the beyond-ethology approach by employing the natural selection theory which requires Tinbergen's four questions. The questions are related to the ontogenetic (development of individuals), proximate (immediate), the phylogenetic (evolutionary history), and ultimate (survival value) causes of behavior. It is a big challenge to yield complementary answers to the four questions. However, together they can provide a more complete picture of behavioral phenomena than the dual approach (proximate and ultimate causation) which sometimes can lead to oversimplified and inappropriate explanations of the patterns of behavior. Endler (1986) stated 'it is important for behavioral ecologists first, to separate proximate and ultimate causes of behavior and second, to evaluate the factors which constitute ultimate causes (phylogeny, natural selection and stochastic processes- such as mutation, genetic drift)'.

When studies of behavior neglect evolutionary aspects, an important set of explanations is lost. For instance, the aim of employing marking pheromones in orchards is to increase the host “choosiness” of the female and thereby increase the probability of her leaving the orchard. The strategy works on the assumption that foraging females reject unhealthy (i.e. infested, parasitized) hosts and subsequently leave the orchard. However, egg-laying behavior is very complex and does not always conform to the immediate and simplistic linking of stimulus and response. When ample healthy hosts are available, a foraging female will reject an unhealthy host. In other situations, the rejection of an unhealthy host would actually decrease fitness and a fly is therefore "better off" laying in an unhealthy host than not laying an egg at all (Charnov and Skinner 1988). Behavioral response to a stimulus may depend on certain information derived from a combination of external and internal stimuli and guided and terminated by the continuous reception of further information (Miller and Strickler, 1984). Evolutionarily valuable signals can be understood and employed within an evolutionary and ecological framework that consider the worth of such signals in relation to fitness.

6.2 Modifying trap characteristics according to the "beyond-ethology" concept

Seasonal trap use for fruit flies should follow regular changes in foraging behavior. Yet, the correlation between fruit size and tendency to oviposit is not always predictable. There is also a change in preference of *D. oleae* for fruit within the same cultivar throughout the season as well as within different varieties (Michelakis 1987). Therefore, "good" and "bad", with respect to different varieties, sizes, shapes, colors and odors, are relative descriptions for hosts. For example, after ovipositing in a host of a certain size (e.g. larger fruits of the macanilha cultivar), a female might encounter another different-sized, healthy host and reject it in the early season when good hosts are common. The increment of fitness is lower not only from laying an egg in a parasitized host than in a healthy one but also from laying an egg in a smaller host than in a big one. By laying an egg in a healthy (and bigger) host a parasite will accrue a larger increment of fitness because the offspring will have a higher rate of survival and a greater likelihood of reproducing. Later in the season, a fly's preference for hosts may change. To reject an unfamiliar, healthy host fruit based on its size would be costly in the late season because few good hosts of any size are available. Thus, initial avoidance of a low-ranking variety (e.g. small size fruit cultivars) is an adaptive phenotypic response in an early-season environment but is maladaptive as the season progresses. This propensity of accepting previously unacceptable hosts is thought to be correlated to female reproductive success. Selection pressure on female oviposition preference should maintain a low level of "choosiness" when "good" host are rare, because the expectancy of surviving in heavily infested areas will increase with a wider degree of acceptance of hosts. In a sense, every host becomes "good" in the late season.

Modifying trap characteristics for quantitative measurement (i.e. monitoring purposes) may be especially important in the early spring (i.e. early detection of pest reservoirs), since favorable weather conditions may permit rapid insect reproduction in the unharvested fruits from the previous year. As the number of flies increase, attacks on new fruits in early summer might follow. For this reason, trap modification must be in accordance with a particular stimulus learned by the fly. Otherwise, its efficacy (i.e. accurate reflection of the fly population size) for monitoring purposes may be compromised. It appears that the use of odor/visual traps for quantitative measurement has, generally, been difficult since variability in factors which affect fly behavior were neglected. More specific knowledge about the olive fly's ability to learn a particular stimulus is needed for traps to be more useful. With improved trap design and placement, early detection of invading flies and the extent of invasion should allow growers to reduce insecticide application and enhance their acceptance of such monitoring programs. More attractive stimuli would trap more flies and, could be used for area-wide population suppression (i.e. mass-trapping).

An example that phytophagous insects can learn properties specific to a host is the egg-laying behavior of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Katsoyannos 1987). There is a corresponding relationship between oviposition in a host of a particular size and later acceptance of host-fruit mimics of the same size due to the recent experience with that host (Prokopy *et al.* 1989). Thus, traps can be made to be more selective which may reduce trap density (i.e. the number of traps per area unit). This is desirable for ecological, economical and practical reasons. A mass-trapping scheme might require adjustment over time to follow the low-crop-high-crop cycle of olives that is observed in olive orchards (i.e. higher population density of flies per olive is expected in a low-crop year) and to adjust to the changes in the susceptibility of the olive fruits among different varieties and within the same variety. For example, the infestation of the fruit of the koroneiki cultivar, which has small olives, is far less than the infestation of the manzanilla cultivar, which has big olives (Michelakis 1987). Locale-associated variations in the female response (i.e. when more than one cultivar is available) should be considered (Katsoyannos and Pittarra 1983).

7.0 Olive grove ecosystems

To understand olive fly behavior, it is useful to be familiar with some of the characteristics of modern day olive agro-ecosystems. The permanence of their plants (olive trees can live for centuries) and long-lasting productivity (though they display year-to-year fluctuations in yield) are the hallmarks of olive groves (Katsoyannos 1992).

Olive trees can grow and produce in hilly, rocky, and dry areas where other permanent crops cannot. Other characteristics common to olives are that they can grow in a variety of soil types (e.g., sand or clay). The stability of the climate in olive groves is generally high throughout the Mediterranean basin. Tree density ranges from 17 trees/ha. in Sfax, Tunisia to an intensive 400 trees/ha. in Italy (Katsoyannos 1992). High grading standards of the olives, in intensive orchard systems, demand that damage to the fruit be very low. The basic structure of olive groves today greatly resembles those of their ancestral environment. The presumed origin of *O. europaea* is Egypt and Ethiopia where *O. chrysophylla* (Lam.) may be an ancestor of *O. europaea* (Katsoyannos 1992). Differences from ancestral habitats include shorter inter-tree distances, and a higher density of hosts per hectare. Each grove is characterized by a particular number of olive varieties and each variety has a certain size, shape and color.

There are different cultural systems including individual trees, small plantations and large plantations. Olives have a biannual fruiting pattern and the fruit generally ripens slowly. However ripening patterns vary within and among trees. The introduction of novel stimuli such as the application of biocides and intensive harvesting practices, have introduced stressful events into the olive fly's habitat.

The resource concentration hypothesis (Andow 1991) postulates that a pest might be more abundant in homogeneous than heterogeneous habitats because hosts are easier to find. Modern olive plantations permit the maintenance of denser populations of flies in the orchard for most of the season. An olive fly can cause more damage in a monoculture than in diverse habitats (e.g. olives and beans) (*pers. obs* 1991). The orchard structure itself might modify fly behavior in both host-finding success and damage level. No attempt has been made to test the plant-odor masking hypothesis (Nottingham 1988) that non-host vegetation in an olive orchard might interfere with flies' short-term memories of encounters with host plants. Thus, work remains to be done to show the possible potential of minimizing pest damage through manipulation of the species composition of the habitat (i.e. monoculture vs. polyculture). The outcome of this strategy might depend on knowing the patterns of the flies' "trivial movements" within the olive groves (e.g. up or down the length of a row) and the ability of non-host plants to interfere, through habituation, with the short-term memories of foraging flies associated with the olives.

7.1 Patterns of olive fly movement and structure of the habitat

Being able to predict an olive fly's movements (both long and short-range dispersal) would allow for behavioral exploitation and better management systems. Bell (1990) reported that variations in distribution, quality and quantity of food is likely to have an impact on the movement of dipteran adults. Fruit flies require energy to support both somatic and gametic functions. Field observation (Katsoyannos 1983) indicate that the movement of olive flies follows a pattern determined by the need for food and host. Flies spend a great deal of time in a back-and-forth movement foraging for food and hosts.

Fundamental resources such as nectar sources and egg-laying sites may be in the same or separate sites. Feeding behavior is influenced by the presence of nutrients, the form of the diet (solid or liquid), and whether the solid and liquid are mixed or separated (Tsiropoulos 1980). Progress has been made on the topic of resource searching by medfly adults (Prokopy *et al.* 1993b). In nature, adult olive flies acquire necessary nutrients from a large variety of food sources (Tsiropoulos 1977). Flies from humid areas, that feed on a liquid diet, lay more eggs and have a shorter preoviposition period than those feeding on a solid diet (Tzanakakis *et al.* 1967). Females from dry areas prefer solid diets. Thus, feeding on a particular diet could lead either to an increase or a decrease of reproductive success.

It is important to understand how the quality and distribution of nectar is related to a fly's oviposition behavior. What kind of tactics does the fly employ? Does it forage in "risk-averse" manner which guarantees it will return to a nectar resource even if the quality of the host is not high or does it act in a "risk-prone" manner searching with a much greater risk of total failure during foraging? If fundamental resources are within the same habitat, then a fly may act in a "risk-averse" manner. It could concentrate its activities within or close to the host plants, even in cases when host sources are not high quality. Instead of searching for a higher quality host at other sites, a fly might decide to stay and occasionally oviposit.

It will be crucial for olive IPM to develop the state-variable modeling approach, with respect to host-site vs. food-site searching behavior and its tradeoffs. Such an approach might provide more profound knowledge about how olive flies respond to events that occur during foraging. For example, a fly that has not acquired sufficient protein to mature eggs is likely to search for nectar sources (energy sources). However, a recently fed fly, may be expected to exhibit a greater search effort for host resources and will be unlikely to feed on proteinaceous food sources regardless of their quality. Simple dynamic models, with a few state variables (e.g. energy reserve vs. nectar availability), could also generate insight into the evolutionary perspective of the proximate and ultimate causes of particular response profiles that have evolved in olive ecosystems. The models could also generate more accurate predictions about the foraging behavior of individual flies over a wide range of different conditions (e.g. choices available under risk of starvation).

When fig-trees bearing ripe fruit (food sites) are located near olive groves, those groves sustain heavier attack by olive flies than other groves (Katsoyannos 1983). Over the same period, captures of olive flies on non-host plants such as fig-trees were higher per trap, per tree, than captures within the adjacent, heavily infested olive groves. These results indicate that the nature of the relationship of olive flies to figs, at least at certain times in the season, may be of fundamental importance to understanding the "foraging strategies" of egg-laying, aggregation to food sites, and "trivial" movements of olive flies. Hypothetically, if flies spend more time on figs acquiring nectar and less time flying between food resources of other plant species (e.g. citrus) while moving back-and-forth between olive trees and fig trees their rate of net energy intake might be increased. Thus, no advantage would be gain from switching to unfamiliar resources.

An insect can learn to store major visual and odor cues associated with its hosts (Prokopy 1986, Papaj and Prokopy 1986, Sheehan and Shelton 1989) as short-term memories of encounters with highly rewarding resources. The olive fly seems to have the ability to recognize the situation where fig trees and olive trees occur together. However, the computational capacity of olive fly memory relative to her simultaneous manipulation of at least two resources is so far untested. Experiments on bees (Koltermann 1974) suggest that this may be possible.

The presence of another alternative major food source for olive flies when figs are not available is currently not known. To understand the temporal foraging dynamics under such conditions (interaction between availability of food and ovipositional sites) it is necessary to take into account the limited capacity of the short-term memories of insects. By preventing insects from accumulating information about the environment indefinitely, insects may be more inclined to exhibit constancy in certain behavioral choices (Menzel *et al.* 1993, Waser 1986). For example, if an olive fly experiences a higher reward than expected on fig trees it may afterward bypass other potentially rewarding food resources. The active status of short-term memory may facilitate a maximum net energy gain on figs and keep flies focused on this food resource. Turlings *et al.* (1993) demonstrated that insects may be focused strongly on a certain resource after repeated successful encounters with it. But the favorable conditions can change dramatically during the season due to the disappearance of figs or their depletion. It makes sense to assume that under these conditions (low or zero expectation rate of net energy gain from figs) it may profit flies to switch to other available host(s). According to the economic theories of behavioral regulation, animals manage to maintain themselves on a positive energy budget (Collier and Rovee-Collier 1981). A practical implication of this is that constraints on an olive ecosystem might motivate flies to adapt to these changes through information collection which would generate modified behaviors. Flies may approximate the optimal solution throughout the season in terms of discriminating rich resources from depleted ones. Olive groves may consist of both risk-prone and risk-aversive foragers. Rather than assuming that a particular single-mix of risk-prone or risk-averse individuals would be maintained in the environment, progressive appearance and disappearance of phenotypes is likely to be expected. Thus, the same individual might be risk-prone in some situations and risk-aversive in others. Like bees (Heinrich 1976), olive flies may be able to learn the spatial positions of host clumps and the flight paths between them. Some butterflies can use landmarks to find familiar locations (Papaj and Prokopy 1989).

Michelakis and Neuenschwander (1981) observed that in the absence of hosts, olive flies tend to move between groves. This indicates that olive flies behave similarly to honey bees (Brown and Demas 1994) and many invertebrate and vertebrate animals, such as rats (Olton and Schlosberg 1978, Olton *et al.* 1981), that have a natural "win-shift" predisposition (i.e. inclination to leave an area depleted of resources). The "win-shift"strategy is based on the premise that an animal has a small but reliable tendency to avoid revisiting locations recently depleted of resources. The "win-shift" condition entails a sequence of behaviors that starts with “win-stay” tendencies (i.e. inclination to stay in an area depleted of resources). Responses to the host might increase significantly through revisiting certain locations until the resources are depleted and 'win-shift' tendencies begin. The assumption has to be made that olive flies are more alert to respond to EVS in certain types of habitats, such as when a fig grove is near an olive grove. Turlings *et al.* (1989) and Eller *et al.* (1992) demonstrated that *Cotesia marginiventris* enhanced her search efficiency after contact with her host. Vet *et al.* (1990a) showed that insect antennae become more sensitive through events that insects experience.

Theoretically, the eradication of nectar sources within or close to orchards would alter the flies’ behavior and force them to leave their host plants. A more thorough understanding of the frequency of such flights, would allow for interference with these patterns. For example, immigrant adults engaged in “trivial movements” could be intercepted by olive mimics placed between olive trees and fig trees. Those mimics should be closer to fig trees, since olive flies show a distinct preference for fig trees. A substantial number of well-fed and mature-hungry flies would probably visit those mimics and try to oviposit there. This alone would probably not be sufficient to provide desirable management in groves, due to within-population behavioral-phenotypic variability. Hungry individuals may show a greater tendency to search for food when both types of resources are present simultaneously and consequently bypass olive mimics. The outcome of this tactic would also depend on the previous experiences of immigrating flies. Papaj *et al.* (1987) demonstrated that the medfly can learn certain features of its host and memorize them for several days. If olive mimics do not match characteristics of olives from the groves where immigrants had ovipositional experiences, the flies might bypass the olive mimics. Thus, it is essential to know specific features that determine whether a fly accepts or bypasses a host.

The future focus, should be to develop a framework where in general behavioral theorems and individual-based dynamic models are linked together. There are two major reasons for this. First, increasingly sophisticated behavioral theory can provide predictions about the expression of various behavioral phenotypes over a broad range of olive ecosystems. Second, modeling can place fitness consequences into a fly's life-history. Even though little has been done on the topic, possible basic combinations should be considered that may influence long and short-range movements of olive flies.

7.2 The roles of seasonality and evolution in host acceptance by *Dacus oleae*

This chapter explores changes across time in the quantity and quality of host availability in the context of the egg-laying behavior. It is important to take the time factor into account, because resource-exploitation behavior (egg-laying decisions, dispersal and non-dispersal movements) is a dynamic process not only determined by endogenous (e.g. age) but also by exogenous factors not yet discussed (e.g. variation in habitat quality as a time function). This aspect has implications for a number of general issues in the study of foraging behavior. I will examine certain of these implications (e.g. environment's overall predictability; life expectancy; the value of the retention of information, the onset of unfavorable conditions) with regard to oviposition behavior. What bears directly on the issue from an IPM prospective is the importance of being able to predict under what conditions a fly would rather reject than accept a bad host. In certain situations, learning and memory will be important for egg-laying decisions, and in other situations, they will be of little or no use.

7.3 Egg laying in the early season

At the beginning of the season, healthy hosts are predictably available in large numbers and flies probably reject bad hosts during this phase. Egg laying is determined largely by the female's preference to lay eggs in more mature hosts (Kapatos *et al.* 1977). A large supply of good hosts is available for immigrants coming from areas with few fruits as well as for flies that emerge in the local olive grove. During this time females may sample the habitat through continuous encounters with good hosts and store this information as short-term memories. The retention of this information has low value because the cues that a fly must remember in the early season do not vary from trial to trial.

Alternatively, the female may have a "hard-wired" expectation that good hosts will be available. In either case, she will reject a bad host.

Based on characteristics of ancestral olive habitats (e.g. predictable good hosts available) and the life history of the olive fly (e.g. most flies will emerge from olives that have matured and fallen to the orchard floor), in the early season, the retention of short-term memory could be more costly than no memory, since there is hardly anything new to learn about the host and its environment. Taken in isolation, and against that background. the general capacity to retain the information might seem implausible. From this perspective one may simplistically assume that memory length is season-dependent. Those assumptions are not logical first because olive groves are only partially regular and invariant and second because to respond appropriately to this kind of environment flies must retain capacity to learn (what changes is the amount learned) throughout the season. To function effectively (respond to changing environment) learning ability should remain constant, whereas response to seasonal changes may vary dramatically.

The relationship between the size of the "memory window" and foraging behavior efficacy was examined by Hughes *et al.* (1992) and MaCkney and Hughes (1995). They demonstrated that the stickleback fish "memory window", in terms of the predictability of hosts, may vary largely between different foraging regimes. Retention of a longer "memory window" and previously learned skills was observed in residents of predictable, unfluctuating habitats (ponds) but not in individuals restricted to more unpredictable habitats (estuaries). These results are in accordance with the theoretical work of Inoue (1983), Cuthill *et al.* (1990), and Valone (1993).

Flies must retain capacity to learn, they must show plasticity, irrespective of the degree of (un)predictability (seasonal patterns) of the environment. The fact that "memory window" may be shorter than later on ,as season goes by, it does not mean that her reproductive decisions will affect negatively her life time fitness.

A pest manager's decisions (e.g. early-season protective spraying with biocide or rigorous removal of infested and uninfested fruits from the orchard floor) are novel stimuli for a fly. The extent to which a fly's preexisting properties of behavioral flexibility can cope with those stimuli is currently unknown.

7.4 Egg laying in the mid-season

Mid-season events are unpredictable in the short term but are seasonably predictable and have been since the ancestral environment. It is important to examine the evolutionary origins and necessity of learning in mid-season, and what factors appear to be most important for its evolution. It is important to understand how the capacity to learn increases fitness for flies in the mid-season.

The ancestors of the olive fly did not need any learning capacity at the beginning of the season when there was plenty of food. However, their offspring living in the mid-season must have experienced strong selection pressure to associate, through learning, a few highly reliable cues (e.g. odor with certain shape) that may lead them to the host.

Some of the olive fly's mid-season generations gradually came to confine their activity where host availability was predictable but its abundance was unpredictable from season to season. Flies can not influence or predict seasonal changes, thus learning as a phenotypic plasticity becomes widespread and eventually universal among individuals across all generations. Natural selection will foster not only learning (Mangel 1993) but also forgetting information (Sheehan and Shelton 1989, Papaj and Vet 1990, McAuslane *et al.* 1991). If there is no tendency to forget there will be no capacity to store the new and different cues. There is a selective advantage also to having a short term memory and this also affects fitness.

The smell of ripening olives, which is material proof of presence of hosts, is perhaps congenitally fixed into the phylogenetic memories of the species and left intact in the course of evolution. Therefore, young flies born in either phase of the season are born knowing how to find a host and to lay its eggs in it.

It is also important to examine the evolutionary relatedness between life span and learning, for mid-season generations of olive flies. The life span of fruit flies can vary dramatically due to environmental factors (Parsons 1978, Hollingsworth 1969). Mangel and Clark (1988) predicted that mid-season individuals would have longer life expectancies compared to those individuals later in the season.

Roitberg *et al.* (1993) showed, both theoretically and experimentally, that an insect-parasite alters its egg-laying decision based on the state of the environment and the time of the year. They provided evidence that some of the most complex sequences of behavior, such as egg-laying, are in principle, the egg versus time trade off (Mangel and Clark 1988). The variations in the ratio of good versus bad hosts are more or less consistent in mid-season. Stephens (1991) wrote “it makes more sense to learn those things that change between generations and are regular within generations”. In mid-season, quite often, the fly's environment consists of high inter-habitat variations (e.g. varieties with different characteristics; habitats with different micro climatic conditions) and low intra habitat variations (e.g. ripest olives are not randomly distributed by the tree).

One must consider not only fruit maturing patterns and biannual fruiting cycles but also the fact that even the same cultivar differs in size, surface smoothness, and colors (Haniotakis and Voyadjoglou 1978). I assume that an olive fly is capable of learning those different cues in various sequences and storing them as short-term memories. By tracking those different cues during each encounter, the olive fly can gather more information about the overall environment in terms of quantity and quality of hosts available and exploit the most profitable habitats. Olive flies probably do not remember individual olives, but rather a series of cues about the olive's characteristics.

In mid-season, a fly would still encounter both good and bad hosts and would make decisions. Through rapid and associative learning about current, local conditions of host quality and quantity, the fly could constantly check the effects of its own performance and base tomorrow's long-range action on today's experience. Roitberg *et al.* (1992) emphasized the importance of changes in oviposition behavior where multiple choices are available regularly season after season. Thus, learning should be maintained and reinforced in the mid-season.

Although highly unpredictable and irregular events (e.g. adverse weather conditions such as cold with prolonged periods of rain and wind; wild fires and man made fires with prolonged periods of heat; extensive use of biocides; natural disasters such as floods or volcano eruptions) are possible during the mid-season from year to year, these conditions are not regular events. It is plausible that if a fly is in an unpredictable situation, for example, deprived of good hosts for excessive periods of time or permanently, the internal neural system would register it as a stress. Such environmental conditions can be of varying degrees of complexity and it is difficult to discriminate between the mid-season phase and the late-season phase. Perhaps the phase change begins when a fly's current understanding of the environment bears no predictable linkage to the future environment and a shifting from learning to a more instinctive behavior becomes a superior strategy.

Hypothetically, an insect may overcome a stressful situation by reabsorbing its oocytes until abiotic conditions become more favorable (Fletcher *et al.* 1978). In some stressful situations, insects show an increase in dispersal movements.

For example, apple maggot flies are known to be repelled or deterred by contact with insecticides (Reissig *et al.* 1983). Such behavior that reduces an insect's exposure to a stressful situation is also observed in german cockroaches (Ebling *et al.* 1966). Evidence in those cases suggest that insects might have at least some capacity to learn (aversion learning) negative associations between a stressor and a location (Sparks *et al.* 1989). Tarsal contact by spider mites with a chemical biocide in an orchard is followed by dispersals into biocide-free orchards (Hall 1979). The mite may have learned that pyrethroid insecticides cause malaise and, in the future, the insecticide will elicit a memory of malaise.

However, there is a great deal of work to do to explain how and why such a mode of response evolved in olive flies and its possible relevance to the use of chemical biocide. Though phenotypic variability among individuals may be partially instinctive ("hard-wired"), some aspects of behavioral responses may be open to a certain degree of flexibility. For example, the use of sub-lethal doses of biocide might mitigate flies to immigrate from an orchard and subsequently recolonize it and cause an outbreak in it (Penman and Chapman 1988). Another example might be the increased tendency of dispersal movements (Michelakis and Neuenschwander 1981) in search for good hosts. Those movements are qualitatively different from trivial movements, which are a regular occurrence within a habitat at a certain locality (Bateman 1972).

Under such conditions, the fly's long-term reproductive success ought to increase by either avoiding the stressful stimuli through dispersal movement or by avoiding the stressor through reduced movement. If a fly has to learn that it is not advantageous to search in a stressful environment, her lifetime fitness is diminished. Unpredictability may be essential for occasional, irregular, dispersal movements of olive flies, and moderate unpredictability may be crucial for 'trivial movements' within the orchard.

7.5 Egg laying in the late-season

As a season progresses, there is a succession from moderately-predictable conditions to highly predictable conditions and this type of progression is a striking feature of the olive fly ecosystem. The end of conditions where good hosts are available may be brought on by the combined effect of host infestation by the fly and the natural fall of the olive fruit from the tree. The result is a decreased supply of healthy hosts and the establishment of a highly predictable condition where healthy hosts are almost totally absent. Harvesting practices also make stress in the late-season predictable because unlike ancestral conditions, potential hosts are removed from the trees.

In accounting for the behavioral effects of inescapable stress, it appears that, in such environments, all members of a species would be restricted to those responses for which the animals were highly prepared and learning would be of little benefit. At this level, a fly cannot expect to find good hosts anywhere. In the late season, flexibility need not be dependent on learning but may be an instinctive response. Insect brains are predisposed to react almost automatically to stressful situations. Flexible, instinctive reactions evolved by means of natural selection and are highly adaptive. Research on multivoltine parasite species (Roitberg *et al.* 1993, Luck 1990) revealed that in the late season, individuals have shorter life-expectancies compared to foragers in the mid-season, since flies are not egg-limited but rather time-limited. Selection has presumably favored females which have been predisposed to accepting bad hosts in the late season. Deficiency of good hosts is a regular occurrence and females adapt by being less choosy.

The aim of research should be to understand and predict certain patterns of response that occur regularly either when flies are not (at least partially) genetically pre-programmed to withstand regular fluctuations of good vs. bad host as in the mid-season, or when flies are reacting more instinctively when good hosts are regularly absent as in the late season. Continuous encounters with bad host will lead to total acceptance of bad hosts.

7.6 Case study

Sufficient basis and conceptual foundations now exist for the development of evolutionary-ecologically integrated management strategies for controlling *D. oleae*. Their relevance of olive fly management strategies to important socio-economic issues can be examined.

The olive fly has marked biological characteristics; it is strictly monophagous; it lays only one egg at a time and, conditions permitting, one in each fruit. The presence of intraspecific competitors is signaled by the presence of HMP.

Heavy-egged adult flies may lay more than one egg in a host during high infestations when all healthy fruits have been exhausted. Such flies will probe and use already infested fruit.

There is a strong synchronization between olive fly development and development of the host. This synchrony is vital since olive fruits directly support a fly's progeny. Therefore, the foraging behavior of olive flies is closely linked to their fitness.

Factors such as the physiological/informational state of the flies have a profound influence on their readiness to accept a particular host. All cultivars of fruit are attacked, and a rank-order of preference for individual hosts is not fixed (except 'supersize' olives which are constantly accepted). A biannual cropping pattern of olive groves and an annual fluctuation in the quality of the host commonly explain a large part of the total environmental change.

The phenotypic response of olive flies to this environmental heterogeneity may facilitate enormous variation in behavioral strategies among individuals and in a single individual from one situation to another. The following case study will examine and evaluate some basic assumptions and predictions of the phenomena discussed earlier from 3 perspectives.

Perspective 1: Biological

Ecological case- Application of host marking pheromones (HMP) in conjunction with interception traps (IP).

Refraining from ovipositing in a pheromone-marked host is a widespread biological phenomenon. Since the "mark" lies on the outside of the fruit and females can discriminate whether or not the fruit was attacked, this phenomenon can be manipulated. (The assumption is that components of the HMP are identified, synthesized and tested in the orchard).

Phase 1 (Deterring flies from accepting s "bad" host): Flies landing on trees with HMP treatment (e.g. foliage and fruits) would encounter one or more bad hosts, causing the females to lower their 'giving up time' and leave the tree due to the prolonged exposure of their tarsal sensilla to the HMP. These assumptions are consistent with earlier discussion on fly's change of acceptance threshold level. Individual flies are able to assess an increase in the quantity of the "bad" host. Consequently, they are correspondingly more choosy. In other words, that kind of response (refrain from oviposition) leads to an increase in inter-tree movement. One critical aspect in this phase is to circumvent the negative effect of continuous pheromone exposure by allowing flies to encounter untreated tree parts. Thus some portions of the tree (e.g. individual fruits) should be left untreated to act as a kind of trap crop.

Phase 2 (Maintenance of higher level of choosiness in foraging females): By drastically reducing residence time on the trees treated with HMP, flies become increasingly mobile. This increased inter-tree movement is desirable only to a certain point, since females deprived of an unmarked host may eventually oviposit. Any effective use of HMP for manipulating the behaviors of flies would depend on maintaining her higher level of choosiness just below the critical threshold level (CTL). When the CTL is reached, flies are not able to distinguish a good host from a bad host due to habituation and they will begin accepting bad host. Another possible explanation is that they may be able to distinguish but choose not to. An important assumption is that flies would refrain from oviposition until suitable hosts are available. Therefore, some trees should be left untreated (e.g. every 8th tree in a row). The first proposition is that the infestation rate will be the highest on those untreated trap trees and adjacent HMP treated trees in their immediate neighborhood. The second proposition is that those trees will be infested sooner than all others.

Phase 3 (Deterring the flies): Two scenarios are possible in this phase. In the first one, flies would encounter few untreated trees. After encountering good hosts they would engage in "area restricted searches" and their residence time would be higher. Eventually, due to natural HMP intensity, they would leave the trees. Here, exploitation of their behavior would be based on their lower level of choosiness. They would be eliminated before reaching adjacent HMP treated trees because of interception traps ringing the perimeter of the untreated trees.

In the second scenario, females would accumulate on trap-trees where they would be eliminated in visual/odor traps or fruit mimics placed in a high proportion of the trap-trees. The assumption is that flies are moving upward not horizontally once they are within a tree. Here, exploitation of flies behavior is based on tephritids attraction to inanimate objects as ovipositional sites. In both scenarios a critical point is to eliminate flies before they start accepting bad hosts as ovipositional sites.

Roitberg and Prokopy (1987) and Roitberg and Angerilli (1986) reported that it is unlikely that the application of HMP as a sole IPM strategic method would provide an acceptable level of control. More satisfactory results could be attained using HMP in conjunction with IT.

Perspective 2: Economics

Previous and present means of control revolve around two features: 1) a small population of olive flies can cause unacceptable high damage and 2) individual units of fruit may be high in value. The major problem in olive IPM is an extremely low economic injury level for table fruits (zero-level tolerance). As a result, management intensity is very high in modern olive groves. Growers are likely to invest heavily in insurance measures that reduce the chance of heavy loses due to pest (Webster 1977, Hall 1983).

The essential question is whether methodologies such as behavior manipulation can successfully reduce damage to an economically acceptable level from a growers point of view.

Perspective 3: Socio-Political

Socioeconomic and political considerations play important roles in the developing and adopting of new management strategies. As Pedigo *et al.* (1989) have pointed out, contemporary EIL does not address environmental concerns. Higley and Wintersteen (1992) have developed a novel approach to assess the level of environmental risk associated with the single use of pesticide (32 insecticides included) to different environmental categories(e.g. ground water, beneficial insects, mammals, human health). Such an approach is able to address the environmental safety directly by establishing environmental costs and EILs for field crop insecticides. For example, the level of environmental risk for single use of dimethoate (a chemical of choice in olive IPM) evaluated for environmental elements such as the aquatic environment, birds, mammals, and human acute toxicity is high. If an olive grower is unwilling to calculate environmental criteria and incorporate their costs into management decisions he will likely to be intolerant of higher levels of pest. Consequently, implementation of environmental EILs would be difficult in such cases and grower decisions would be based largely on economic cost of available options (most likely insecticide treatments).

Although some "correct" ecologically and environmentally approaches are already available (e.g. fruit mimics) their large-scale implementation is questioned because of complex economic-socio-political reasons.

Historical record shows that chemical-based approach , with respect to economics (high returns to farmers; low labor inputs), sociology (support tradition of individuality and low government involvement), and philosophy (fits farmer mind set of man's dominance over the nature) is highly attractive to growers (Perkins 1982). The basic tenet of business, that producers manage their resource for profit in a free enterprise system, is an ultimate obstacle , in my opinion, for new products such as HMP, to be adopted as a pest management tool. Clearly, at present, employment of behavioral-ecological "tools" according to standard EILs would neither cost less nor provide enhanced control of pests (Roitberg 1992, personal communication). Re-education of the growers has to be carried out first, because their attitudes and the way they make their decisions are based on the basic conviction that spraying insecticides will reduce the risk of crop loss. By assigning more realistic costs to pesticide use (e.g. enormous cost to farmers and public health; overall environmental quality) behavioral-ecological methods with negligible environmental and personal health costs may become more economically feasible in the near future. Moreover, economics is a system that measures values in its own terms exclusively. For instance, Pearce (1988) argue that: "the only way to get the environment onto economic agenda is to demonstrate that environment matters to the economy". Gordon and Suzuki (1990) strongly disagreed with this stance. Their argument is that " it is economy that has to fit into environment not the other way around". When calculating the cost of insecticide usage economists tend to completely ignore all other indirect costs and often associated negative consequences (Zimmerman 1995). They refer to them as externalties. Currently, ignoring all those externalties associated with olive IPM, there can be no argument that there is an enormous distance in pricing particular technologies meaningfully (e.g. HMP vs. insecticides). However, unless, those externalties are considered and integrated into olive agroecosystem enterprise, behavior-based management decisions will not prove realistic and justifiable.

If it is assumed that a behavioral-ecological approach is desirable to growers, how is it to be practiced? An assumption is that greater yield losses (above 30%) from a pest would be acceptable for growers who employ environmentally oriented EILs. Pedigo and Higley (1992) provide suggestions on the issue of paying the cost associated with avoiding environmental injury. One approach consider the manipulation of the crop market value of the crop by increasing the cost for pesticide-free products. The assumption is that consumers would be willing to pay more for such products. HMP and SHM might be "socially acceptable" technique tools to individuals with zero-risk mentality (e.g. members of various environmentally-oriented groups and organizations; organic growers) and to the large number of lay people who are generally distrustful of synthetic chemicals. Such shift toward "softer" technologies for food production may create a "dual market " for those who can afford to pay more for "safer food" and the those who cannot . According to Pedigo and Higley (1992) a higher price of such products is presumed necessary to compensate for more expensive management practices or for reduced productivity. An argument can be made that it would be appropriate for growers to accept some costs in order to minimize effects on the environment, since they are the once who enjoyed the most high returns from pesticide usage. In my opinion, governments should subsidy growers to compensate their lower profit margins by employing ecologically based technologies in order to keep them attractive.

To conclude, first, environmental cost should not be the only selection criterion when deciding amongst the IPM methods available, but it should be a major one. In particular that would help to select the least environmentally damaging methods and break a never-ending cycle that was established in which management practices were designed solely to reduce the costs for farmers. Second, the overreaching objective of maximum social value must include critical ecological requirements, since some environmental commodities are priceless.

8.0 Conclusion

The intent has been to show that evolutionary questions are important and testable and should be incorporated into current and future management strategies. Furthering our understanding of fruit flies' foraging behavior from an evolutionary perspective will have strong implications for their management since most of the currently used tactics of olive fly IPM are strongly linked to its foraging behavior (e.g. odour bated traps for interception of immigrating flies). I have demonstrated that the general ability to learn is widespread in insects, including fruit flies. This recently acquired knowledge challenges the traditional view that insect behavior is "hard-wired".

I have argued that learning by fruit flies has a profound effect on the success of management tactics and neglecting the role of learning in insects contributes to failures of current management practices. Data have been published showing that fruit flies can learn host characteristics (i.e. trap characteristics) and that this prior ovipositional experience with locale-associated variations among present cultivates should be considered in designing traps. Applied entomology should become more experimental than observational in approach.

Exploring a topic such as this within the context of BE provides the potential for advancement, especially for predicting fly behavior. It is clear that BE and IPM are much more closely intertwined than was formerly assumed.

I have argued that one of the fundamental differences between the BE approach and all other forms is that the former takes into full account the dynamics and interrelatedness among various important parameters, an account that can be verified by both theoretical (dynamic, state-variable models) and empirical work (laboratory and field study). Other approaches could be multivariate but they are proximate. Advances in current research illustrate how the interplay between the internal physiological state of flies and information about host-biotic resources may influence fly behavior. This information has great practical value, because it allows pest managers to predict behavior and particular conditions under which some specific behavior, such as egg-laying, over a season, is likely to occur. This new integrative, multilevel approach is a departure from the way that behavior has been characterized in the past. It regards behavioral plasticity as a response to variations in physiological and informational state; the result of a particular individual fly life history that includes both phylogenetic and ontogenetic memories. I have suggested that one of the aims of establishing a new working framework is to obtain background information and predictive hypotheses against which experimentation can be done. Achieving this goal will provide a more realistic and precise understanding of behavior. However, research confirms that a behavioral-ecological approach to managing fruit flies, such as employing HMP and SHM, causes a significant reduction in fruit infestation by fruit flies.

Although a BE approach is not yet sufficiently developed for a general transfer of technology to take place (e.g. HMP as a substitute, alternated with, or combined with insecticidal control or other management methods), its high selectivity and environmental soundness make it superior to insecticidal control, and it already presents real opportunities for field application. It is likely that the active compound of olive juice will be chemically identified, synthesized and formulated. A deeper understanding of olive fly resource foraging behavior is needed with respect to the ecological, physiological, and behavioral data.

The disadvantage of the BE approach, which promotes the centrality of ecological elements in decision making, is that it would be expensive.

It would be difficult to maintain capital-intensive farming concurrent with the introduction of "tools" that would force growers to accept higher levels of crop injury and lower profit margins. Perhaps public health and environmental issues may damage the image of insecticides as reliable mechanistic means in dealing with pests .

From the socio-political point of view, BE " tools" should be publicly accepted, due to their negligible effect on the environment. It is hoped that the principles emerging from an evolutionary perspective on olive fly behavior will be used in the near future to derive effective management tactics.

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