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THE EFFECTS OF HUE, INTENSITY, AND SATURATION ON FOLIAGE AND FRUIT FINDING IN THE APPLE MAGGOT, *RHAGOLETIS POMONELLA* WALSH

A Dissertation Presented
By
ELIZABETH DOLI OWENS

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of
DOCTOR OF PHILOSOPHY
May 1982
Entomology

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THE EFFECTS OF HUE, INTENSITY, AND SATURATION ON FOLIAGE AND FRUIT FINDING IN THE APPLE MAGGOT, *RHAGOLETIS POMONELLA* WALSH

A Dissertation Presented

By

ELIZABETH DOLI OWENS

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DEDICATION

I dedicate this dissertation to my friends, all of them, whose unending support, encouragement, and faith in me as a person helped me to persevere.

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ABSTRACT

The Effects of Hue, Intensity, and Saturation on Foliage and Fruit Finding in the Apple Maggot, Rhagoletis pomonella Walsh

(May 1982)

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Directed by: Ronald J. Prokopy

The complex of reflective properties of apple maggot hosts (apple and hawthorn) were analyzed using methods embodied in visual ecology (spectrophotometry, spectral radiometry, photography). Properties of the host which may be utilized by apple maggot flies to detect resource structures were identified, described, and quantitatively characterized. Mimics of host structures were created to test attractiveness of surface components to apple maggot flies in nature and in a laboratory flight chamber. Properties of color (hue, saturation, intensity) were emphasized. Apple maggot flies were most attracted to pigmented panels resembling foliage in spectral hue, and were less attractive to panels of unsaturated foliage hues than to those of pure hues.. They were captured in higher numbers on the least reflective fruit mimic regardless of hue. Results were compared with observations of apple maggot fly behavior in nature and spectral sensitivity function as measured from the apple maggot fly compound eye.

The apple maggot fly compound eye was found to be highly sensitive to light in the spectral region where host foliage reflects and transmits highly. However, the eye is very insensitive to the spectral region where ripe host fruit reflect maximally. Detailed descriptions of the theory and methods of techniques in visual ecology applicable to the study of insect vision and the design of attractive devices are discussed. An ecological approach is suggested as a valid method of studying insect vision.

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CHAPTER I

INTRODUCTION

Insects have an anatomical diversity of visual receptor structures, suggesting that vision plays a major role in their behavior (Mazokhin-Porshnyakov 1969). Dartnall (1975) states that it is logical to assume that mechanisms of vision are adapted to suit the needs of the animal for locating resources and avoiding dangers in the context of its environment. Therefore, visual studies should provide information on the nature of the environmental structures to be perceived as well as information on the visual mechanisms doing the perceiving. This is the basic thrust of the emerging discipline known as visual ecology (Lythgoe 1979).

In this study, I have adapted visual ecology methods to the study of a visual orienting insect, the apple maggot fly (AMF), to increase the understanding of how it locates food and oviposition resources within a host tree. In so doing, I have drawn extensively on the literature of both vertebrate and invertebrate vision studies, concentrating particularly on visual contrast. Visual contrast enables the detection of patterns which differentiate an object from the remainder of the visual environment. It is dependent upon: (a) the inherent properties of the object; (b) the perceiver; (c) the spectrum and energy of illumination; and (d) the inherent properties of the optical background. For the studies discussed herein, I have concentrated on properties of AMF host tree structures, particularly aspects of color. I used artist oil pigments on solid forms as host mimics in both field and laboratory situations to determine what aspects of color (hue, intensity, saturation) were attractive to AMF. Surface properties of host structures and mimics were measured and documented using photography, spectrophotometry, and spectral radiometry.

A parallel study of the AMF compound eye visual sensitivity function, conducted in collaboration with Dr. Gary D. Bernard of Yale University, provided information on the visual mechanism of the perceiver. It is obvious, from the results of this study, that mechanisms for detection of hues are present in AMF compound eyes.

Two areas of importance, the effects of the illuminant and of the optical background, received only superficial coverage during this study. That does not reflect their importance in visual detection of resource objects, only the lack of time and understanding needed to investigate thoroughly their properties. To understand thoroughly AMF visual orientation, more effort should be directed towards *in situ* measurements of illumination and reflectance of natural environments (Hailman 1979).

Applying the visual ecology approach to insect vision studies will contribute toward understanding adaptation in visual mechanisms among insects; but, of equal importance, this approach will improve the design of insect traps. Prokopy and Owens (1978) demonstrated that gaining an understanding of the nature of resource items and the behavior of an insect species within the context of its environment is a logical first step toward developing an appropriate monitoring trap. The widespread adoption of integrated pest management (IPM) has produced a need for more specific methods of monitoring pest and beneficial insect populations. Therefore, in the future, research of the type discussed herein will gain in application.

CHAPTER II

LITERATURE REVIEW

VISUAL HOST LOCATION IN PLANT FEEDING INSECTS: COLOR

Introduction

A review of visual orientation to plants by insects requires an approach enabling the reader to visualize host plants from an insect's view. As was so eloquently stated by Tinbergen (1951) "each animal has its own *Merkwelt* (perceptual world) and this world differs from its environment as we perceive it, that is to say from our own *Merkwelt*". This statement certainly applies to the difference between visual worlds of insects and humans! Visual ecology approaches the comparative study of visual mechanisms by presuming that specialized visual systems have an adaptive advantage for the life style of a particular animal. Visual ecologists quantify physical attributes of the animals environment, particularly resource items. Combining this information with information on ocular morphology and physiology produces a theoretical picture of the world the animal "sees".

Definition of vision. Vision is defined as the ability to perceive spatiotemporal arrays of photon fluxes (visual patterns). As an active, complex process, vision depends upon events in the entire visual field as well as patterns of expectation in the visual processing system itself, some of which are established through prior visual experience. Spatiotemporal photon arrays differ in total energy and frequency composition, providing the visual cues of brightness, hue, and saturation. The arrangement of the arrays provides information on shape, form, size, distance, and motion.

Insect photoreceptors. Insects, as well as other animals, have a variety of photoreceptors, not all of which contribute to visual perception. I have chosen to exclude from my discussion those mechanisms, extra-ocular receptors, which do not contribute to visual perceptions *per se*, although they may influence metabolic functions and biological rhythms, important to maintaining temporal insect-plant relationships. Therefore, discussions concern compound eye perception with some information on ocelli and stemmata. Structures and functions of extra ocular receptors are well reviewed elsewhere (Wolken 1975, Truman 1976, Bennett 1979, Underwood 1979, Yoshida 1979).

The morphology and physiology of ocular receptors of insects is very different from that of humans. On the adult insect, compound eyes and ocelli function in light detection and image formation. The compound eye is the primary visual image receptor (Goldsmith and Bernard 1974, Horridge 1975, Bernard 1981). Ocelli are poor image formers, but may function in the spectral or intensity characterization of ambient light or in orientation (Goodman 1975, 1981, Laughlin 1981, Waterman 1981). Recent research on compound eye optics provides a more complete picture of the limitations of insect vision (Mazokhin-Porshnyakov 1969, Horridge 1975, Autrum 1979, 1981a,b). It is now possible to compare and contrast insect optical imaging with that of humans to provide perspective on the relative levels of "seeing". Combining these comparisons with quantification of attributes of the environment accessible to "seeing" produces a visualization of the plant world in insect terms.

The purpose of this review is to discuss color and how insects may use the perception of color to locate host plants within nature. The approach is that embodied by visual ecology. Thus the theory and methodology applied by visual ecologists will be discussed first. Sections following this initial discussion will cover: (a) color and color perception, (b) color vision in nature; (c) attributes of plant color; (d) mechanisms of insect color vision; (e) insect attraction to natural plant colors; (f) yellow as a foliage mimic; (g) infra-red light; (h) polarized light. Visual mechanisms and behavior in

Rhagoletis pomonella and related species will be included within sections.

Descriptive Methodology of Visual Ecology

Visual patterns depend upon the nature of the viewed surface, the optical background, and the illuminant, and the viewer's angle of view and sensitivity. Visual ecology attempts to identify and characterize important visual patterns by understanding the ethology and optical system of the animal and quantitatively measuring the physical surface characters of resource items and optical backgrounds. Methods were first adapted to the study of sea fishes, where spectral sensitivity of visual pigments was shown to be correlated with the spectrum of downwelling light (McFarland and Munz 1975a,b, Munz and McFarland 1977, Lythgoe 1979, Levine and MacNichol 1982). The visual ecology approach has subsequently been adapted to studies of land-dwelling animals as well (Lythgoe 1979, Hailman 1979, Snodderly 1979) including insects (Kevan 1978).

The theory and methodology embodied in visual ecology is covered in depth elsewhere (Dartnall 1975, Hailman 1977, 1979, McFarland and Munz 1975a,b, Munz and McFarland 1977, Lythgoe 1979, Gates 1980).

It has long been known that colors vary in their attractiveness to certain insects (Weiss 1943) and that certain colors can be utilized as components of effective trapping devices (Mazokhin-Porshnyakov 1969, Boller and Prokopy 1976, Moericke 1976, Prokopy and Owens 1978). What has been lacking is a cohesive research approach combining studies of: attractiveness of artificial surfaces, attributes of natural structures attractive to insects, environmental illumination, and sensitivity characteristics of insect visual mechanisms. Without such an approach, we may learn much about visual mechanisms, but little about vision (Dartnall 1975, Wehner 1981). Adapting methods of visual ecology to insect study is a possible approach to learning about insect vision.

Color and Color Perception

Color is defined as the aspect of vision which includes everything but spatial and temporal inhomogeneties of light. It is so important in human perception that hue is often considered a direct physical attribute of objects. Color blind individuals frequently learn colors by identifying colors with objects.

Although of broad definition, color is generally described in terms of hue (dominant wavelength), saturation (bandwidth, chroma, tint, or purity), and intensity (brightness, total energy, value, or shade) (Science of

Color 1963, Wyszecki and Stiles 1967). The red appearance of an apple is due to hue. If an apple appears pink it is of an unsaturated or tinted red hue. If it appears maroon, it is of a less intense or shaded red hue. The hue (red) remains the same in both cases (tint and shade). Only the relative values across the spectrum change (tint, increased; shaded, decreased).

Quantitative measurements of color are made (using spectrophotometers, or spectral radiometers) or relative or absolute reflectance values/wavelength in the extended visible spectrum[1] (near UV (300nm) to near IR (800nm)). Quantification by relative reflectance values eliminates the confusion caused by descriptive color names, enabling comparisons among results of separately conducted studies. Direct comparisons can also be made between relative values and relative absorption spectra for visual pigments. Relative values lack "units" and therefore, can be considered equivalent to direct photon counts (Lythgoe 1979). Measurements in units of absolute energy must be converted to photon number prior to comparison with absorption spectra of visual pigments (Dartnall 1975).

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[1] Photons of wavelengths below 300nm cause destruction of visual pigments due to their high energy. Photons above 800nm do not carry sufficient energy to excite visual pigments (Dartnall 1975)

Hue is frequently referred to as "color". Hue discrimination curves describe the visual system's ability to differentiate spectral regions to produce the sensation of "color". While a theoretical hue is as small as a single nanometer bandwidth, most visual systems are incapable of making such fine distinctions. Therefore, hues, varying among visual systems, represent spectral regions rather than nanometer bands. Hue discrimination requires a visual system consisting of a minimum of two receptor types, each with a pigment absorbing maximally in a different spectral region. Finest hue discrimination occurs at regions of overlaps in pigment absorption spectra (Davson 1980). The system must be capable of discriminating hue independently of intensity to possess true "color" vision (Gruber 1979, Davson 1980). A system capable of color vision would require a minimum of three receptor types (Davson 1980).

Evolution of Color Vision

The evolution of hue discrimination in both invertebrates and vertebrates is a topic of considerable debate (Wolken 1975, Autrum 1979, Menzel 1979, Lythgoe 1979, Burtt 1979, Davson 1980, Levine and MacNichol 1982). Good hue discrimination may be of importance for food location in diurnal species (Snodderly 1979). The coloration of some ripening fruits is a signal to seed dispersing birds and mammals. Floral color is similarly a signal to pollinators. Both situations suggest possible co-evolution with color vision (van der Pijl 1972). Color vision is also important in inter- and intra-specific optical signaling in many animals (Hailman 1977, Rowland 1979). Evolution of insect color vision is not well understood, but probably is a function of food location (Menzel 1979).

Color Vision in Natural Environments

Natural illumination. Ability to discriminate hues is found primarily among diurnal species, as it is an energy inefficient process. Nocturnal animals have visual systems which optimize the capture of photons at the expense of hue discrimination (Lythgoe 1979). For nocturnal insects, therefore, the world may be black, gray, and white. Under natural daylight conditions sufficient energy is available in all regions of the visible spectrum to enable fine hue discrimination. Daylight energy is composed of two different irradiance sources: direct sunlight and skylight. The latter contains the greater proportion of short wavelengths (<500nm), including UV, as a result of Rayleigh scattering (Henderson 1970, Sustare 1979, Lythgoe 1979, Gates 1980). Environmental factors such as suspended pollutants (moisture, dust, other) and reflective surfaces (vegetation, soil, water, other) affect the spectrum of the irradiance (Hailman 1977, 1979, Lythgoe 1979). The detection of behaviorally significant hues via mechanisms of color contrast is influenced by the environmental irradiance falling on both the object to be detected and its background. For insects, this may be at the microenvironmental level (Land 1981).

Animals within terrestrial environments are subject to frequent changes in irradiance, i.e. sunlight to shadow, open space to vegetation, time of day, weather changes due to the mechanism of color constancy, which is thought to have some component of memory (Davson 1980). Color contrast and color constancy appear to function also among other animals possessing color vision (Hailman 1977, Lythgoe 1979), including some insects (Moericke 1955, Hamdorf 1979, Menzel 1979, Neumeyer 1980, 1981, Rose and Menzel 1981). The exact nature of these mechanisms is poorly understood.

Backgrounds. Optical background has considerable effect on the detection of objects. Discrimination of an object from a background requires that an animal be able to detect differences in hue (color contrast), intensity (relative brightness), or motion. Detectability of each difference varies independently with viewing conditions. For example, the hue of small objects is lost as background intensity increases because of lateral inhibition, a visual mechanism which enhances intensity differences. Lateral inhibition silhouettes natural objects viewed against an optical background of sky, as sky is nearly always of higher intensity (Hailman 1977). This mechanism is thought to be of importance to insects locating prey or mates against the sky (Wehner 1981). Ability to detect color contrast is essential when the entire visual field is subject to the same level of irradiance. When neither color nor intensity contrasts are sufficient, objects can still be detected by variations in movement (Hailman 1977, Lythgoe 1979, Wehner 1981).

The influence of visual mechanisms coupled with those of the physical environment can affect the perception of surface color. Insects seeking plant hosts must cope with variation in visual attributes of plants and optical environments. To detect host plants, insects may have developed specialized mechanisms, visual and behavioral, to enhance plant color features. These mechanisms may result in specific wavelength regions triggering specific responses, or they may be a type of true color vision.

Attributes of Plant Color

Plant color is remarkably consistent (Woolley 1971, Vaishampayan et al. 1975a, Gates 1980). This consistency is due to the absorption properties of chlorophyll, present in most plants and responsible for the dominant green hue (dominant wavelength = 520-580nm) (Woolley 1971, Wolken 1975, Gates 1980). Carotenoids and other plant pigments also contribute to plant color through selective absorbance or reflectance in specific spectral regions. Carotenes, for example, are yellow pigments which absorb maximally in the blue and reflect in the green to red region. They are the pigments primarily responsible for the yellow to red appearance of living and senescent leaves. These pigments, of plant origin, are the chemical precursors of visual pigments in animals (Fox 1979).

Although foliage hue as produced by chlorophyll is nonvariable, the color appearance of foliage may change by unsaturation through the addition of other pigments, growth patterns, surface texture, spectrum of illuminant, or angle of view. Changes of saturation are accompanied by changes in intensity, sometimes of a regional rather than of a uniform distribution across the visible spectrum. Gates (1980) reviewed evidence that saturation changes in foliage represent increases in reflection of either short wavelength light energy (<500nm), causing a whitish appearance, or long wavelength light energy (>500nm), particularly around 600-700nm, causing a yellow appearance. Most changes in plant physiology produce vegetation color changes of the latter type. Surface texture is primarily responsible for short wavelength reflection.

Wax (glaucousness), specular reflectance (glare), pubescence (hairiness), and cellular water increase short wavelength reflectance. Specular reflectance mirrors the illuminant and is a function of the glossiness of the surface, the angle of illumination, and the angle of view. Glaucousness significantly increases the relative reflectance across the entire spectrum, including the UV, regardless of viewing angle or illumination (Mulroy 1979). Pubescence selectively absorbs UV while reflecting highly in other regions (Kevan 1979). Long-wavelength energy is enhanced by transmission through foliage (Moericke 1969, Woolley 1971, Vaishampayan et al. 1975a). Wilting increases the ratio of long wavelength to short wavelength reflectance (Kennedy et al. 1961). Decreases in chlorophyll concentration reduce the absorption peak at 680nm, thereby increasing long wavelength reflectance. Yellow appearance is characteristic of new growth, or diseased or senescent foliage. Yellowness, caused by an increase in relative reflectance of long wavelength light, accompanies changes free of nitrogen to fluid concentrations.

Insect Mechanisms for Detection of Color Differences

That plant feeding insects are frequently attracted to yellow suggests that they may have mechanisms enabling discrimination of foliage-like hues. In invertebrates, visual systems are found which enhance the spectral difference between vegetation and sky (Kennedy et al. 1961, Menzel 1979). Visual systems composed of two broad-band receptor types, one absorbing maximally below ca. 500nm and one absorbing maximally above ca. 500nm, are the minimum requirement for wavelength discrimination between foliage and sky. Discrimination between foliage and soil would require an additional receptor to detect hue and intensity differences in the red region (600-700nm), such as in the case of trichromatic birds and monkeys (Lythgoe 1979, Snodderly 1979). Both systems would theoretically be capable of hue discrimination, and therefore color vision. Menzel (1979) states, however, that the existence of a chromaticity-coding visual system does not prove the existence of color vision. Such a system may also serve as the releaser mechanism for wavelength-specific behavioral patterns (spectral specific responses) defined as response patterns elicited by light intensity in a specific spectral region. Color vision implies more than spectral preference within a specific behavior response pattern (feeding, oviposition, mating, shelter seeking). It also implies memory

(Davson 1980). The most reliable method of demonstrating insect color vision is the training procedure to monochromatic light, in which light intensity and wavelength are varied in the test. This procedure has been applied to relatively few insect species: bees, which have been shown to use color memory in nectar foraging (Daumer 1956, Menzel 1967, von Helverson 1972), ants (Wehner and Toggweiler 1972, Kretz 1979, Mote and Wehner 1980), and butterflies (Ilse and Vaidya 1956, Swihart and Swihart 1970). Behavioral observations, action spectra, and electrophysiological determination of different receptor types, while suggestive of color vision in a wide variety of insects (Goldsmith and Bernard 1974, Menzel 1979), cannot prove the presence of true color vision as opposed to spectral specific behavioral response patterns. In plant feeding insects, alightment on foliage or yellow pigment suggests a spectral specific response (Moericke 1955, Kennedy et al 1971, Moericke et al. 1966, Vaishampayan et al. 1975a, b, Coombe 1981).

Fly Color Vision

Flies have receptors of varied sensitivity, providing a basis for hue discrimination (Hamdorf 1979, Bernard and Stavenga 1979). Within the open rhabdome of a single ommatidium, receptor cells are arranged into two general types: exterior cells (R1-6) and interior cells (R7-8)

(Hamdorf 1979, Kunze 1979). Apple maggot flies have typical ommatidium morphology (Agee et al. 1977). Spectral sensitivity in the generalized fly may vary according to receptor cell types (Hardie et al. 1979, Hardie 1979, Smola and Meffert 1979). Receptor cell types may vary in their contribution to hue, motion, and polarization sensitivity (Menzel 1975, Hu and Stark 1977, Hardie et al. 1979, Waterman 1981). The spectral sensitivity of Tephritidae is similar to that of other higher Diptera (Agee, unpublished data).

In addition to differences among receptors within an ommatidium, differences in general sensitivity between regions of the compound eye have been shown (Bernard and Stavenga 1979, Franciscini et al. 1981). In the bee, eye regions of differing spectral sensitivity have been shown to function in different types of behavior (Menzel 1975, Moore et al. 1981). Flies have compound eye regions of differing spectral sensitivity, but it has not been demonstrated that these regions correlate with specific behaviors. It is apparent that the compound eye of higher Diptera is far too complex to dismiss as a structure of uniform sensitivity and function. Thus, fly vision offers numerous possibilities for adaptation to plant location.

Phytophagous flies have been demonstrated to exhibit spectral preferences for reflective surfaces under field conditions. Foliage selection in Tephritidae (Prokopy 1977b) and in several anthomyiids (Kring 1968, Rötteger 1979, Dapsis and Ferro 1982) is a response to visual stimuli, primarily hue and intensity.

Training experiments necessary to prove color vision in flies have met with little success (Menzel 1979). Only two examples, one involving houseflies (Fukushi 1976) and one involving drone flies (Ilse 1949), indicate that classical training to colors may be useful in proving the existence of true color vision.

Insect Attraction to Natural Plant Colors

Insect attraction to color attributes of plants has been most intensively studied in Homoptera. Unfortunately, very little information is available on the morphology and physiology of homopteran eyes, possibly because both the eye and insect are small, making them difficult to study (Kring 1977, Mazakhin-Porshnyakov and Kazyakina 1979). Nonetheless, there are sufficient data provided by action spectra (spontaneous response to monochromatic lights) to suggest that the visual sensitivity extends from the UV (300nm) to the orange-red (600nm), with a long wavelength peak at approximately 550nm (foliage hue) (Mound 1962, MacDowell 1972, Dickman 1974, Vaishampayan et al. 1975, Coombe 1981). Whitefly visual action spectra, compared to reflectance and transmission spectra of the host plant, suggest that the spectral sensitivity of the eye is adapted to detect plant hues. Whiteflies appear to detect host foliage solely by vision and cannot distinguish hosts from non-hosts prior to alightment (Moericke et al. 1966, Vaishampayan et al. 1975b).

Much behavioral work on visual host plant location has been conducted on plant feeding aphids (Moericke 1955, 1962, 1969, Kennedy et al. 1971, Kennedy and Booth 1963a, b, Kring 1966, 1967, 1969). The aphid visual spectrum has theoretically been divided into two hues; vegetation or earth hue (>500nm), and non-vegetation or sky hue (<500nm) (Kennedy et al. 1961). Vegetation hue elicits a settling response in feeding aphids, whereas sky hue stimulates continued flight activity in dispersing aphids. Kennedy et al. (1961) discuss the importance of assessing the physiological state of the aphid prior to running tests on attractants.

Aphid attraction to host plants is affected by color saturation but not by hue. The hue of foliage is too consistent among aphid hosts and non-hosts to be important in host plant discrimination. However, foliage color tint and brightness vary sufficiently to be a plant species specific character (Moericke 1969). Random alightment, which Moericke termed a spectral specific response, occurs among plants of equal hue saturation. Aphid species utilizing specific hosts having foliage spectral components reflecting below 500nm alight in greater numbers on unsaturated (tinted) yellows than on saturated yellow hue. The same lack of saturation repels aphid species which feed on hosts of more saturated hues. This is the only demonstrated visual host plant discrimination mechanism in aphids.

The hue and saturation of color also affect the attraction of olive flies to host foliage within host trees (Prokopy et al. 1975). The undersurfaces of olive leaves, which are pubescent and light gray-green in color, are less attractive to alighting flies than the dark green upper non-pubescent surfaces. The olive fly does not prefer strong yellow tints over pure yellow.

The angle of insect approach may affect the insect's perception of color attributes of host plants. Alightment observations show that in nature, aphids and whiteflies approach vegetation from underneath, where visible energy is primarily transmitted through leaves (Moericke 1955, 1969; Vaishampayan et al. 1975b). Many tephritid species also approach from below leaves (Prokopy 1975a, 1976). Behavioral response tests, on the other hand, are typically conducted with horizontal or vertically placed reflective surfaces which attract insects approaching from above or horizontally. Alightment from below may increase leaf hue attractiveness by elimination of spectral reflectance and surface texture reflectance, thereby enhancing saturation of foliage hue (Kennedy et al. 1961, Vaishampayan et al. 1975b). The approach behavior of alighting insects may provide cues as to the importance of surface features in attraction. Kennedy et al. (1961) describes two types of orientation behavior: distance and closeby. They state that different stimuli may be triggering responses in each case. Distance attraction to whole plants may be a response to leaf surface reflection whereas close-range response may be to transmitted energy, at least in some species (Moericke 1955).

Yellow as a Foliage Mimic

Yellow has been described as a super-normal foliage stimulus because it is more attractive to plant feeding insects than is natural foliage (Prokopy 1968, 1969, 1972, Moericke 1969). Attractiveness is due to reflectance intensity above 500nm. Yellow hue is a broad spectral region hue, excluding only blue components (<490nm). Herbivorous insect visual sensitivity and response to monochromatic light peaks in the green, declining rapidly above 550nm (Menzel 1979). Therefore, green components of yellow surfaces are assumed to be more important to insect attraction than are red components. Few studies have been conducted to determine which components of yellow attract plant feeding insects or how attractive components compare to peak visual sensitivity. The majority of field studies on surface attractiveness to plant feeding insects have compared white, blue, green, yellow, and red paint colors selected by the human eye. In only a few studies has the importance of devising tests based on spectral rather than subjective color differences been considered (Kennedy et al. 1961, Kring 1967, Moericke 1969, Prokopy et al. 1975, Vaishampayan et al. 1975a, b, Prokopy and Haniotakis 1976, Coombe 1981). Such tests are necessary to determine the importance of changes in green spectral components to attractiveness of yellow to insects. From studies which have included series of hues and tints of yellow, it appears that increase of spectral reflectance below 520nm inhibits maximum attraction of plant feeding insect species.

Unsaturated yellows. Plant feeding insects may be able to distinguish between the UV and blue spectral regions, as do bees (Moericke 1969). Certain aphids seeking the unsaturated foliage hue of marsh reeds are more attracted to yellow tints having a component of UV than to a tint without UV. Thus, for these aphids, the two tints must be perceived differently (Moericke 1969). Many species of reeds and grasses have surfaces which differentially reflect shortwave components, including UV (Hailman 1979). On the other hand, plants with pubescent surfaces absorb

UV strongly, while simultaneously reflecting across the visible spectrum (Woolley 1971, Kevan 1979). Tints reflecting UV may not be as attractive to insects utilizing pubescent host plants as they are to plant feeders whose hosts are grasses or waxy-coated broad leaves, such as cabbage. However, little information is available on the importance of unsaturated plant hues for insects seeking pubescent vegetation. Prokopy et al. (1975) found that olive flies are less attracted to strong tints of yellow with or without UV reflectance. Weak tints are not preferred over saturated yellow hue.

Effects of Background on Yellow Preference

Attraction to yellow surfaces is affected by optical background (Prokopy et al. 1975, Prokopy and Haniotakis 1976, Kring 1970). Optical backgrounds are seldom described, and even less so quantitatively measured, in attractance studies. Soil backgrounds have been shown to increase yellow water-trap captures of alate aphids compared to backgrounds of vegetation (Kring 1972). Aluminum mulches, which reflect sky energy uniformly, are thought to repel alighting alates (Kring 1972). Backgrounds can affect stimulus quality by: (1) enhancing color contrast; (2) providing or removing competing attractive surfaces; (3) increasing or decreasing general irradiance; or

(4) providing contrasting optical patterns (Hailman 1979). There is almost no information available on how insects react to the presence of various optical backgrounds in nature. It is known that single plants, surrounded by no vegetation, are more attractive to ovipositing insects than are plants mixed with nonhost vegetation (Rausher 1978).

Fluorescent yellows. Fluorescent colors enhance true reflection by absorbing in the shorter wavelengths (UV to blue) and re-radiating this captured energy in longer wavelengths (green to red). Most fluorescing compounds have both narrow absorption as well as narrow emittance bands. Field studies comparing yellow commercial enamels with fluorescent paints of similar hues show that the increased radiant energy of the latter enhances insect trap captures (Prokopy and Boller 1971, Prokopy 1972, Greany et al. 1977, Finch and Skinner 1974). The spectrum of the irradiance source affects fluorescent paints differently than non-fluorescent paints. Therefore, quantitative measurements conducted under test conditions would provide clearer comparisons of surface spectral differences than would relative reflectance measured with a spectrophotometer. Many natural and artificial surfaces have some component of fluorescence. This frequently results in a noticeable small increase in UV reflectance when surfaces are quantified using a standard reflectance spectrophotometer. Therefore, fluorescent paints are best measured under test condition, to provide reliable comparison data for insect attraction interpretation.

Yellow hues and oviposition. Not all phytophagous insects, particularly those seeking sites for oviposition, are attracted to yellow hues over other bright surfaces (Kring 1967, Owens and Prokopy 1978, Prokopy and Owens 1978, Röttiger 1979, Dapsis and Ferro 1982). Certain foliage-feeding Lepidoptera prefer green hues, although of lower reflectance, to yellow hues for oviposition substrates (Saxena and Goyal 1978). Knowledge of the physiological state of the test species is required to evaluate insect attraction (Kennedy et al. 1961).

Infra-red Importance to Visual Host Plant Location

Plant spectral reflectance curves show the highest variation in the infrared region (>800nm). This region is important for vegetation identification in remote sensing (Gates 1980). At night, vegetation re-radiates heat energy, absorbed during the day, in the infrared region. However, photons of infrared do not carry sufficient energy to initiate a response in visual pigments (Dartnall 1975).

Therefore, vision in the infrared is unlikely. Insect vision is limited to wavelengths <650nm (Burkhardt 1964, Goldsmith and Bernard 1974, Menzel 1979).

Orientation to infrared energy has, however, been shown in Coleoptera. Bupresiid beetles, attacking trees recently burned by forest fires, have a specialized heat sensing pit (Evans and Kuster 1980). Alfalfa weevils, and other members of the family Curculionidae, have IR sensitive areas in the vertex of the head which may function in orientation to plants (Meyer 1976, 1977). Speculation on IR sensitivity has centered primarily on body surface structures, which may function as dielectric waveguides for this longer wavelength electromagnetic radiation (Callahan 1965a,b). None of these sensors represent true visual mechanisms as defined. However, they do suggest that insect sensitivity to the environment may be more sophisticated than our own. This is all the more reason to pause and reflect on the perceivable physical attributes of the environment.

Polarized Light

All light energy reflected from surfaces contains some component of polarization (Gates 1980, Waterman 1981). Polarization sensitivity in insects has been linked to long distance orientation and home recognition (Wehner

1976), but the prevalence of polarized reflectance from surfaces suggests that polarized light may also contribute to object detection (Waterman 1981). Within the compound eye, retinular cell membrane orientation limits absorption of light to one plane of polarization. Thus, as in a polarizing filter over a camera lens, this mechanism can detect patterns of polarized light directly or can filter out specular reflectance which obscures visual pattern details (hue, texture, shape) (Waterman 1981). Certainly, the contribution of polarized light to surface orientation of insects deserves the intense evaluation that ultraviolet patterns have received for pollinators (Mazokhin-Porshnyakov 1969, Waterman 1981).

CHAPTER III

THE IMPORTANCE OF COLOR COMPONENTS TO WITHIN-TREE FOLIAGE FINDING IN APPLE MAGGOT FLIES, RHAGOLETIS POMONELLA WALSH

Introduction

Insect behavior frequently involves response to visual signals. Behavior elicited by spectral components of environmental light, such as alightment on yellow pigments by plant feeding insects, has been referred to as a spectral specific response (Kennedy et al. 1961, Moericke 1969, Vaishampayan et al. 1975b, Menzel 1979, Coombe 1981). Vegetation reflects and transmits maximally in the yellow-green spectral region (500-600nm) and minimally in the blue (400-500nm), where skylight energy peaks. Researchers (Kennedy et al. 1961, Menzel 1979) have hypothesized that the visual system of plant feeding insects has evolved to maximize the contrast between sky and vegetation. Therefore, insects exhibiting spectral specific responses to plant foliage should have mechanisms capable at the very least of discriminating light energy below ca. 500nm from that above ca. 500nm. If so, it suggests that proportion of total energy above and below 500nm might be used to predict alightment on a specific surface (Kennedy et al.

1961, Coombe 1981). Alternatively, energy measurement from specific narrow regions of the spectrum might prove equal or better in predicting alightment response (Vaishampayan et al. 1975b, Greany et al. 1977). Resolution of this difference requires a quantitative approach to the description and measurement of attractive host plant reflectance patterns, precise methods for isolating various components of the reflectance patterns for behavioral response analysis under natural conditions of illumination and background, and determination of the visual spectral sensitivity function of the insect. Visual ecologists suggest that studies of the reflective properties of an animal's resources combined with observation of the animal's orientation behavior may provide clues as to how visual mechanisms have been shaped for satisfying specific needs of the animal.

The apple maggot fly (AMF) Rhagoletis pomonella, is a destructive pest in commercial fruit orchards in much of North America. Adult flies seek food (eg. insect honeydew) on foliage within host trees. AMF are more attracted to yellow rectangles than to other colors (Prokopy 1968, 1972). Prokopy hypothesized that yellow is a super-normal foliage stimulus eliciting food seeking behavior. Therefore, reflected yellow light may be a visual signal which elicits a spectral specific response in AMF of alightment and feeding behavior.

The spectral reflectance patterns of most foliage, including AMF host plants, is an unsaturated hue of yellow-green, reflecting maximally at 550nm. For humans, changes in observable, foliage color do not result from changes in the spectral maximum (hue), but rather are the consequence of increasing reflectance (unsaturation) either (a) below 550nm, resulting in a whitish appearance (tint), as in densely pubescent or glaucous leaf surfaces, or (b) above 500nm, resulting in a more yellowish appearance, as in senescent leaves (Gates 1980). Therefore, insects that respond visually to foliage may be affected by hue unsaturation as well as by changes in hue intensity of foliage (Kennedy et al. 1961, Moericke 1969, Prokopy et al. 1975). The aims of this study were to determine (a) which features of AMF host plant structures are least variable in natural conditions; (b) how important yellow-green hue is to AMF attraction to foliage mimics; (c) what portion of the yellow-green foliage spectrum is most attractive to AMF; (d) how unsaturation of yellow hue affects foliage mimic attractiveness; and (e) whether AMF visual sensitivity shows a correlation with spectrum of host foliage reflectance.

Alightment behavior in plant feeding insects has been studied using reflective surfaces and filtered lights (Kennedy et al. 1971, Moericke 1969, Prokopy 1968, 1972, MacDowell 1972, Prokopy et al. 1975, Vaishampayan et al. 1975a,b, Greany et al. 1977, Coombe 1981). Both systems represent valid approaches. Selection of one or the other should be based on specific goals of the study. In this study, the former approach was used. High quality artist oil pigments were selected for the preparation of host structure mimics that were used to study responses to reflected light components under both laboratory and field situations. Studies of foliage reflectance and transmission patterns were conducted on host AMF trees: Crataegus (hawthorn) and Malus (apple). Apple trees in abandoned orchards were the field sties for studying AMF responses to host structures and to mimics during summers (1978-1981). Responses to mimics under laboratory conditions were conducted in a specially constructed flight chamber.

Materials and Methods

Mimic surfaces. Large (15x20cm) and small (7.5x10cm) rectangles cut from 2 mm pressboard (E.H.V. Weidman Ind., Inc., St. Johnsbury, VT), undercoated with white, were covered with (a) London and Winsor Newton artist oil pigments (Winsor-Newton Co., London, England) applied evenly using a palette knife; (b) lemon yellow (LYE) or black (BE) cadmium yellow light pigment (CYL) (Pearl Paint Co., N.Y.C.) mixed with Liquitex clear acrylic gel (Perm. Pigments Co., Cincinnati, OH) to form a spreadable paste; (d) yellow fabric; or (e) leaves. Controls were 3mm clear Plexiglas rectangles (Plex) or pressboard rectangles painted with non-reflecting enamel undercoat No. 29 (SWE) (Sapholin Co., Brooklyn, N.Y.).

Artist oil pigments used were: (a) London series: cadmium lemon (LCL), cadmium yellow light (LCYL), cadmium yellow (LCY), cadmium orange (LCO), titanium white (LTW); (b) Winsor-Newton series: cadmium yellow lemon (WCYL), cadmium yellow pale (WCYP), cadmium yellow (WCY), cadmium yellow deep (WCYD), cadmium scarlet (WCS), winsor green (WWG), winsor blue (WWB), flake white (WFW), and mars black (WMB).

Pigment mixtures used consisted of the following weighed proportions: (a) Greens (referenced by nm peak of reflectances): 500 I (2.5% WWB, 5% WWG, 92.5% LCL); 500 II (95% 500 I, 5% LTW); 520 I (5% WWG, 95% LCYL); 520 II (90% 520 I, 10% LTW); 550 I (1.5% WWG, 98.5% LCY); 550 II (90% 550 I, 10% LTW); 580 I (1% WWG, 99% LCO): 580 II (90% 580 I, 10% LTW); 500-600 I (2% LCL, 98% WMB), 500-600 II (90% I, 10% LTW); (b) Green intensity (GREINT): GREINT 1 (50% 550 I, 50% LTW); GREINT 2 (90% 550 I, 10% LTW);

GREINT 3 (88.8% 550 I, 11.2% WMB); (c) Gray: 10gray (90% LTW, 10% WMB), 2.5gray (97.2 LTW, 2.5% WMB); and (d) Diluted yellow: DIL 1 (85% WCYP, 15% WFW); DIL 2 (50% WCYP, 50% WFW); DIL 3 (10% WCYP, 90% WFW).

Fabrics were purchased from local retail outlets. Composition of selected fabrics was: (a) - cotton polyester broad cloth; (b) - 100% cotton; (c) - 100% polyester knit; (d) - 100% nylon knit. Commercial traps were also used. Unbaited yellow Pherocon® traps (Zöecon Co., Palo Alto, CA) were stapled and trimmed to 15x20cm size. Fresh apple leaves were attached to pressboard rectangles using double stick tape.

Field studies. For field tests, all rectangle surfaces were coated with a thin layer of Tangletrap® (The Tanglefoot Co., Grand Rapids, MI) and vertically suspended by wire within the canopy of host trees at ca. 2m height. Panels were hung a minimum of 1m apart, in sites selected to provide a foliage and fruit surround at ca. 18-25cm. Tests were conducted in two abandoned Amherst, MA apple orchards. Captured flies were counted and removed at daily intervals. Traps were rotated among positions so that each treatment received equal exposure at each position.

Flight chamber studies. A flight chamber (Kring 1966, Prokopy 1972) was constructed for laboratory tests of pigment preference. The interior surface of the 1m diam x 1.5m tall cylinderical chamber was painted with SWE. Interior temperature was regulated between 23.9-26.7°C using a space heater below the chamber. Humidity was maintained between 45 and 65% by misting with water between tests. Lighting was provided by a circular cool white fluorescent lamp (General Electric Co.) at the top of the chamber. The spectra of the lamp and of the pigments tested under its irradiance were measured using a spectral radiometer (Gamma Scientific Inc., Palo Alto, CA). The lamp energy spectrum and the relative reflectance of pigments are presented in Figs. 1 and 2, respectively.

Mature (2-4 wk post emergence) AMF (50-75/group) were introduced a minimum of 30 min prior to beginning a replicate. Flies were not sexed prior to introduction because preliminary tests indicated that males and females respond similarly under flight chamber conditions. Generally, test groups included 10-20% more females than males. Flies were allowed to feed on a standard yeast and sucrose diet prior to introduction into the chamber, after which no food was provided. Water was provided through misting. Counts were made by observing the alightment (=arrival)

Figure 1. Irradiance measurement, made with a Gamma Scientific Spectral Radiometer, of the flight chamber lamp (FCL). Radiance reflectance from rectangle surfaces illuminated by the flight chamber lamp: Sapholin white latex enamel (SWE); Winsor-Newton artist oil pigments - cadmium yellow lemon (WCYL), cadmium yellow pale (WCYP), cadmium yellow (WCY), cadmium yellow deep (WCYD); green pigments, mixtures of winsor green and cadmium yellows, are noted by peak reflectance wavelength number (500, 520, 550, 580).

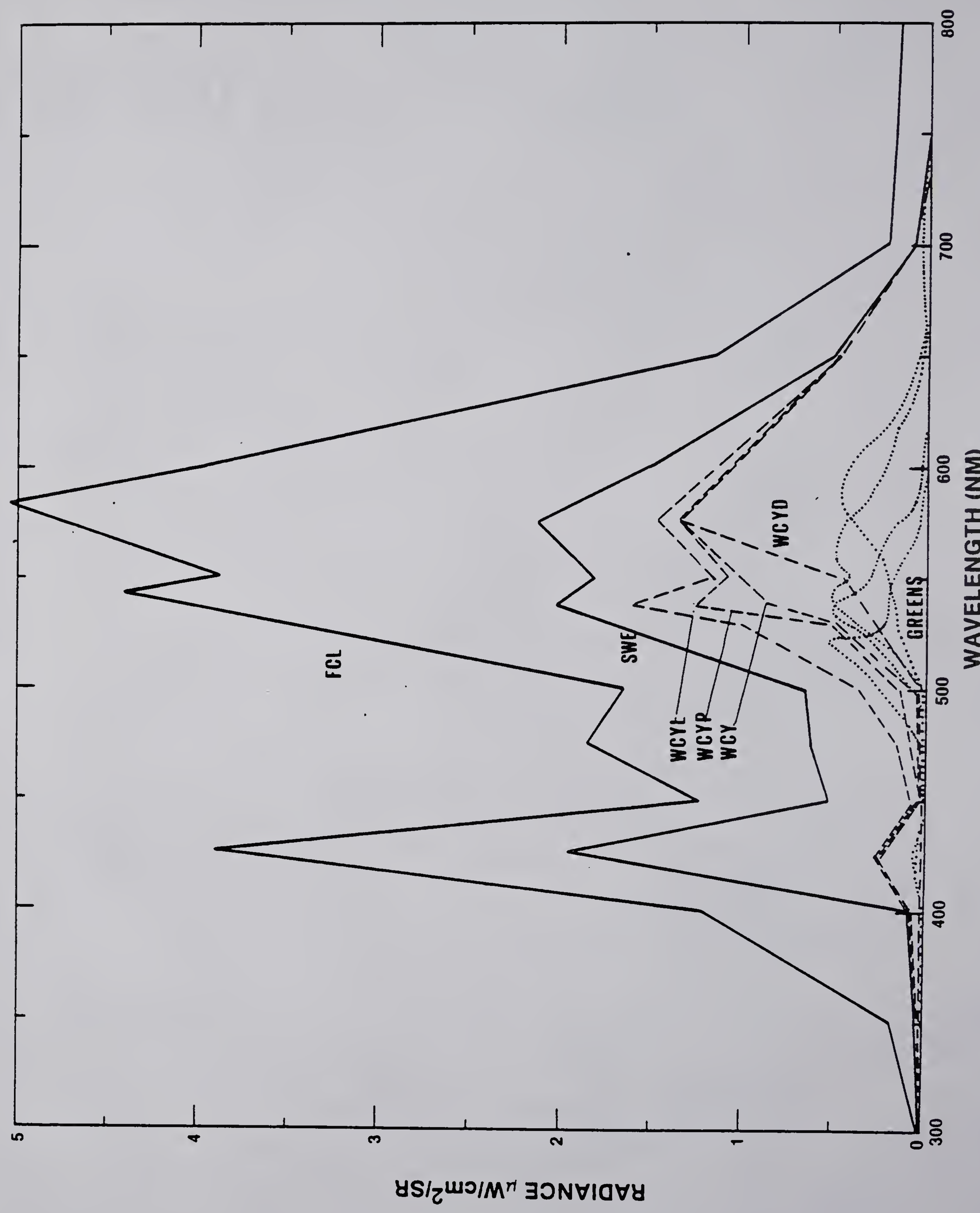

RADIANCE µW/cm²/SR
0
1
2
3
4
5
WAVELENGTH (NM)
300
400
500
600
700
800
FCL
SWE
WCYL
WCYP
WCY
WCYD
GREENS

Figure 1

Figure 2. Relative reflectance spectra mathematically calculated from spectral irradiance-radiance measurements shown in Figure 1. Pigments used: Sapholin white enamel (SWE); Winsor-Newton artist oil pigments - cadmium yellow lemon (WCYL), cadmium yellow pale (WCYP), cadmium yellow (WCY), cadmium yellow deep (WCYD), cadmium scarlet (WCS); green pigments, mixtures of winsor green and cadmium yellows, are noted by peak reflectance wavelength number.

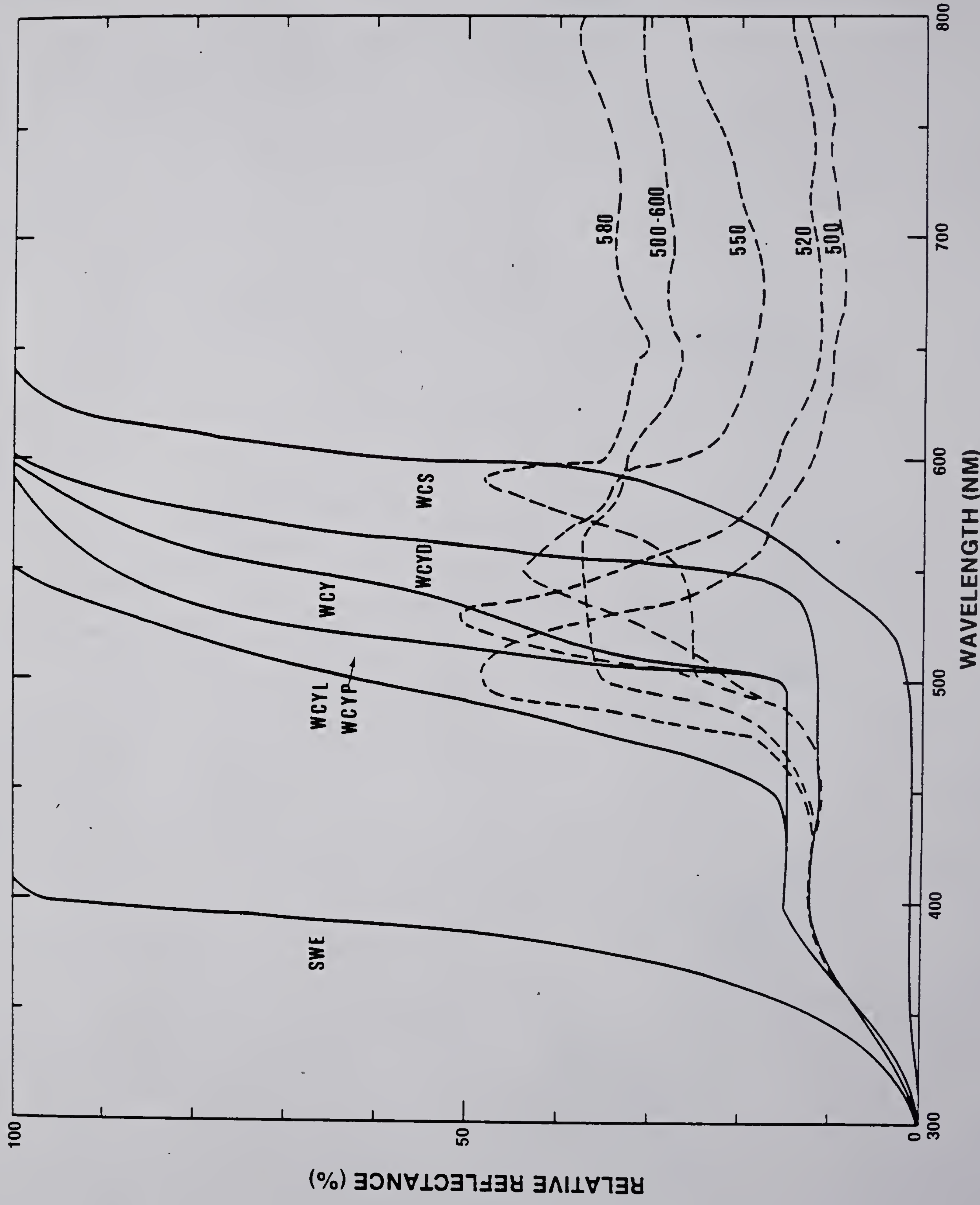

RELATIVE REFLECTANCE (%)
0
50
100
WAVELENGTH (NM)
300
400
500
600
700
800
SWE
WCYL
WCYP
WCY
WCYD
WCS
580
500-600
550
520
500

Figure 2

of flies on test rectangles attached to the chamber wall 20-25cm below the ceiling, across from a small clear plastic viewing port. Tests were conducted from 8am to 4pm (photoperiod of lab flies = 5am-11pm).

A replicate (rep) ended and rectangles were rotated after 10 arrivals total were observed on all rectangles. Observation time per rep ranged from 5-45min, and varied with treatment combinations and fly activity. A minimum of 15 min lapsed between reps. Results represent data for those reps conducted using a minimum of two groups of flies and all possible positional combinations of treatments. A single group of flies was used on only one day. A maximum of 10 reps (mean = 6) was conducted on each fly group. In one experiment (Table 2, Exp. 5), flies were captured on sticky-coated rectangles. Otherwise, all flight chamber data was gathered through direct observation of alightments.

Background effects. The effect of the color of the visual background on alightment preference was studied by covering the flight chamber interior with backdrops made of artist canvas. The canvas was primed with SWE and then painted with 500 I green, shaded with WMB to match foliage reflection intensity (Fig. 3), and diluted to brushable consistency with boiled linseed oil. Back-

Figure 3. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of: host leaf surfaces - apple (A), hawthorn (H), face (F), back (B), transmission (T); foliage mimic backdrops for the flight chamber - light foliage mimic backdrop (L), dark foliage mimic backdrop (D).

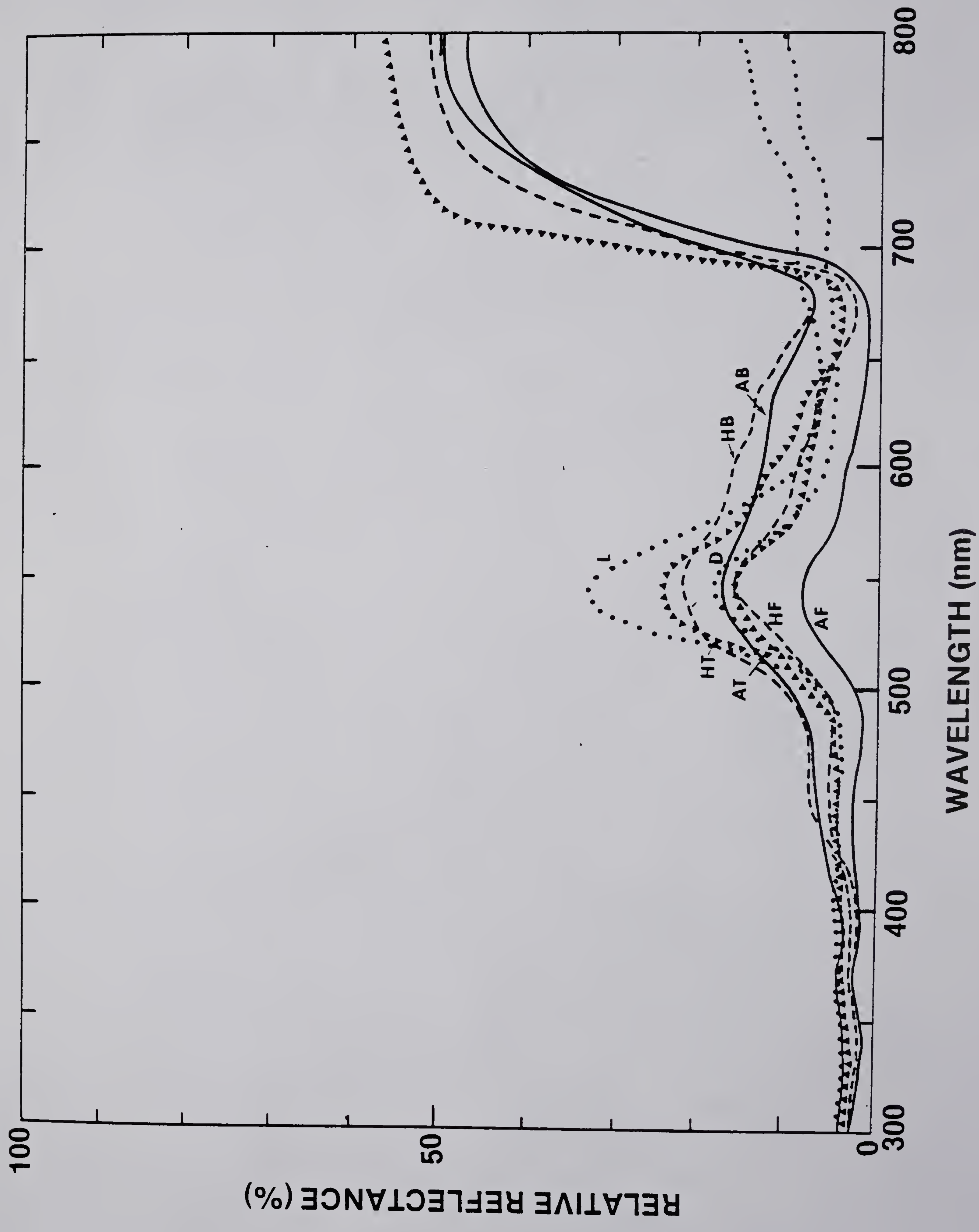

RELATIVE REFLECTANCE (%)
0
50
100
WAVELENGTH (nm)
300
400
500
600
700
800
L
D
HT
AT
HF
AF
HB
AB

Figure 3

drops were air dried for 3 months prior to use.

Quantification of reflective properties. Measurements of the relative reflectance spectra of foliage mimics and host structures were made with a Shimadzu UV-210 spectrophotometer (Bausch and Lomb, Inc.). Magnesium oxide (MgO) was used as a reflectance standard. Reflectance spectra for host foliage and all surfaces used are presented in Figs. 3, 7-11. The spectral radiometer was used to measure apple foliage radiance in nature (Fig. 4). A Pentax 35mm camera with either a 100mm macro or 50mm lens was used for color field photography utilizing Kodak Kodachrome 64 film (Fig. 5, 6) (Chapter VI).

Analysis. Data were submitted to analysis of variance and Duncan's Multiple Range Test at the 5% level. Arrival index was computed as total fly response to each surface relative to the most attractive surface or to WCYL for each experiment.

Results

Properties of foliage environment.

Color. Naturally growing, disease-free leaves of host hawthorn and apple trees had a broad-band reflectance spectrum peaking at 550nm (Fig. 3). The upper surfaces reflected a more saturated yellow-green hue than

Figure 4. Radiance spectra of: apple host leaves - (1) transmission; (2) face reflection; (3) Winsor-Newton cadmium yellow pale (WCYP). Measurements made from within the tree canopy using a Gamma Scientific Spectral Radiometer.

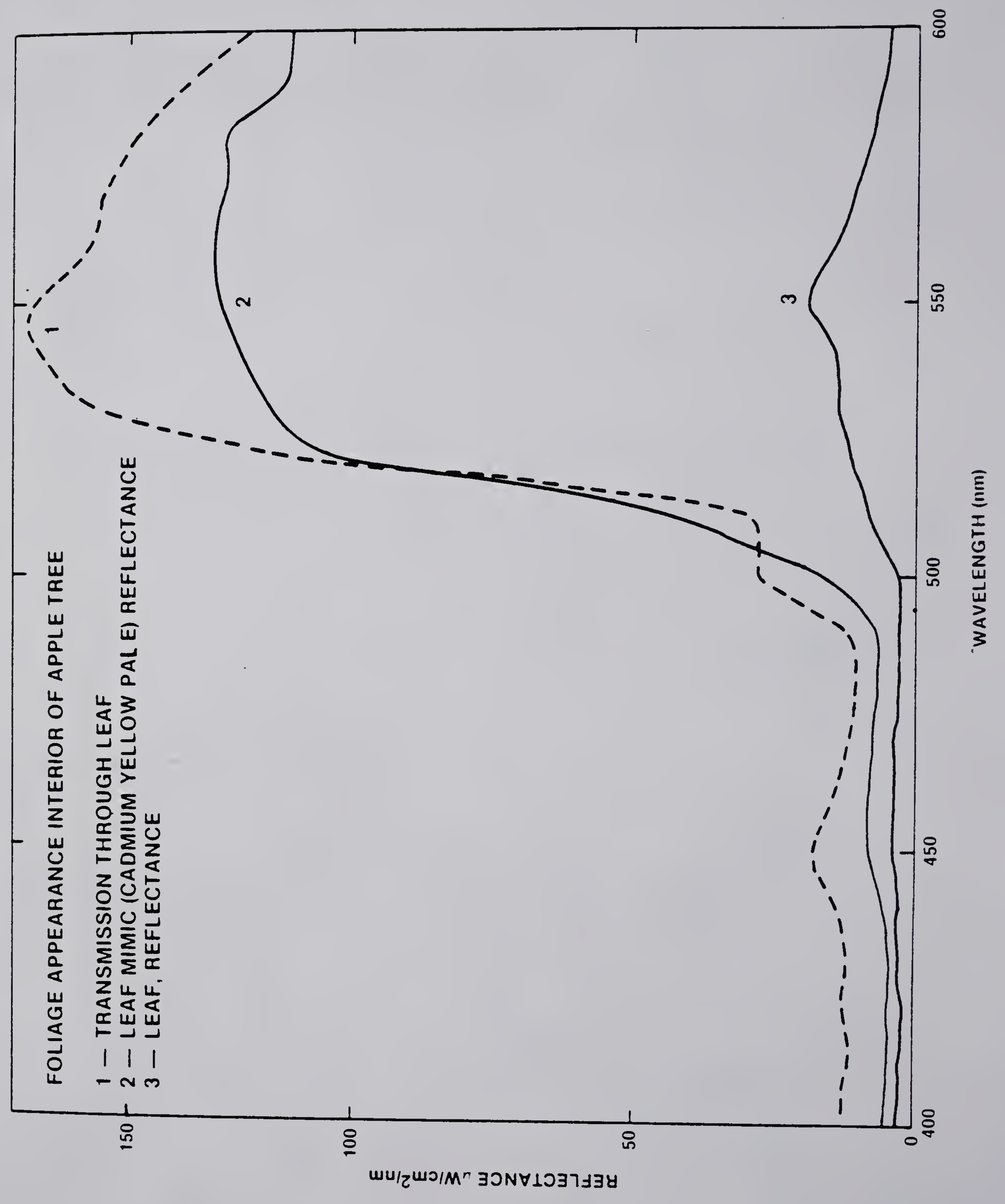

FOLIAGE APPEARANCE INTERIOR OF APPLE TREE
1 — TRANSMISSION THROUGH LEAF
2 — LEAF MIMIC (CADMIUM YELLOW PALE) REFLECTANCE
3 — LEAF, REFLECTANCE
1
2
3
REFLECTANCE μW/cm²/nm
0
50
100
150
WAVELENGTH (nm)
400
450
500
550
600

Figure 4

Figure 5. Individual leaves of host apple trees photographed: (a) from above, showing specular reflectance from leaf face; (b) with leaf backs turned toward sunlight; showing reflective pubescence; and (c) from beneath showing light transmitted through leaf surfaces. Photographed on Kodachrome 64 film without filtration.

the pubescent undersurfaces, which reflect more energy below 500nm. Peak reflectance of both surfaces never exceeded 20% (relative to MgO), regardless of leaf maturity. Upper surfaces of mature leaves collected in July and August had lower maximum reflectance (<8%) than developing leaves (8-15%). Transmitted energy passing through the leaves also peaked at 550nm and was highly saturated, containing no energy component below 500nm (Fig. 3,4). Field photography showed that light passing through foliage was more intensely yellow-green in appearance than light reflected from upper or lower foliage surfaces (Fig. 5). Upper surfaces varied in appearance because of specular reflection, which included spectral components characteristic of the illuminant (skylight) as well as the leaf surface (Fig. 5).

Vegetation hue is consistent among species of plants and among varied conditions of natural illumination, although to humans the apparent color may be variable due to increases in unsaturation and intensity (Woolley 1971, Vaishampayan et al. 1975, Gates 1980). Hue of AMF host foliage, with maximum reflectance at 550nm, was consistent among measurements of surface reflectance and transmission, therefore it was the least variable feature of foliage (Fig. 3,4). Saturation and intensity varied with viewing angle (Fig. 5). Highest saturation was

was measured from foliage transmission, and lowest from undersurface leaf reflectance (Fig. 3,4). Individual leaf shape and size was inconsistent as well.

Pattern. To the observer, the physical appearance of reflected light from the exterior of the foliage canopy of an AMF host tree was heterogeneous in visual pattern (Fig. 6). Leaves within the tree canopy varied in size, shape, and orientation, and the trees varied in general leaf characters among localities. On uncultivated hosts, disease and insect damage often caused distortion of leaf appearance, particularly of intensity of measured surface reflectance and leaf shape. Hue of transmitted energy changed relatively little, and the overlapping growth pattern of leaves rendered the appearance of light passing through foliage more homogeneous than reflected patterns (Figs. 5,6). Reflective patterns of branches and fruit appeared more homogeneous than the foliage background.

Background. It appears from observations of AMF behavior that skylight was frequently the background against which AMF viewed foliage. Spectral measurements of skylight show that peak energy occurs in the blue (ca. 450nm) largely as a result of Rayleigh scattering (Henderson 1970, Lythgoe 1979, Gates 1980). The saturation of blue hue is dependent upon the amount of moisture

Figure 6. Foliage, fruit, and branches photographed from (a) exterior to canopy; (b) interior of canopy. Photographed on Kodachrome 64 film without filtration.

and particulate matter in the atmosphere. Peak energy is always below 500nm during daylight hours.

Fly behavior within trees

Sex differences. Observations of AMF behavior within host trees located in abandoned Amherst, MA, orchards showed that on warm, sunny days most females were resting, feeding, or crawling on foliage, with only a few on fruit. In contrast, males were mostly noted on fruit, where mid- and late season mating is initiated (Prokopy et al. 1971, Prokopy and Smith 1980). Detailed observations of within tree movements and activities of AMF have been described elsewhere (Prokopy et al. 1971, 1972; Prokopy and Bush 1973; Prokopy and Smith 1980).

Within tree movement. Movement within host trees by both sexes consisted primarily of short hops (4-12cm) and short flights, which returned flies to the canopy near the point of flight origin. Movement was most frequently initiated at an outer upper edge of a leaf and terminated on the undersurface of a nearby leaf. Landing orientation to leaf undersurfaces has also been noted for plant feeding whiteflies (Vaishampayan et al. 1975b), and *R. fausta* flies (Prokopy 1975). Hops and flights by AMF were often preceded by a side to side rocking motion of the fly, suggesting visual orientation (Reichardt and Poggio 1979). Flies crawled to upper leaf surfaces following landing, and the sequence was repeated. Flies also flew from upper leaf surface to upper leaf surface, and from fruit to fruit. Departure and direction of flights and hops were (in order of frequency of observation): leaf to leaf, leaf to fruit, fruit to leaf, fruit to fruit, and leaf or fruit to twig.

AMF response to natural foliage. Attractiveness of natural foliage of two reflectance intensities (8% (dark) and 15% (light) maximum reflectance at 550nm) to alighting flies was tested in the flight chamber. Significantly more flies alighted on the light-foliage-covered rectangles than on the dark-foliage covered ones when rectangles were displayed against the white (SWE) chamber interior (Table 1, Exp. 1). A similar test conducted within host apple trees captured too few flies for comparison.

AMF response to green pigment foliage mimics

Field. Under field conditions, five green pigments having reflectance spectra approximating those of natural leaves (green pigments are referred to by wavelength number of maximum hue: 500, 520, 550, 580, and 500-600)

Table 1. Adult AMF attraction to 15x20cm rectangles covered with fresh leaves or various green pigments (Fig. 1,2,4). Arrivals within apple trees were measured by number of AMF captured in the Tangletrap which coated the rectangles. Arrivals in the flight chamber measured by direct observation of AMF alightments on rectangles. Numbers within each experiment followed by the same letter are not significantly different (P < .05).

			Arrivals		Arrival Index**		
Experiment	Location	Rectangle*	M	F	Total	M	F
1	Flight Chamber	Leaves Light	83a		100		
		Leaves Dark	37b		45		
2	Tree	550I	159a	340a	100	100	100
		520I	147a	303ab	90	92	89
		500I	104ab	275ab	76	65	81
		500-600I	104ab	215 b	64	65	63
		Plex	47 b	112 c	32	30	33
3	Tree	550II	15a	102a	100	100	100
		500II	23a	64 b	74	153	63
		Plex	6a	39 b	38	40	38
4	Tree	550II	48a	129a	100	100	100
		580II	47a	118a	93	98	91
		Plex	11 b	31 b	24	23	24
5	Tree	520II	58a	119a	100	100	100
		500-600II	27ab	67 b	53	47	46
		Plex	5 b	20 c	14	9	17

Table 1. continued

Experiment	Location	Rectangle*	Arrivals			Arrival Index**		
			M		F	Total	M	F
6	Flight Chamber	550I		38a		100		
		500I		8 b		21		
		SWE		4 b		11		
7	Flight Chamber	550I		144a		100		
		520I		117 b		81		
		SWE		19 c		13		
8	Flight Chamber	550I		46a		100		
		580I		24 b		52		
		SWE		10 c		22		
9	Flight Chamber	580I		18a		100		
		500I		13a		72		
		SWE		19a		105		
10	Flight Chamber	550I		28a		100		
		500-600I		6 b		21		
		SWE		5 b		18		
11	Flight Chamber	550I		55a		100		
		10Gray		10 b		18		
		2.5Gray		11 b		20		
12	Flight Chamber	550II		35a		100		
		550I		14 b		40		
		SWE		11 b		31		

Table 1. continued

			Arrivals		Arrival Index**		
Experiment	Location	Rectangle*	M	F	Total	M	F
13	Tree	GREINT1	45a	87a	100	100	100
		GREINT2	47a	65a	85	104	75
		Plex	12 b	24 b	25	27	28
14	Flight Chamber	GREINT1	41a		100		
		GREINT2	17 b		42		
		SWE	12 b		29		
15	Tree	GREINT1	40a	110a	100	100	100
		GREINT3	17 b	19 b	24	43	17
		Plex	14 b	26 b	27	35	24
16	Flight Chamber	GREINT1	38a		100		
		GREINT3	9 b		24		
		SWE	13 b		34		
17	Flight Chamber	GREINT2	26a		100		
		GREINT3	12 b		46		
		SWE	12 b		46		

*Wavelength of maximum reflectance (green hue). GREINT - series of 550 green tints (1=light, 3=dark)

**Computed as: $\frac{\text{total arrivals/rectangle}}{\text{total arrivals on the most preferred rectangle or WCYP rectangle}}$

(Fig. 2,7) were more attractive to AMF than clear Plexiglas (Table 1, Exp. 2-5). Males and females showed equal relative responses to green pigments although total female capture was higher. Green pigments, having peak hue reflectance at 520 or 550nm (closest to natural foliage peak hue reflectance at 530-560nm) were more attractive than pigments having peak hue reflectance at 500 or 500-600nm. Female captures on 550 green pigment rectangles were ca. 1.2-1.6 times higher than on the 500 green pigment (Table 1, Exp. 2,3).

Flight chamber. AMF responded to green rectangles displayed within the flight chamber (white, SWE, interior) with the same preferences as shown under field conditions. AMF were slow in responding to rectangles under these conditions (10 arrivals/15-45 mins of observation), indicating that green rectangles were not strong attractants. Nonetheless, flight chamber experiments did show that AMF response significantly differed among the five green-hued pigments. Arrivals on 550 I green rectangles were 5.8 times greater than on 500 I green ones and 4.7 times greater than on 500-600 green ones (Table 1, Exps. 6, 10). Arrival total on 550 I green was only 1.2 times greater than on 520 I green, and 1.9 times greater than on 580 I green (Table 1, Exp. 7,8). Arrival on 550 I green was

5-5.5 times greater than on either gray (Table 1, Exp. 11). Flies did not significantly prefer 580 I green over 500 I green (Table 1, Exp. 9). However, in this case, neither 580 I green or 500 I green was significantly more attractive to alighting flies than the SWE white rectangle.

<u>AMF response to unsaturated 550 green pigment foliage mimics</u>. To increase attractiveness to alighting AMF, green pigments were tinted with titanium white to increase reflection (green series II) (Fig. 7). 550 II green (= GREINT 2, Fig. 8) (15% higher in reflectance at the 550nm hue peak than 550 I) was significantly more attractive within the flight chamber to alighting AMF (Table 1, Exp. 12). Further tinting of 550 I green to produce GREINT 1 (75% reflectance at hue peak) (Fig. 8) significantly increased AMF arrival under flight chamber conditions when compared to both shaded 550 green (GREINT 3, Fig. 8) (5% reflectance at hue peak) and GREINT 2 (Table 1, Exp. 14, 16). No significant differences were found under field conditions in comparisons between GREINT 1 and 2 (Table 1, Exp. 13). However, GREINT 1 was more attractive to alighting flies than GREINT 3, (Table 1, Exp. 15). Captures on shaded GREINT 3 did not differ significantly from captures on either clear Plex-

Figure 7. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of green pigments used to mimic host foliage. Dashed lines are for series II, tinted with white. Solid lines are for series I, untinted mixtures of winsor green and cadmium yellows.

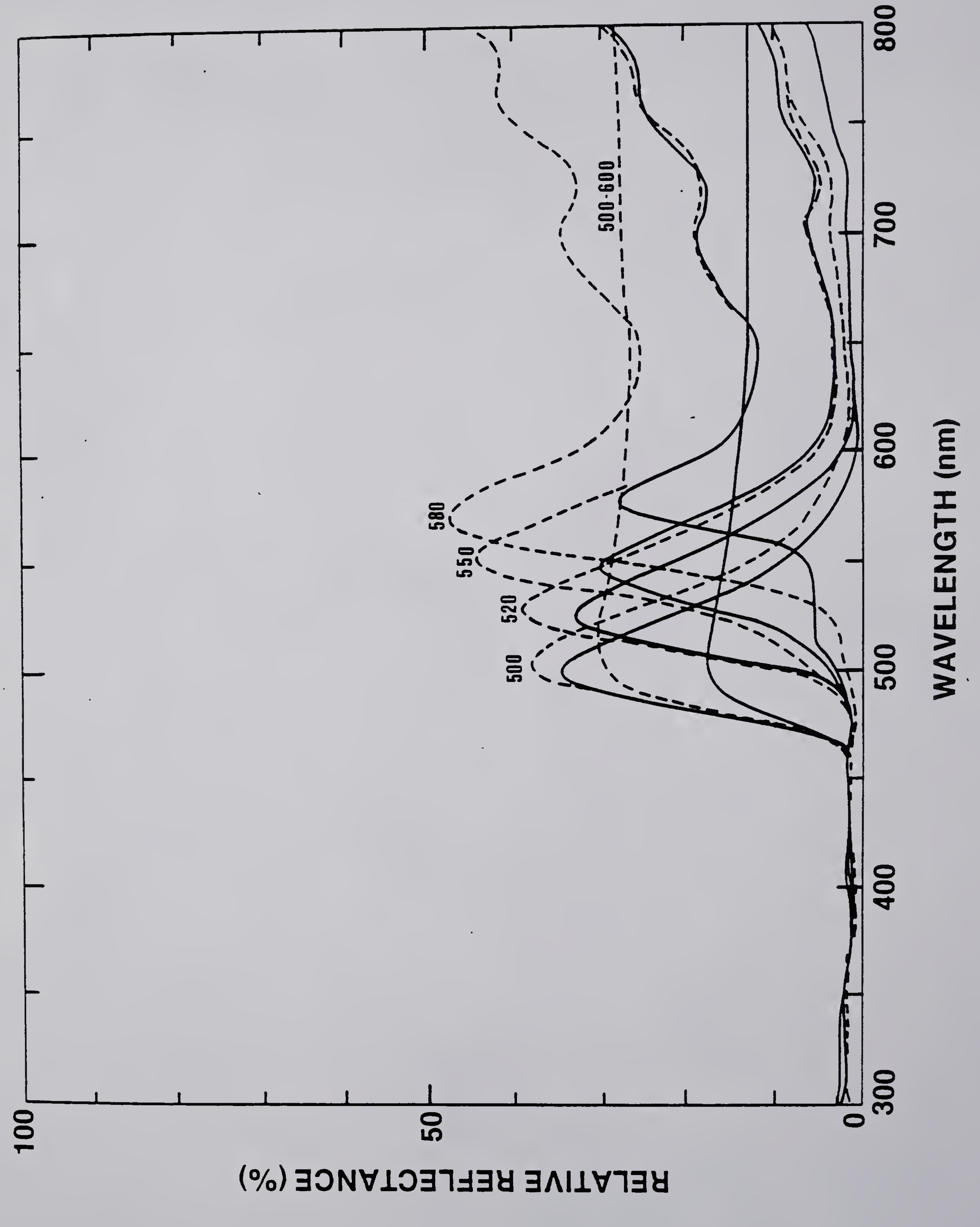

100
50
0
RELATIVE REFLECTANCE (%)
300
400
500
600
700
800
WAVELENGTH (nm)
500
520
550
580
500-600

Figure 7

Figure 8. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of unsaturated pigments of: (a) 500 green tinted with London titanium white or shaded with mars black (GREINT 1,2,3); (b) mars black tinted with titanium white (Gray 2.5, 10), (c) Sherwin Williams black enamel (BE).

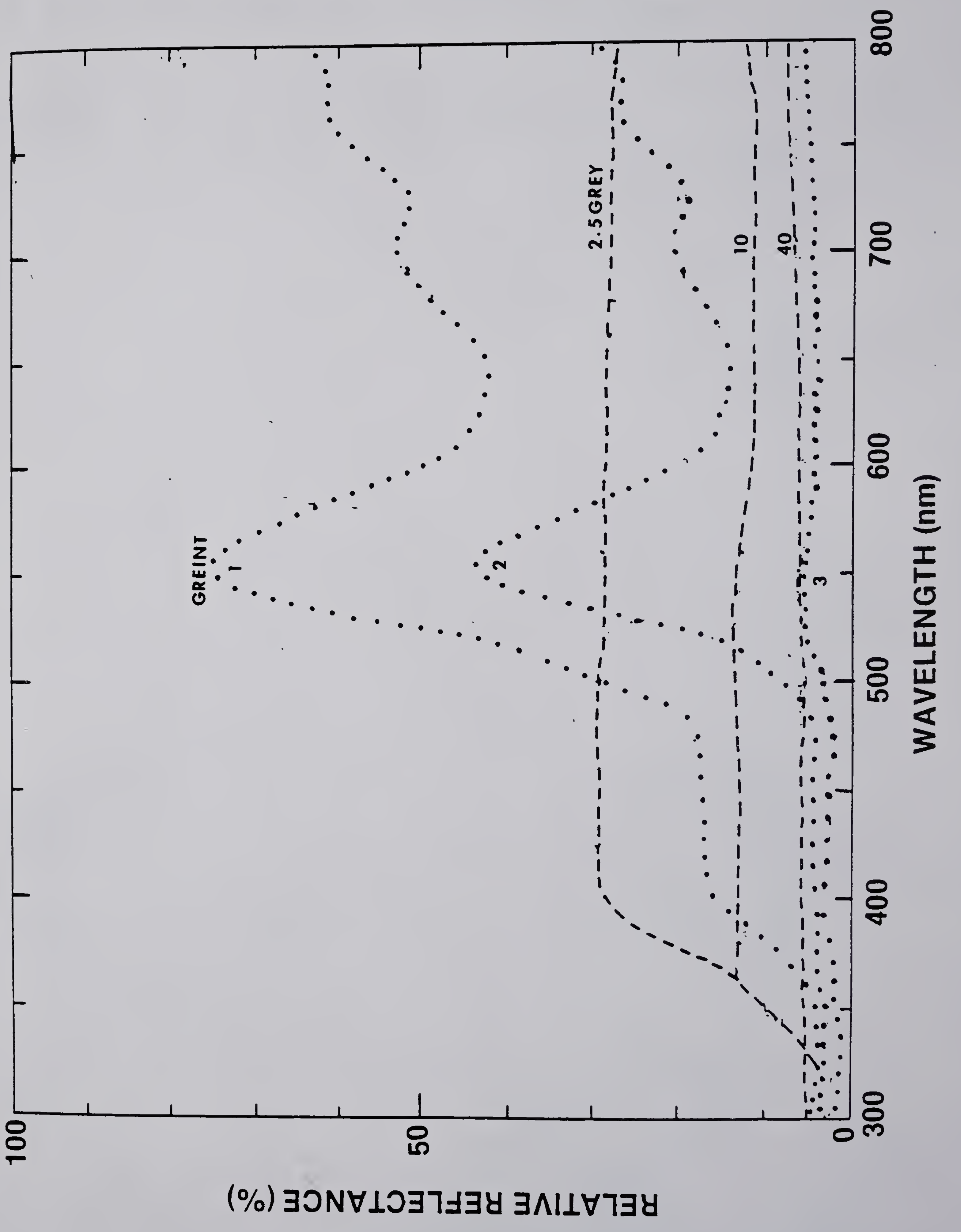

RELATIVE REFLECTANCE (%)
100
50
0
WAVELENGTH (nm)
300
400
500
600
700
800
GREINT
1
2
3
2.5GREY
10
40

Figure 8

iglas or white (SWE) rectangles (Table 1, Exp. 15, 16). Captures on GREINT 2 were variable in comparison with captures on Plexiglas and SWE (Table 1, Exp. 13, 14, 17).

Fly response to yellow pigment foliage mimics

Field. A series of yellow hued pigments (peak reflectances: WCYL = 500, WCYP = 520, WCY = 560, WCYD = 590, and WCS = 610nm) (Fig. 2, 9) were compared for AMF attraction within apple trees. Yellow pigmented (WCYL, WCYP, WCY and WCYD), black enamel (BE), and clear Plexiglas (Plex) rectangles (7.5 x 10cm) were compared initially (Table 2, Exp. 1). Yellow pigments were significantly more attractive to females than were either BE or Plex. However, BE was equally as attractive as yellow pigments to males. These results suggest that male response to rectangles of this small size may not have represented a response to foliage (Owens, unpublished data). Subsequent studies were conducted with larger panels (15x20cm) to eliminate, as much as possible, arrivals not associated with foliage seeking behaviors.

Comparisons among (a) WCYP, WCY, and WCYL, (b) WCYP and WCYD, and (c) WCYP and WCS showed that WCYP was significantly preferred over all other yellow pigments except WCYL (Table 2, Exp. 2-4). For females, arrival on

Figure 9. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of: (a) yellow artist pigments (Winsor-Newton, Inc.) - cadmium yellow lemon (WCYL), cadmium yellow pale (WCYP), cadmium yellow (WCY), cadmium yellow deep (WCYD), cadmium scarlet (WCS); and (b) apple leaves - face (AF) and back (AB).

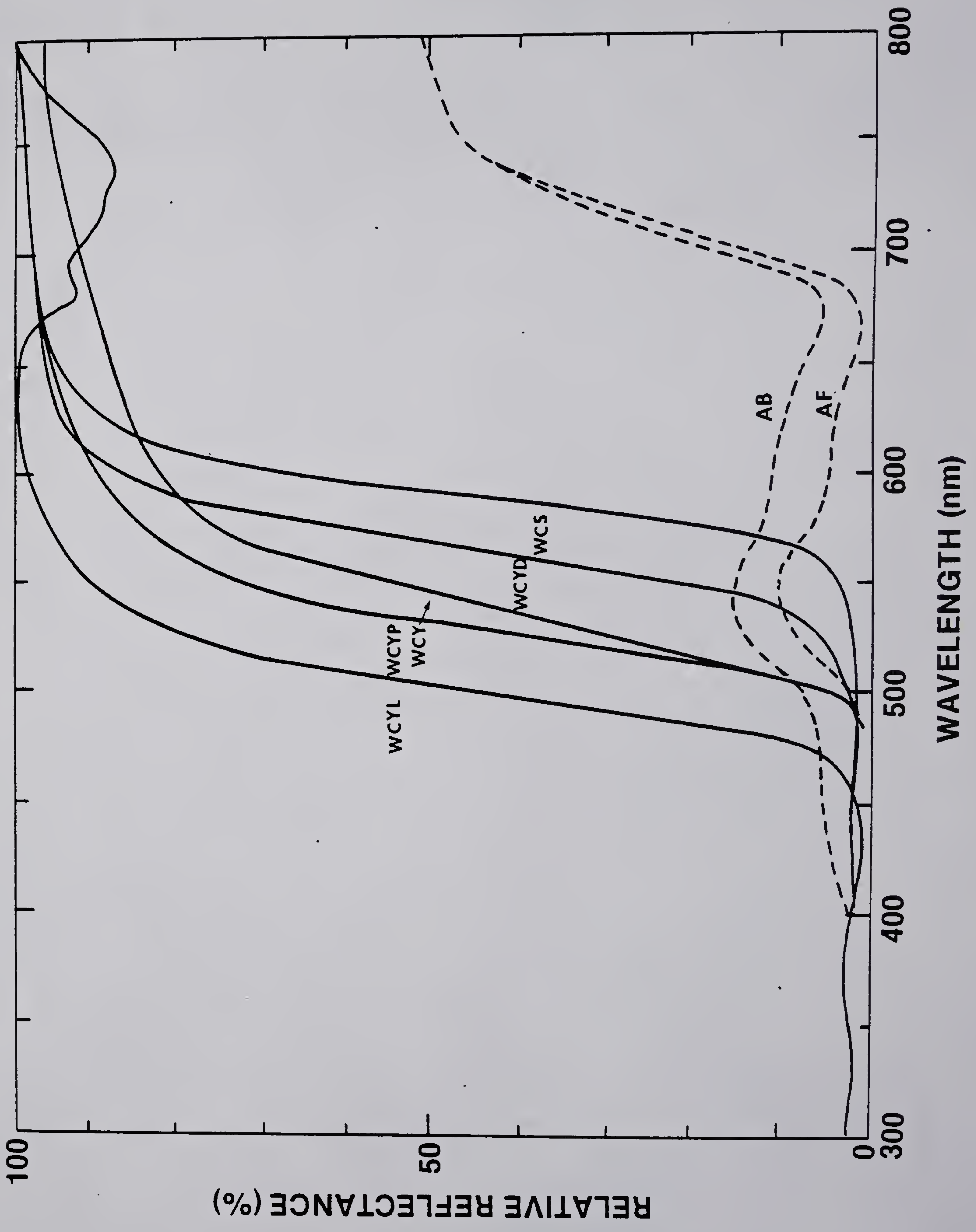

RELATIVE REFLECTANCE (%)
100
50
0
300
400
500
600
700
800
WAVELENGTH (nm)
WCYL
WCYP
WCY
WCYD
WCS
AB
AF

Figure 9

Table 2. Adult AMF attraction to 15x20cm rectangles covered with various yellow pigments (Fig. 2,7). Arrivals within apple trees and in Exp. 5 were measured by number of AMF captured in the Tangletrap which coated the rectangles. Arrivals in the flight chamber were measured by counts made via direct observation. Numbers within each experiment followed by the same letter are not significantly different (P < .05).

			Arrivals		Arrival Index**		
Experiment	Location	Rectangle*	M	F	Total	M	F
1	Tree	WCYP	196a	226a	100	100	100
		WCYL	178a	217a	94	91	96
		WCY	160a	191a	87	82	85
		WCYD	96 b	173a	63	49	76
		BE	147ab	119 b	63	75	53
		Plex	24 c	38 c	15	12	17
2	Tree	WCYP	108a	257a	100	100	100
		WCYD	55 b	127 b	64	51	49
		Plex	17 c	43 c	16	16	17
3	Tree	WCYP	24a	118a	100	100	100
		WCS	2 b	15 b	12	8	13
		Plex	0 b	13 b	9	0	11
4	Tree	WCYP	51a	164a	100	100	100
		WCYL	51a	159a	98	100	97
		WCY	27 b	97 b	58	53	59
		Plex	2 c	10 c	5	4	6
5	Flight Chamber	WCYP	80a		100		
		WCYL	49 b		61		
		WCY	45 b		56		

Table 2. continued

			Arrivals			Arrival Index**		
Experiment	Location	Rectangle*	M		F	Total	M	F
6	Flight Chamber	WCYP WCYL SWE		250a 175 b 18 c		100 70 7		
7	Flight Chamber	WCYP WCY SWE		253a 232 b 46 c		100 66 13		
8	Flight Chamber	WCY WCYL SWE		202a 134 b 23 c		100 66 11		
9	Flight Chamber	WCY WCYD SWE		144a 57 b 19 c		100 40 13		
10	Flight Chamber	WCYP 10Gray 2.5Gray		53a 4 b 3 b		100 8 6		
11	Flight Chamber	WCYD 10Gray 2.5Gray		53a 10 b 7 b		100 19 13		

*WCYP=cadmium yellow pale, WCYL=cadmium yellow lemon, WCY=cadmium yellow, WCYD=cadmium yellow deep, BE=Sherwin Williams black enamel, WCS=cadmium scarlet, SWE=Sapholin white enamel.

**Computed as: $\dfrac{\text{total alightments/hue}}{\text{total alightment on most preferred hue or WCYP}}$

WCYP was 7.9 times greater than on WCS, 2.0 times more than on WCYD, 1.8 times than on WCY, and approximately the same as on WCYL. The most attractive yellow hues, WCYL and WCYP, had broad bands of high reflectance between 500 and 600nm (Fig. 2,9).

Flight chamber. Flight chamber studies (Table 2, Exp. 5-11) confirmed the field results. Yellow rectangles were highly attractive to alighting AMF under flight chamber conditions (10 arrivals/3-20 mins). Arrivals on WCYP rectangles were significantly greater than on any other yellow pigmented ones (Table 2, Exp. 5-7). Yellow pigmented (WCYL, WCYP, WCY, WCYD) rectangles were significantly preferred over white (SWE) rectangles by alighting AMF (Table 2, Exp. 6-9). WCY was preferred over WCYL and WCYD (Table 2, Exp. 8,9). WCYP and WCYD pigmented rectangles were significantly preferred over either of two intensities of gray pigmented (Fig. 8) rectangles (Table 2, Exp. 10,11).

AMF response to yellow pigmented mimics when displayed within or against varied shades of host foliage or foliage mimics. The shade (light = 15% maximum reflectance, dark = 8% maximum reflectance, sky) of the background (natural apple foliage or sky for field experiments; pigmented artist canvas foliage backdrop mimics or SWE for flight chamber experiments) affected relative AMF arrivals on WCYL and WCY, but not on WCYP (Table 3, Exp. 1-8). WCYP was the most attractive yellow pigment (although not usually significantly so) under all conditions where it was included (Table 3, Exp. 1, 4, 7). WCYP hue lies between the hues of **WCYL** and WCY (Fig. 9). Hence, it was omitted from the remaining experiments (Table 3, Exp. 2, 3, 5, 6, 8). Within both light and dark foliage trees, WCYL was consistently, although significantly in only one test (Table 3, Exp. 5), preferred over WCY (Table 3, Exp. 1, 2, 4, 5). WCYL was significantly preferred within the flight chamber against the light as well as dark foliage mimic backgrounds (Table 3, 6). WCY panels were slightly, although not significantly, more attractive to AMF when hung within trees lacking foliage (sky) (Table 3, Exp. 7). WCY was significantly more attractive than WCYL within the confines of the white (SWE) flight chamber (Table 3, Exp. 8).

Under field conditions, relative numbers of flies attracted to WCY compared to WCYL successively increased from when within a dark foliage background (70-78% of WCYL), to when within a light foliage background (70-98% of WCYL), and finally to when within a bare-of-foliage (sky) background (127% of WCYL) (Table 3, Exp. 1, 2, 4, 5, 7). Similarly, in flight chamber studies, relative AMF

Table 3. Adult AMF attraction to 15x20cm rectangles covered with various yellow pigments and displayed against various backgrounds. Arrivals within apple trees were measured by number of AMF captured in the Tangletrap which coated the rectangles. Arrivals in the flight chamber were measured by counts made by direct observation. Numbers within each experiment followed by the same letter are not significantly different (P < .05).

<table>
<tr><th rowspan="2">Experiment</th><th rowspan="2">Location</th><th rowspan="2">Background</th><th rowspan="2">Rectangle*</th><th colspan="2">Arrival</th><th colspan="3">Arrival Index**</th></tr>
<tr><th>M</th><th>F</th><th>Total</th><th>M</th><th>F</th></tr>
<tr><td>1</td><td>Tree</td><td>Foliage Dark</td><td>WCYP</td><td>14a</td><td>67a</td><td>111</td><td>64</td><td>131</td></tr>
<tr><td></td><td></td><td></td><td>WCYL</td><td>22a</td><td>51a</td><td>100</td><td>100</td><td>100</td></tr>
<tr><td></td><td></td><td></td><td>WCY</td><td>6ab</td><td>51a</td><td>78</td><td>27</td><td>100</td></tr>
<tr><td></td><td></td><td></td><td>Plex</td><td>2 b</td><td>3 b</td><td>7</td><td>9</td><td>6</td></tr>
<tr><td>2</td><td>Tree</td><td>Foliage Dark</td><td>WCYL</td><td>29a</td><td>55a</td><td>100</td><td>100</td><td>100</td></tr>
<tr><td></td><td></td><td></td><td>WCY</td><td>19a</td><td>40a</td><td>70</td><td>66</td><td>73</td></tr>
<tr><td></td><td></td><td></td><td>Plex</td><td>2 b</td><td>3 b</td><td>6</td><td>7</td><td>5</td></tr>
<tr><td>3</td><td>Flight Chamber</td><td>550 Dark</td><td>WCYL</td><td colspan="2">302a</td><td>100</td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>WCY</td><td colspan="2">155 b</td><td>51</td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>Plex</td><td colspan="2">23 c</td><td>8</td><td></td><td></td></tr>
<tr><td>4</td><td>Tree</td><td>Foliage Light</td><td>WCYP</td><td>35a</td><td>88a</td><td>124</td><td>140</td><td>119</td></tr>
<tr><td></td><td></td><td></td><td>WCYL</td><td>25a</td><td>74a</td><td>100</td><td>100</td><td>100</td></tr>
<tr><td></td><td></td><td></td><td>WCY</td><td>30a</td><td>67a</td><td>98</td><td>120</td><td>91</td></tr>
<tr><td></td><td></td><td></td><td>Plex</td><td>1 b</td><td>3 b</td><td>4</td><td>4</td><td>4</td></tr>
<tr><td>5</td><td>Tree</td><td>Foliage Light</td><td>WCYL</td><td>67a</td><td>149a</td><td>100</td><td>100</td><td>100</td></tr>
<tr><td></td><td></td><td></td><td>WCY</td><td>37 b</td><td>114 b</td><td>70</td><td>55</td><td>77</td></tr>
<tr><td></td><td></td><td></td><td>Plex</td><td>10 c</td><td>22 c</td><td>15</td><td>15</td><td>15</td></tr>
</table>

Table 3. continued

				Arrivals			Arrival Index**		
Experiment	Location	Background	Rectangle*	M		F	Total	M	F
6	Flight Chamber	550 Light	WCYL		270a		100		
			WCY		176 b		65		
			Plex		34 c		13		
7	Tree	Bare	WCYP	78a		176a	149	134	156
			WCYL	58a		113 b	100	100	100
			WCY	67a		151ab	127	116	134
			Plex	3 b		10 c	8	5	9
8	Flight Chamber	SWE	WCYL			173 b	100		
			WCY		211a		122		
			SWE		37 c		21		

*WCYP=cadmium yellow pale, WCYL=cadmium yellow lemon, WCY=cadmium yellow, SWE= Sapolin white enamel.

**Computed as: $\frac{\text{arrivals/rectangle}}{\text{arrivals/WCYL rectangle}}$

response to WCY compared to WCYL successively increased when against dark green (51%), light green (65%), and white (122%) (Table 3, Exp. 3, 6, 8).

AMF response to unsaturated yellow foliage mimics

Field. Field experiments comparing fabrics of hue similar to the hue most attractive to AMF yellow hue (WCYP) (Fig. 10), or comparing tints of WCYP (Fig.11) indicate that yellow tints are not as attractive as pure yellow (Table 4, Exp. 1, 2). More female AMF were captured on those rectangle fabrics (eg. cadmium, Zöecon Pherocon yellow) and tints (eg. WCYP, DIL 1), exhibiting the most saturated yellow hue (Fig. 10,11, Table 3, Exp. 1, 2, 3). Captures were fewer on rectangles of the brightest yellow, which had high reflectance in the green region, 480-510nm (i.e. Zöecon Pherocon yellow) (Table 4, Exp. 1, 3). Relative captures of males and females were nearly equal among all rectangles although total female captures were greater than that for males in each experiment. GREINT 1 (green tint) and non-UV-reflecting SWE (white), equally attractive to AMF, were not as attractive as either yellow (Table 4, Exp. 3). Female captures on WCYP were ca. 3 times higher and male captures on WCYP were ca. 5-8 times higher than on GREINT 1 or SWE. Female captures on WCYP were 1.4 times higher and male captures were 2.1

Figure 10. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of: (a) yellow fabrics - cotton-polyester broad cloth (A), 100% cotton (B), 100% polyester knit (C), and 100% nylon knit (D): (b) yellow Zöecon Pherocon® trap (Z); and (c) paints - cadmium yellow light in acrylic gel (CYL), and Sherwin Williams lemon yellow enamel (LYE).

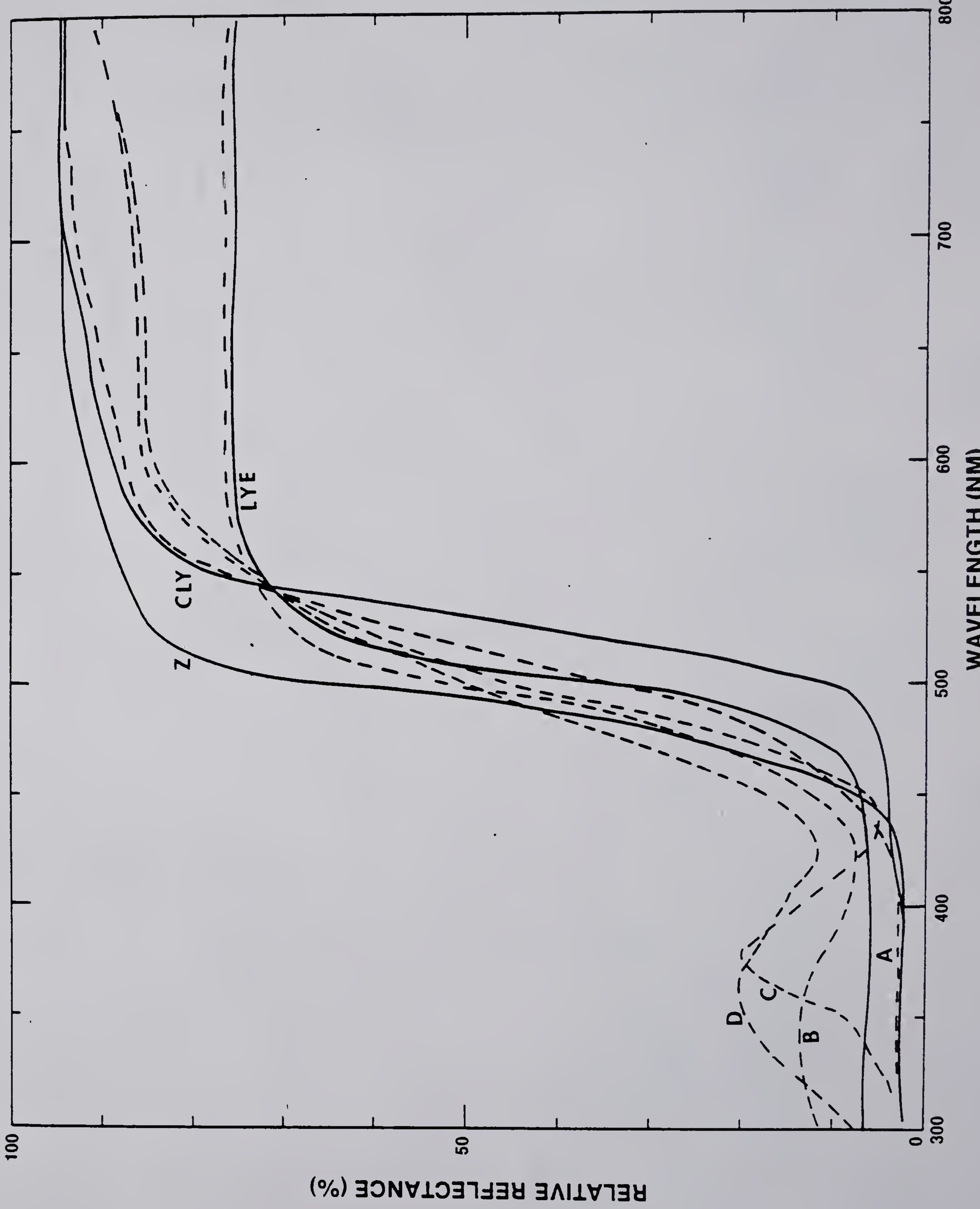

RELATIVE REFLECTANCE (%)
100
50
0
WAVELENGTH (NM)
300
400
500
600
700
800
Z
CLY
LYE
A
B
C
D

Figure 10

Figure 11. Relative reflectance, measured with a Shimadzu UV-210 spectrophotometer, of Winsor-Newton cadmium yellow pale (WCYP) tinted with flake white (Pb) (DIL 1,2,3).

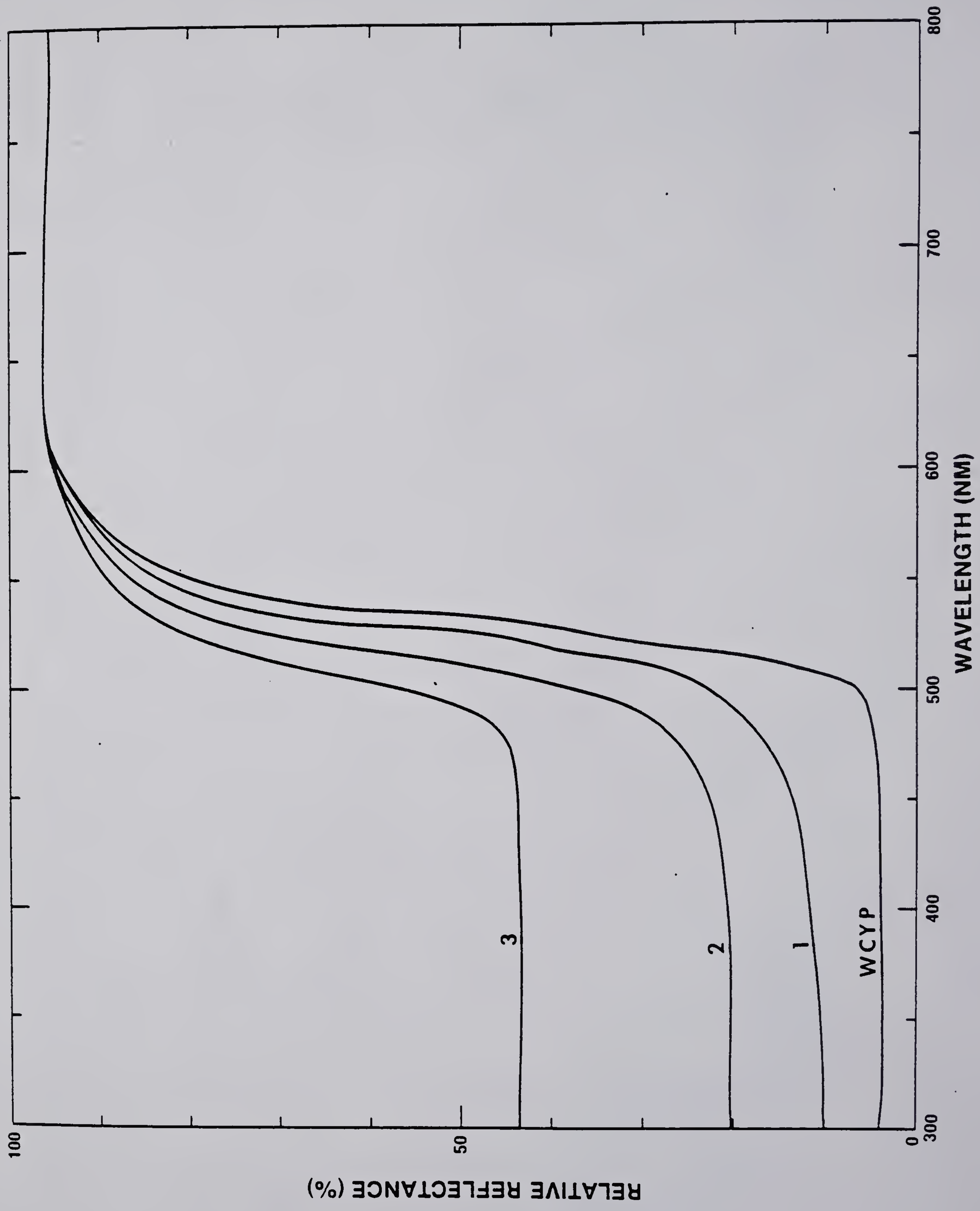

RELATIVE REFLECTANCE (%)
100
50
0
300
400
500
600
700
800
WAVELENGTH (NM)
3
2
1
WCYP

Figure 11

Table 4. Adult AMF attraction to 15x20cm rectangles covered with various diluted yellow hues, pigments and fabrics hung within host apple trees (Fig. 8,9). Arrivals were measured by counting the number of AMF captured in the Tanglefoot which coated the rectangles. Numbers within each experiment followed by the same letter are not significantly different (P < .05).

				Arrival Index**		
Experiment	Rectangle	M	F	Total	M	F
1	CYL	128a	586a	100	100	100
	ZOECON	98ab	413 b	72	77	70
	FABRIC A	63 b	358 b	59	49	61
	LYE	69 b	312 bc	53	54	53
	FABRIC B	51 b	282 bc	47	40	48
	FABRIC C	44 b	212 c	36	34	36
	FABRIC D	48 b	207 c	36	38	35
2	WCYP	152a	184a	100	100	100
	DIL1	126ab	134ab	78	83	73
	DIL2	76 b	127 b	60	50	69
	DIL3	96ab	101 b	59	63	55
	Plex	17 c	15 c	10	11	8
3	WCYP	248a	279a	100	100	100
	ZOECON	116 b	196 b	59	47	70
	GREINT1	46 c	94 c	27	19	34
	SWE	30 cd	91 c	23	12	33
	Plex	14 d	25 d	7	6	9

*CYL=cadmium yellow light, LYE=lemon yellow enamel, WCYP= cadmium yellow pale, DIL=cadmium yellow diluted with Pb white, GREINT1=light 550 green tint, SWE=Sapholin white enamel.

**Computed as: $\frac{\text{arrivals/rectangle}}{\text{arrivals/WCYP or CYL rectangle}}$

times higher than on Zöecon Pherocon yellow.

AMF response to neutral surfaces (controls). Clear Plexiglas rectangles (field, flight chamber green backdrop) and SWE rectangles (flight chamber, white interior) were considered as neutral surfaces for measuring rates of random AMF arrivals. Arrivals on these rectangles served as a basis for measuring relative attractiveness of various pigmented rectangles. Arrivals on Plexiglas averaged 24-38% of the number on 550 green (Table 1, Exp. 2, 3, 4) and 5-16% of the number on WCYP (Table 2, Exp. 1-4, Table 4, Exp. 2, 3). White rectangle arrivals averaged 10-22% of those on the most preferred green (550 I) (Table 1, Exp. 6, 7, 8, 10) and 6-13% of those on the most preferred yellow (WCYP) (Table 2, Exp. 6, 7). Relative AMF arrivals on clear Plexiglas varied little compared to arrivals on yellow pigments when experiments were conducted within or against various backgrounds (Table 3).

AMF maturity in field experiments. There were no consistent differences in ovary maturity of captured females regardless of the pigment. More females were captured on foliage mimic panels than males. Female maturity within the total population increased from July through August.

Discussion

The results of my studies confirm Prokopy's (1968) earlier hypothesis that AMF react to yellow pigment as if it were foliage on which to find food.

AMF were most attracted to those pigmented rectangles which were most similar to natural foliage in reflected or transmitted yellow-green hue. Background and unsaturation of foliage hue affected AMF alightment on rectangle surfaces. These results suggest that foliage hue may be perceived by AMF principally as a broad band of energy from ca. 510 to ca. 580nm, the spectral region where AMF visual sensitivity has a peak.

Natural foliage showed more variability in intensity of reflected and transmitted energy than in dominant hue of reflected and transmitted energy, suggesting that hue is the lesser variable surface feature. Light reflected from both host leaf face and back surfaces contained a strong component above 500nm, peaking as a yellow-green (550nm) hue. Spectral radiometry indicated that leaf transmission, under bright sunshine field conditions, was higher in hue saturation and in intensity than was leaf reflectance (Fig. 4). The reflectance spectrum of WCYP more closely resembled the leaf transmission spectrum than did any other yellow or green pigment tested.

All bright-appearing yellow surfaces (eg. foliage-filtered light; pigments such as WCYP and Zöecon Pherocon traps) contain a strong green component (490-550nm). True spectral yellow occupies a very narrow band (550-580nm) and is seldom encountered in natural conditions. It is partly the presence or absence of a red component, particularly the chlorophyll absorption band at 680nm, that determines for the human eye whether a surface will appear yellow or green (Science of Color 1963, Wyszecki and Stiles 1967, Snodderly 1979). Lack of red reflectance from leaf surfaces, but strong transmission of red through leaf surfaces, explains why humans perceive apple leaves as dark green when viewed in diffuse reflected light and as a more intense yellow when viewed in transmitted light (Fig. 4, 5, 6). The hue peak of foliage (550nm) is characteristic of chlorophyll reflectance and therefore changes little or not at all with viewing angle or among plant species (Gates 1980). Results from these spectral studies of AMF host foliage support Gate's suggestion that to humans, an increased yellow appearance of foliage is characterized by an increase in intensity of the red component (>580nm) and not a change of hue.

Vegetation-feeding birds use spectral changes in red reflectance to select food plants. Pigeons, which have been intensively studied, have trichromatic vision. They have a red receptor, enabling peak wavelength discrimination ability at approximately 610nm, where leaf surface reflectance shows the greatest variability (Lythgoe 1979). AMF lack a red receptor (Chapter V), and therefore must use cues from some other portion of the foliage reflectance spectrum for visual foliage selection. They may have discrimination mechanisms functioning as birds, but in shorter wavelength regions. The region around 500nm has been suggested as one of particular importance to alighting insects (Kennedy et al. 1971).

Field behavior studies showed that AMF frequently hop to the under surfaces of leaves. Under leaf surfaces observed and photographed from the point of hop origin showed that transmitted light obscured lower leaf surface reflectance (Fig. 5). Photographs of leaf face and back surfaces turned toward the light (Fig. 5) show the appearance effects of specular reflectance (due to surface gloss from wax and pubescence, both of which are less apparent in spectrophotometer measurements (Fig. 3)). UV was not involved in saturation changes except as specular reflectance. Photography indicated that UV reflectance is not a component of white-appearing surface pubescence in AMF apple hosts. Pubescence absorbs UV, but reflects all other wavelengths (Kevan 1979). Foliage hue saturation within the AMF host tree environment can be considered a component of viewing angle.

Leaf-hopping, movement patterns of *Rhagoletis* flies within trees are particularly well developed in extrafloral nectary feeding species, such as *R. fausta* (Prokopy 1976). These movement patterns may be partly a response to the greater attractiveness of transmitted yellow-green foliage hue. Moericke (1955) suggested that alightment behavior in aphids is a direct response to energy transmitted by plant foliage visible to the aphid during its horizontal, close-to-the-ground phase of dispersal flight. Although the reflected energy of plants may initially direct the orientation of a plant feeding insect's flight away from sky, alightment may be more dependent on closer range signals where transmitted energy offers a stronger cue than reflected energy (Kennedy et al. 1961). The strength of the transmitted energy cue may result from both lack of specular components and from higher intensity of energy above 500nm transmitted through foliage. In addition, aphids may use intensity of transmitted or reflected energy above 500nm as an indication of nitrogen (Kennedy 1958, Kring 1972, Dixon 1972). Nitrogen concentration is highest in new and senescent foliage, which transmits and reflects more energy above 500nm than mature foliage. AMF, which utilize honeydew as a food source, may, be using the same intensity cues as aphids to locate areas of homopteran feeding (Prokopy 1968). Indeed, flight chamber results assessing AMF response to apple host foliage of different reflectance intensities suggest that higher reflectance increases alightments (Table 1, Exp. 1). That the most attractive yellow (WCYP) was the one closest to the foliage transmitted energy spectrum also suggests that AMF may be responding to the purest natural foliage hue.

Insect detection of foliage within an environment illuminated by daylight, and subsequent insect alightment on host plants, may be mediated by a visual system capable of comparing as few as two spectral regions (Kennedy et al. 1961). Aphid alightment behavior may be dependent upon the aphid's ability to compare the amount of energy above and below 500nm. This requires a minimum of two receptors: one sensitive to energy > 500nm, and one sensitive to energy < 500nm. Relative reflectance rising above a 30% intensity level at less than 510nm reduces whitefly alightment, indicating a strong visual discrimination ability at 510nm and thus implicating two receptor types (Vaishampayan et al. 1975a,b).

Studies of AMF compound eye spectral sensitivity (Chapter V) suggest that two receptor types are found. A short wave receptor type, comparable to that found in

Drosophila receptors 1-6 (Bernard and Stavenga 1979), has broad reception range peaking in the UV (350nm) and blue-green (475nm). A second, more weakly responding receptor, peaks at 560nm and shows a decline of response below 500nm. This receptor may be equivalent to a longer wavelength receptor noted in central cells of studied Diptera (Hardie 1979, Hardie et al. 1979, Smola and Meffert 1979). The maximum sensitivity of the second receptor type corresponds closely to the peak of foliage reflectivity and transmission. The shorter wavelength receptor has little sensitivity in this area, with maximum capacity for detecting reflected energy at or below 500nm. The overlap of the receptors suggests that maximum hue discrimination for the fly, if indeed the mechanisms necessary for discrimination are present, would be between 500 and 550nm. Unlike the pigeon, AMF would not be able to discriminate host foliage on the basis of variability in red reflectance, as AMF have no demonstrated red receptor. However, discrimination ability in the blue to yellow-green region is possible, which corresponds both with the measured spectral reflectance and transmission hues of foliage and AMF preference for green and yellow hues. AMF were most attracted to those green hues which did not have a component at or below 500nm (Table 1, Exp. 2-10). This suggests that AMF may be capable of discriminating hues around 500nm, where leaf reflectance begin to increase. At the 5% intensity level, attractive green have no 500nm component, whereas less attractive greens (e.g. 500, 500-600) have reflectance above 30% intensity at 500nm (Fig. 7). 580 green apparently approaches the far edge of AMF visual sensitivity. Thus such a hue may not be very visible to AMF.

AMF preference for yellow hues likewise showed a positive relationship with wavelengths above but not below 500nm. Yellows with green components below 510nm (WCYL) were less attractive than those with green components above 510nm (WCYP). As reflected hue became more reddish, with less green component (WCYD, WCS), attractiveness to AMF declined. Therefore, foliage hue for AMF may be represented by a broad band from ca. 510 to ca. 580nm, peaking at ca. 550nm, where both peak foliage hue and peak AMF long wavelength sensitivity occur.

Unsaturation of WCYP or similar fabric yellows, through increase of reflectance below 500nm without altering that above 500nm (Figs. 8,10,11), resulted in a decrease in AMF alightment under field conditions (Table 4), suggesting that the additional reflectance made yellow less attractive (Kennedy et al. 1961, Moericke 1969, Prokopy et al. 1975). Unsaturation of 550 green (GREINT 1) increased alightment when compared to darker shades

(GREINT 2, 3) (Table 1, Exp. 13-16). It is not possible to determine if this alightment increase was due to 550 green unsaturation or to the increase of total reflectance intensity. I suggest that is was due to the latter, and that the increase in unsaturation through addition of reflectance components below 500nm detracted from the attractiveness of the higher yellow-green hue intensity. GREINT 1 was not significantly more attractive than non-UV-white SWE and was significantly less attractive than WCYP under field conditions. I suggest that AMF may be detecting rectangles of GREINT 1 much the same as they might be detecting open spaces (Kennedy et al. 1961). Open space has been described as areas of homogeneous visual patterns of broad-band spectral irradiance, i.e. white. Hailman (1977) suggested that for animals within their natural environment, sky appears homogeneous in visual pattern. That both white and GREINT 1 captured more AMF than clear Plexiglas suggests that there was positive attraction. AMF have been observed to fly from leaf edges into open spaces between leaves. While intensity of yellow-green hue may affect attractiveness to AMF, I suggest that pigment mimics of foliage hue must be of maximum hue saturation to ensure that AMF are responding as to foliage and not as to open space.

The intensity and color appearance of a surface is relative to the properties of the optical background against which it is viewed (Moericke 1955, Lythgoe 1979, Neumeyer 1980, 1981). Backgrounds of varied green foliage can affect the preference of tephritids for yellow hues (Prokopy et al. 1975). For AMF, the relative attractiveness of a green-yellow hue containing a 500nm component (WCYL) declined with high intensity backgrounds (sky and SWE) (Table 3). In contrast, the attractiveness of a non-green yellow hue (WCY) increased. Against all backgrounds tested, WCYP, which reflects in the green but not below 410nm, was most preferred. These results suggest that yellows of spectral reflectance similar to WCY have maximum attractiveness under bright conditions, whereas yellows similar to WCYL are most attractive to AMF against dark foliage. A mid hue (WCYP) is least affected by background variability. Data is insufficient to permit detailed explanations. Nonetheless, results do suggest that background differences may be a major reason accounting for literature discrepancies in describing the particular yellow hues most attractive to tephritid flies (Greany et al. 1977). Certainly, analysis of optical backgrounds surrounding the attractive object should be included in studies of insect attraction to reflective surfaces.

Differences in attractiveness of foliage-mimicking rectangles to male vs. female AMF may be explained by sex-related differences of within tree behavior. No visual sensitivity differences were noted between the sexes (Chapter V). From mid-season onward (i.e. when the bulk of these studies were conducted), males frequent foliage less often than females. At that time, males are more frequently noted on fruit, where they establish territories (Prokopy and Bush 1973). Females frequently forage on foliage and spend less time than males on fruit, even when engaged in ovipositional behavior (Prokopy et al. 1972). Fruit mimic studies yielded equal to slightly higher male:female capture ratios (Chapter IV), which contrasts with the findings here.

In conclusion, AMF showed consistently stronger attraction to the foliage mimics which most closely resembled the foliage reflectance - transmission spectrum of natural hosts. Greens of intensity close to that of natural host leaf reflectance were less attractive than yellow. Attraction to yellow may be, as Prokopy (1968) suggested, an attraction to a supernormal foliage stimulus or an attraction to the energy spectrum transmitted through foliage. AMF visual sensitivity may provide the flies with maximum ability to discriminate on the basis of hue differences between foliage and other visual stimuli in the 500nm spectral region. Whether this represents true color vision remains undetermined. Quite likely, alightments of AMF on foliage are in response to the ratio of foliage hue (510-580nm) to non-foliage hue (350-510nm) in a manner similar to spectral specific responses described for aphids (Kennedy et al. 1961) and white flies (Coombe 1981). These responses may be affected by both the spectrum of the surface and that of the optical background.

CHAPTER IV

THE EFFECTS OF HUE AND INTENSITY ON FRUIT FINDING OF THE APPLE MAGGOT FLY, *RHAGOLETIS POMONELLA* WALSH

Introduction

The apple maggot (AMF) is a serious pest of commercial fruits in New England. It was primarily restricted to the fruit production areas of the northeastern and midwestern United States and Canada prior to its recent introduction into Oregon. AMF now threatens to infest the major U.S. fruit production areas of Washington and California. The latter state also faces continued threat of invasion by other fruit-infesting Tephritidae, several of which would raise havoc with a multi-billion dollar agricultural industry (Hagen et al. 1981). Sensitive monitoring traps capable of detecting very low levels of a fruit fly infestation are an important component of tephritid detection and control programs. Since many tephritids use vision in host selection (Prokopy 1977a), further research on visual host location is essential to the development of more effective design and use of monitoring methods.

AMF frequent host fruits, which are sites of mating and oviposition (Prokopy 1968, Prokopy et al. 1971).

Fruit-mimicking monitoring traps (sticky red spheres) are important for predicting need and timing of control measures in IPM programs (Prokopy 1975b, Prokopy and Hauschild 1979). Within-tree fruit location by AMF is primarily visual. Prokopy (1968, 1977) found color, shape, and size to be important to fruit mimic attractiveness. He hypothesized that AMF locate fruits within trees primarily by form and intensity of reflectance in contrast against background, rather than by hue. The red hue of fruits may be a major color-contrast signal for vertebrate seed dispersers (van der Pijl 1972). Little is known about the role of hue in the foraging behavior of fruit feeding insects. Butterflies may use the red hue of flowers as a signal to stimulate nectar feeding (Kevan 1978). The compound eye of some butterflies has been shown to be sensitive to red wavelengths whereas most insect eyes are not sensitive at such long wavelengths (Bernard 1979). Precise determination of fruit hue importance to AMF attraction requires careful analysis of fruit color components. By so doing, important natural surface components can be identified, quantified, and mimicked.

Using this approach, I studied AMF attraction to fruits in relation to those host fruit features which appeared least variable among different fruit species or varieties. I investigated (a) spectral reflectance patterns of natural host fruits (*Crataegus* and *Malus*) and background, (b) normal AMF activity under natural field conditions, (c) captures of AMF on variously pigmented fruit mimics (size = ca. natural fruit) under field conditions, and (d) spectral sensitivity function of the AMF compound eye (Chapter V).

Materials and Methods

Quantification of reflective properties. A Shimadzu UV-210 spectrophotometer (Bausch and Lomb, Inc.) and a 35mm camera with a 100mm macro or 50mm lens (Pentax, Inc.) (Chapter IV) were used to characterize spectral reflectance patterns of host fruits and fruit mimic surfaces. Relative reflectance measurements are given as a % of reflectance from a MgO standard (Fig. 12-14). For color photography, Kodak Kodachrome 64 film was used.

Observations of AMF behavior were made in apple and hawthorn trees having high natural fly populations, on days with warm, sunny weather (Chapter III).

Artificially pigmented fruit. To study AMF attraction to artificially pigmented (growing) host fruits, randomly selected green fruits on apple trees in an abandoned Amherst, MA orchard were artificially pigmented in place

Figure 12. Natural green growing apple fruits (ca. 4 cm diam) (NGF) and artificially pigmented fruit (growing). Winsor-Newton watercolor pigments: cobalt blue (WCB), cadmium lemon (WCL), alizeran crimson (WAC), black (WMB). Liquitex alizeran crimson plus clear acrylic gel (AC2). Spectral measurements made 7/25/80.

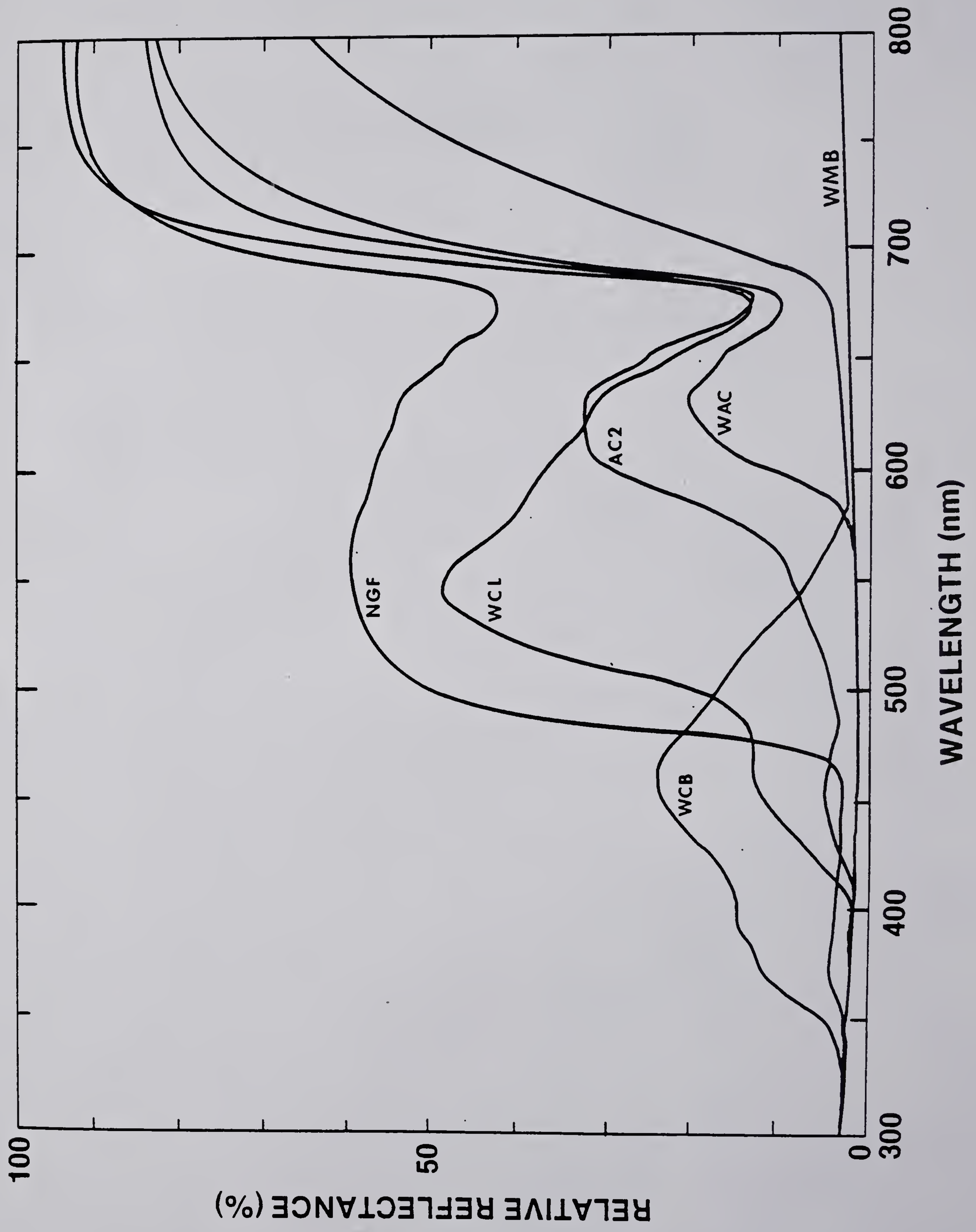
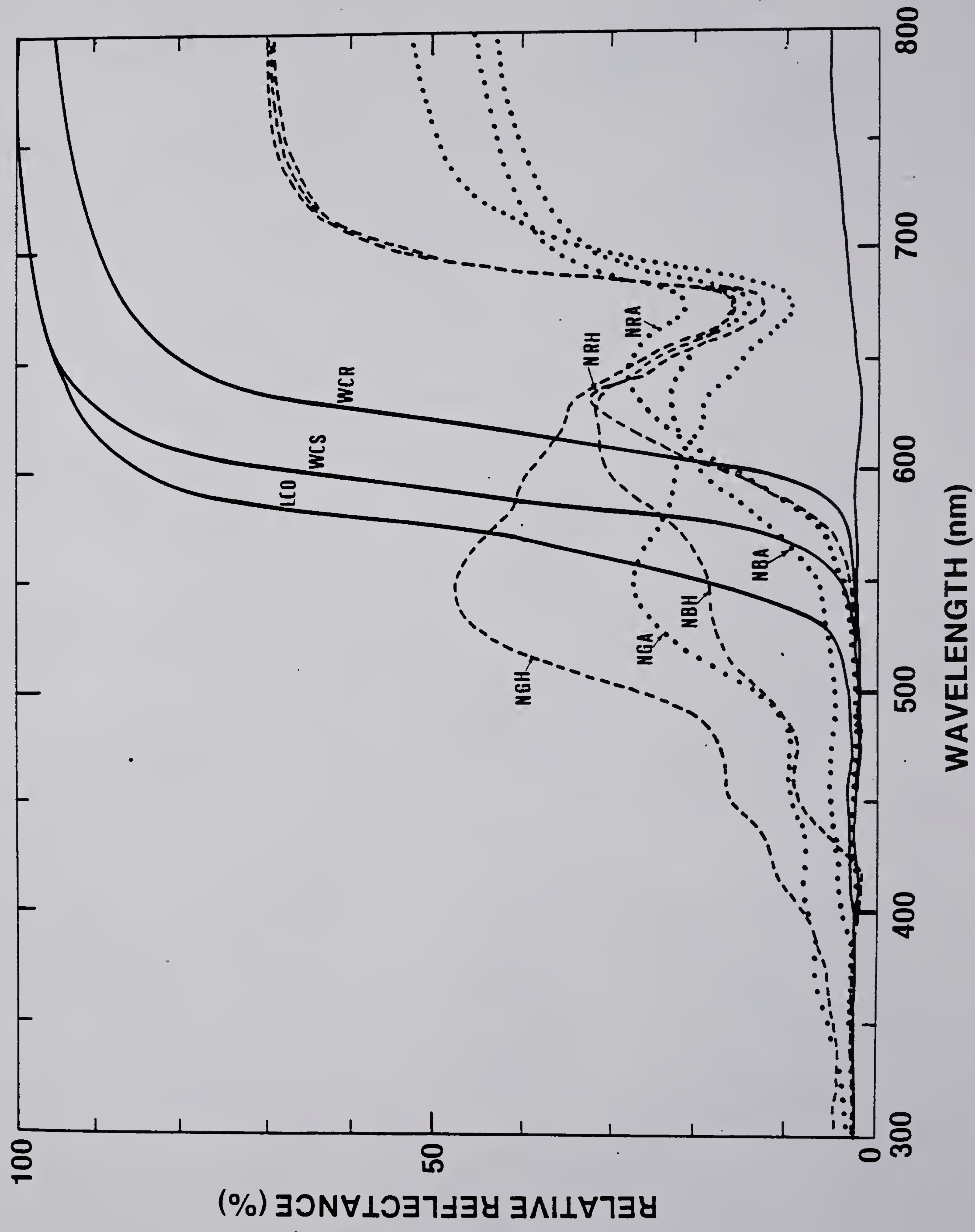

RELATIVE REFLECTANCE (%)
100
50
0
WAVELENGTH (nm)
300
400
500
600
700
800
NGF
WC1
AC2
WAC
WCB
WMB

Figure 12

Figure 13. Natural growing fruits and pigmented sphere mimics. Fruits: apple-unripe green (NGA), unripe blushed (NBA), ripe red (NRA); Hawthorn - unripe green (NGH), unripe blushed (NBH), red (NRH). Pigments: London cadmium orange (LCO); Winsor-Newton cadmium scarlet (WCS) and cadmium red (WCR). Sherwin Williams black enamel (BE).


RELATIVE REFLECTANCE (%)
100
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300
400
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NGA
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NBA

Figure 13

Figure 14. Pigmented sphere mimics. Winsor-Newton - cobalt blue (WCB3), 75% LTW (WCB2), 90% LTWC (WCB1); GREINT series (Chapter III) - GREINT 3, 2, and 1: London - cadmium orange (LCO), 10% WMB (LCO2); gray series (LTW+WMB or pigment B+ZnO), 40% black + 60% white (40%G), 10% black + white (10%G), 2.5% black + white (2.5%G). Lead white combinations are 3% lower in intensity across the spectrum and continue reflecting to 350nm prior to declining.

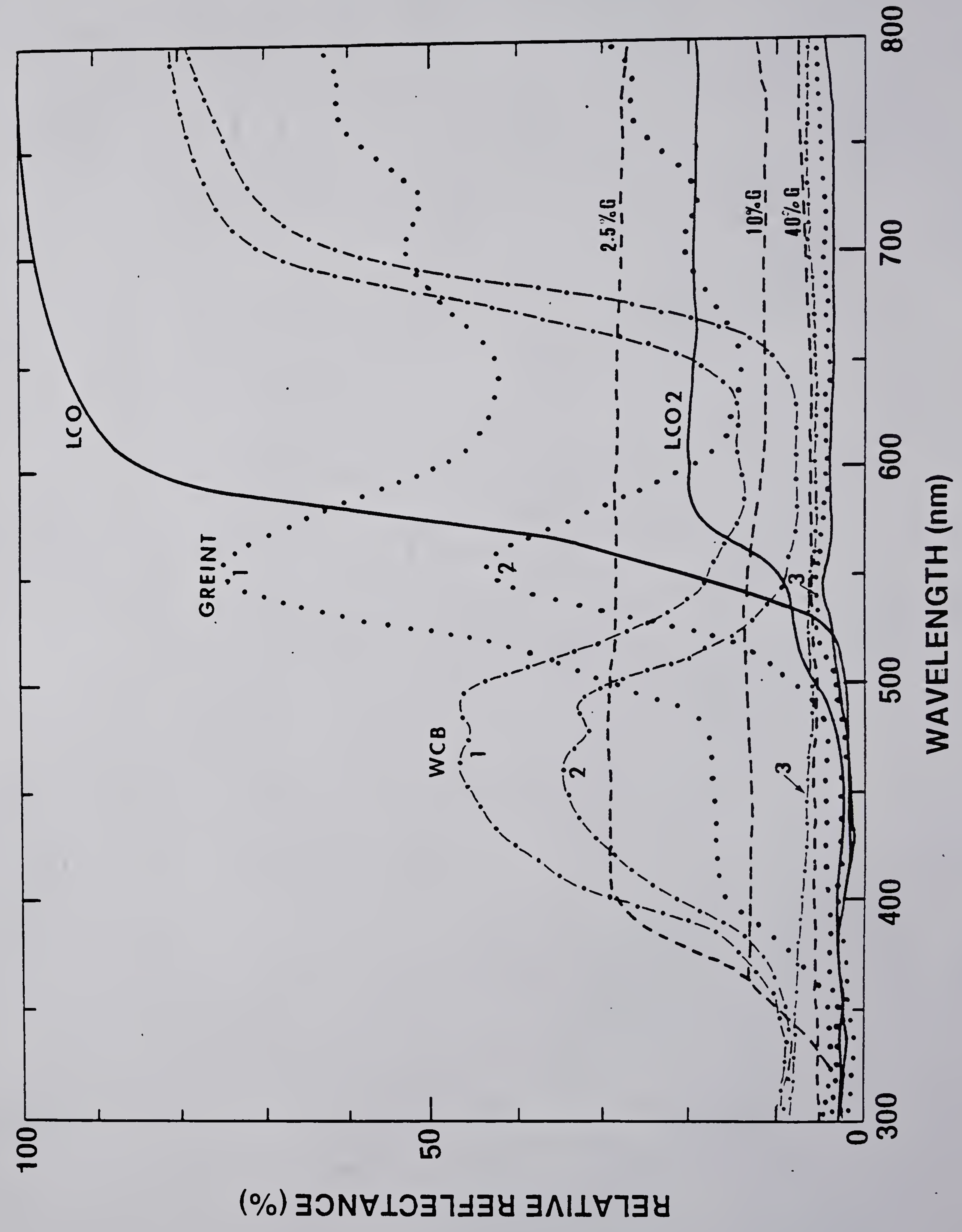

RELATIVE REFLECTANCE (%)
100
50
0
WAVELENGTH (nm)
300
400
500
600
700
800
LCO
LCO2
GREINT
1
2
3
WCB
1
2
3
2.5%G
10%G
40%G

Figure 14

with mixtures of artist water color pigments (Winsor-Newton, Inc., London) and Liquitex acrylic gel (Perm. Pigments Co., Cincinnati, Ohio) (Fig. 12,15). Pigments used were: cadmium lemon (WCL), cobalt blue (WCB), alizeran crimson (WAC), and ivory black (WIB). Liquitex alizeran crimson acrylic artist pigment thinned with clear acrylic gel was used to mimic blush (AC2). Fruits were thinly coated with Tangletrap® (The Tanglefoot Co., Grand Rapids, MI) to capture alighting flies. Counts were taken daily for 3 consecutive days in July, 1980, when all but artificially pigmented fruits were green (Fig. 12,15). Captured flies were removed and sexed.

Pigmented fruit mimics. Experiments to determine AMF response to host fruit hue, as well as to fruit intensity, were conducted in the field. Plastic spheres (3.5cm diam.) were coated with either: (a) artist oil pigments, all manufactured by Winsor-Newton, Inc., London; (b) black enamel (BE) (Sherwin Williams, Co., Cleveland, Ohio); or (c) powdered black pigments A and B (supplied by V. Moericke) alone, or combined with either ZnO (Zn) or $(PbCo_3)_2$ $PbCOH_2$ (Pb) powders (Mallinckrodt, Inc., Bedford, MA) in clear acrylic gel to make gray).

Artist oil pigments used were: (a) London series: cadmium orange (LCO); titanium white (LTW); (b) Winsor-

Figure 15. Apple fruits artificially pigmented with alizeran crimson, and natural green fruit within apple tree experimental sites. Photographed on Kodachrome 64 film without filters.

Newton series: cadmium scarlet (WCS), cadmium red (WCR), mars black (WMB), winsor green (WWG), cobalt blue (WCB); (c) GREINT: 1, 2, 3 (Chapter III); and (d) the following mixtures by weight: LCO_2 (90% LCO, 10% WMB); WCB 1 (10% WCB, 90% LTW); WCB 2 (25% WCB, 75% LTW); 10% gray (90% LTW, 10% WMB). The powdered pigment grays were black powders A or B combined with white powders Zn or Pb in the following percentages of black: 2.5%, 10%, 40%. Relative reflectance spectra of all fruit mimic colors are shown in Fig.13,14. Pigment grays involving Pb are not shown but are equal to those of Zn based grays shown in Fig.14, except that reflectance extended to 350nm before declining and was 3% less than shown for the Zn-type group.

Spheres were thinly coated with Tangletrap and hung by wire at ca. 1.75m height in abandoned apple trees. An area free of branches and foliage was created ca. 15-20cm around each sphere, with abundant vegetation beyond. There was a minimum distance of ca. 1m between spheres within a tree. Spheres were rotated within replicates to minimize variability due to position effects. Flies were removed, counted, and sexed at 1-2 day intervals.

Analysis. Count data, untransformed, were submitted to analysis of variance and Duncan's multiple range or students t-test at the 5% level.

Results

Properties of host fruit.

Color. Spectrophotometer studies conducted from late May into September, 1980 documented the change in hue that accompanies the ripening of AMF host fruits (Fig. 13). The timing and amount of hue change with ripening varied within and between trees. In general, relative reflectance of yellow-green hue (550nm maximum) decreased and that of orange-red hue (625-650nm maximum) increased with ripening for both hawthorn and red apple variety fruits. Unripe fruits resembled foliage in reflected hue (Chapter III), but were 3-5 times higher in reflective intensity (Fig. 13). Ripe fruits reflected maximally above 600nm, with little reflectance at 550nm. All vegetative host spectra showed a reflectance dip at ca. 680nm, representing an absorption band for chlorophyll (Fig. 13). This dip could not be mimicked by pigmented natural fruit (Fig. 12). The reflectance of fruits rose rapidly beyond 680nm and peak in the near infrared (IR) (>800nm). As in other natural surfaces measured, ultraviolet (UV) reflection was minimal. Photographs showed a UV reflectance associated only with the bloom present on some apple varieties, but the effect was too little to measure quantitatively (<5%). Waxy bloom (glaucousness) is associated with high UV reflectivity in certain desert plants (Mulroy 1979). Specular reflectance, less from fruits than foliage, contained a UV component. The angle of viewing affected this component as well as affected the overall intensity contrast between fruits and foliage. Photographing fruits from a point of fly orientation within a tree showed that fruits viewed against a foliage-sky background appeared dark (Fig. 15). However, viewed from outside of the tree canopy, both ripe and green fruits appear lighter than a background of leaf reflectance (Figs. 16,18,19).

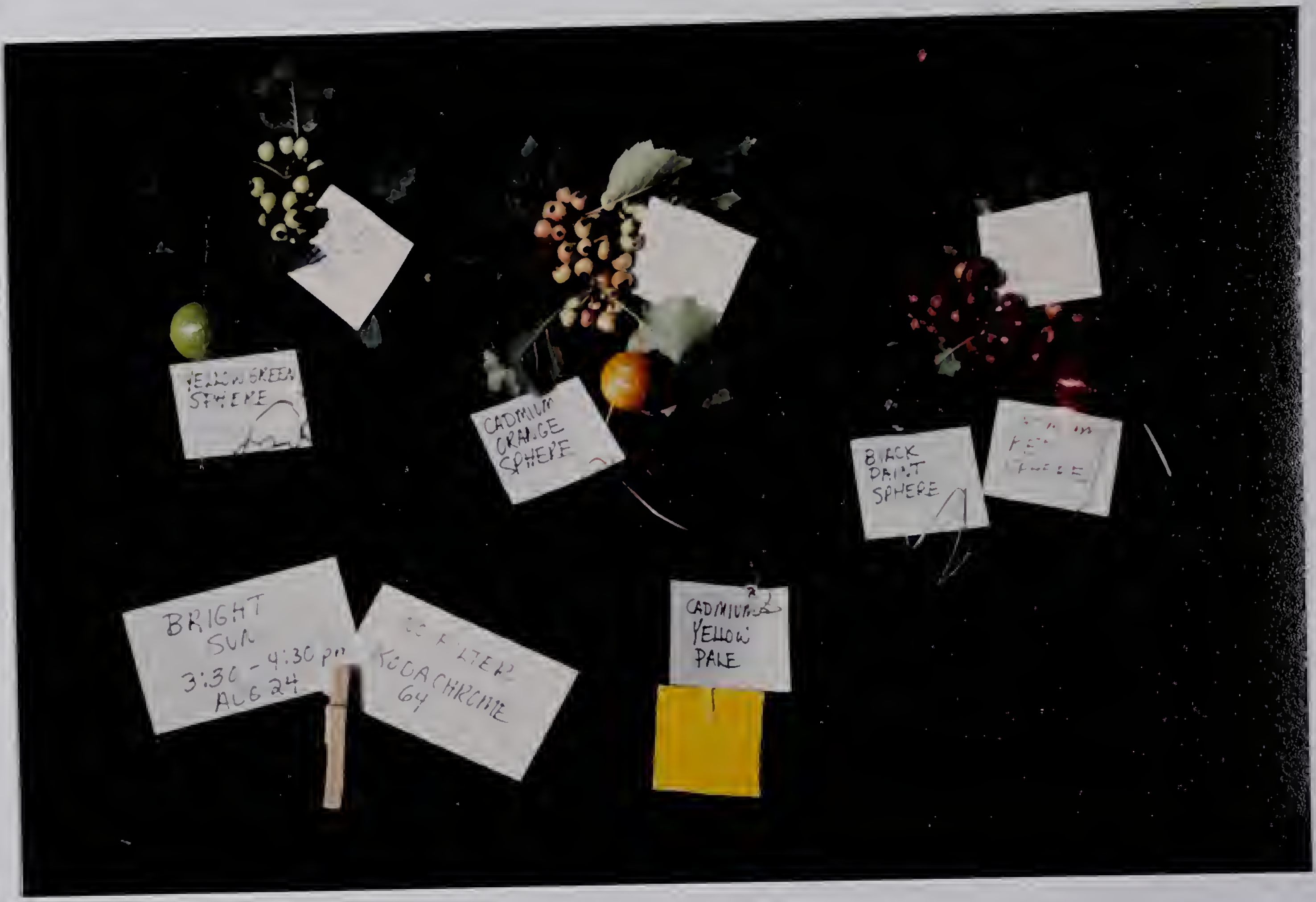
Fly behavior within trees. The sexes varied in type of activity and time spent on host structures within trees (Chapter III). AMF were observed to orient towards and hop or fly to a fruit from leaves or another fruit at distances of 30cm or less. Males were frequently observed on fruits, often on the reddest fruit in a cluster (Fig. 17), guarding territories (Prokopy and Bush 1973). During the same periods as when males were observed in abundance on fruits (late morning to early afternoon), females were frequently sighted on foliage (Prokopy et al.

Figure 16. An apple fruit photographed from a point of observed AMF approach, 12cm from fruit. Photographed on Kodachrome 64 film without filters.

Figure 17. Male AMF (arrow) guarding the reddest fruit within a hawthorn berry cluster. Photographed on Kodachrome 64 film without filters.

Figure 18. Apple fruit mimics displayed against apple leaf upper surfaces. From left to right: cadmium orange (LC), black enamel (BE), 550 green tints (GREINT 1,2,3), cadmium red (WCR), green unripe apple fruit, red ripe apple fruit, cobalt blue tint (WCBl), cadmium yellow pale (WCYP) rectangle. Photographed on Kodachrome 64 film without filters.

Figure 19. Hawthorn fruits photographed with appropriate mimics against black velvet background. Unfiltered Kodachrome 64 film was used with afternoon daylight illumination. Left to right: green unripe fruits, GREINT 1 fruit mimic; blushed fruits, cadmium orange fruit mimic; red ripe fruits, black enamel and cadmium red fruit mimics.


YELLOW GREEN SPHERE
CADMIUM ORANGE SPHERE
BLACK PAINT SPHERE
BRIGHT SUN 3:30 - 4:30 pm AUG 24
NO FILTER KODACHROME 64
CADMIUM YELLOW PALE

1972), where they occasionally fed. Females were observed attempting oviposition into both red and green fruits. Observations of alightments on fruit mimics indicated that flies made both direct flights to the mimics from nearby leaves and apparently less direct spiralling flights to the mimics from greater distances.

Fly response to artificially pigmented host fruits. Experiments with artificially pigmented natural fruits were performed in unsprayed apple trees bearing heavy crops of green, unripe fruits (Figs. 12,15). AMF captures were greater on dark pigmented fruits than on fruits of lighter pigments (Table 5). Artificially blushed fruits (AC2) were less attractive than artificially pigmented red fruit (Table 5, Exp. 1), WAC and WIB fruits were equally attractive and significantly more attractive than WCL, or WCB (Table 5, Exp. 2). WCB and WCL were proportionately more attractive than WIB or WAC, but not to males.

Fly response to artificial fruit mimics.

Red pigments. Captures on pigmented 3.5cm diam spheres were highest for both AMF sexes on those pigments (Figs. 13,14) which were least reflective, regardless of hue (Tables 6-8). Red pigments (WCS, WCR), reflecting energy maximally above 600nm (Figs. 13,18,19), were equally

Table 5. Number of adult AMF captured in Tangletrap which covered artificially-pigmented natural fruits (ca. 4cm diam.) (Fig.12,15) within host apple trees. July 23-Aug. 25, 1980. Numbers within each experiment followed by the same letter are not significantly different.

		Capture		Capture Index**		
Experiment	Pigment*	M	F	M	F	Total
1	WAC	64a	60a	100	100	100
	AC2	22 b	29 b	34	48	41
2	WMB	41a	90a	100	100	100
	WAC	42a	73a	102	81	88
	WCB	13 b	32 b	32	36	34
	WCL	6 b	29 b	15	32	27

*WAC=alizeran crimson red, AC2=alizeran crimson plus clear gel, WMB=black, WCB=cobalt blue, WCL=cadmium lemon yellow.

**Computed as: $\frac{\text{No. AMF captured}}{\text{No. AMF captured on the most attractive pigment}}$

Table 6. Number of adult AMF captured in Tangletrap which covered artificial fruit mimics (ca. 3.5cm diam), painted with pigments of various red hues (Fig. 13,14), and hung within host apple trees. July 23-Aug. 25, 1980). Numbers within each experiment followed by the same letter are not significantly different.

Experiment	Pigment*	Capture		Capture Index**		
		M	F	M	F	Total
1	BE	97a	89a	100	100	100
	WCR	77a	93a	79	104	91
	WCS	65a	81a	67	91	78
2	BE	88a	122a	100	100	100
	LCO	31 b	61 b	35	50	44
3	BE	126a	75a	100	100	100
	LC2	68 b	48 b	54	64	58
	LCO	61 b	47 b	48	63	54

*BE=black enamel, WCR=cadmium red, WCS=cadmium scarlet, LCO=cadmium orange, LCO2=cadmium orange plus 10% black.

**Computed as: $$\frac{\text{No. AMF captured}}{\text{No. AMF captured on BE}}$$

Table 7. Number of adult AMF captured in Tangletrap which covered artificial fruit mimics (ca. 3.5cm diam), painted with pigments of various hues and intensities (shades or tints) (Fig. 14), and hung within host trees. July 16 to Aug. 17, 1980. Numbers within each experiment followed by the same letter are not significantly different.

Experiment	Host tree	Pigment*	Capture		Capture Index**		
			M	F	M	F	Total
1	Apple	WCB3	79a	115a	100	100	100
		WCB2	45 b	68 b	57	59	58
		WCB1	16 c	23 c	20	20	20
2	Apple	GREINT3	185a	117a	100	100	100
		GREINT2	85 b	57 b	46	49	47
		GREINT1	51 b	43 b	28	37	31
3	Hawthorn	GREINT3	352a	162a	100	100	100
		GREINT2	136 b	87 b	39	54	43
		GREINT1	95 b	76 b	27	47	33
4	Apple	LCO	80ab	79a	100	100	100
		10%Gray	96a	60a	120	76	101
		WCB1	60 bc	42 b	75	53	65
		GREINT1	36 c	38 b	45	48	47

*WCB=cobalt blue and tints, GREINT=550 green and tints, LCO=cadmium orange.

**Computed as: $\frac{\text{No. AMF captured}}{\text{No. AMF captured on the most attractive pigment}}$

Table 8. Adult AMF captured in Tangletrap which covered artificial fruit mimics (ca. 3.5cm diam), painted with gray pigments of varied intensity (Fig. 14), and hung within host apple trees. Aug. 8-24, 1978. Numbers followed by the same letter are not significantly different.

		Capture		Capture Index**		
Experiment	Pigment*	M	F	M	F	Total
1***	A	218a	49a	100	100	100
	2.5A+Pb	164ab	29a	75	59	72
	2.5A+Zn	86 b	25a	39	51	42
	A	273a	52a	100	100	100
	10A+Pb	229a	41a	84	79	83
	10A+Zn	224a	27a	82	52	77
	A	161a	43a	100	100	100
	40A+Pb	185a	53a	115	123	117
	40A+Zn	176a	31a	109	72	101
2***	B	218a	43a	100	100	100
	2.5B+Pb	93a	29a	43	67	47
	2.5Zn	104a	26a	48	60	58
	B	239a	33a	100	100	100
	10B+Pb	181a	20a	76	61	74
	10B+Zn	179a	28a	75	85	76
	B	150a	42a	100	100	100
	40B+Pb	152a	42a	101	100	101
	40B+Zn	132a	35a	88	83	87
3	A	227a	43a	100	100	100
	40A+Pb	207a	31a	91	72	88
	10A+Pb	146a	35a	64	81	67
	2.5A+Pb	92a	31a	41	72	31

*A=IR reflecting black, B=non-IR reflecting black, Pb= lead white, Zn= zinc white.

**Computed as:

$$\frac{\text{No. of AMF captured}}{\text{No. of AMF captured on A or B pigment}}$$

***Difference in total captures on solid A and B pigment spheres not significant at .05 level (t-test) for either sex.

as attractive as black (BE) (Table 6, Exp. 1). Captures on LCO, which reflected more energy than WCS and WCR below 600nm (Fig. 13,18,19) were significantly lower than on BE (Table 6, Exp. 2,3). Shaded LCO (LCO2) (Fig. 14) was also significantly less preferred than BE (Table 6, Exp. 3). Females were relatively less selective among pigments than males.

Green and blue pigments. Attractiveness of WCB and GREINT (Fig. 14,18) significantly decreased with unsaturation, which increased reflected intensity (Table 7, Exp. 1-3). WCB3 and GREINT 3, the least reflective of these series, were significantly more attractive than WCB1 and GREINT 1 (Table 7, Exp. 1-3). Females were relatively less selective among the GREINT series pigments than were males. No sexual difference was seen in the WCB series, where there were significant differences in capture rates of both sexes among all three intensities. Captures on WCB1 and GREINT 1 were not significantly different from those on LCO and 10% gray, although both of the former were significantly less preferred than either of the latter by females and than the 10% gray by males (Table 7, Exp. 4). Relative captures on the GREINT series did not vary between the two hosts (Table 7, Exp. 2,3). Both hosts had very abundant green fruit, but no red fruit.

Gray pigments. Spheres coated with gray pigments showed increased attractiveness with decreased reflectance, but (with one exception) the difference was not significant (Table 8). In Exp. 1 (Table 8), pure A was significantly preferred by males over 2.5A+Zn. Comparative amounts of UV and IR reflectance had no discernable effect on captures. Overall, male captures were higher than female captures, possibly reflecting low numbers of females in the trees. These experiments were conducted in late season, when natural fruits were dropping. Males frequently stay longer on host trees than females, which readily disperse to other host trees under such conditions (Roitberg et al. 1982).

Black pigments A and B differ in reflected energy above 700nm. Pigment A reflects highly above 800nm whereas pigment B absorbs highly in this region (as do black enamel paints). There was no significant difference in AMF attraction tp either A or B black pigments (Table 8). Further studies comparing only pure A and B yielded similar results (Owens and Prokopy, unpublished data). Therefore, it is unlikely that energy in the region above 800nm affected AMF captures on pigmented fruit mimics used in these studies.

Discussion

Prokopy (1968) suggested that AMF detect host fruits visually on the basis of contrast against the background.

He suggested that intensity of reflectance was more important to contrast than hue. The results presented here support the importance of reflectance intensity and not hue to within tree fruit selection by AMF.

Wehner (1981) suggested that objects which are darker than the background, and of certain size and velocity of motion, are most apt to elicit a positive response when imaged within a specific portion of a predatory insect's field. He suggested that visual contrast provided by the background plays an important part in the detection of resource objects. Visual contrast between an object and background may be increased by: (a) color hue contrast between an object and background; (b) decreased object reflectivity relative to background; (c) increased object reflectivity relative to background; (d) matching of visual sensitivity to background spectrum; and (e) decreased visual sensitivity to object spectrum. Animals detecting food objects within natural environments may employ any or all of these mechanisms (Dartnall 1975, McFarland and Munz 1975b, Hailman 1977, Kevan 1978, Lythgoe 1979, Snodderly 1979).

The evolution of color vision in higher vertebrate species which disperse seeds of fruit may have co-evolved with the development of fruit hues (van der Pijl 1972). The need to detect yellow to red fruit within brownish, dry habitats could have been an important selective force in the development of long wavelength discrimination ability within old world monkeys (Snodderly 1979). Long wavelength discrimination within some species of new world monkeys is poorly developed. These monkeys consistantly locate preferred foods against green foliage backgrounds, where intensity contrasts should be sufficient for fruit detection (Snodderly 1979). The red hue of some ripe AMF host fruit is more likely to have evolved to attract seed dispersing birds, rather than to attract insects (van der Pijl 1972). Some insects, notably butterflies, have been shown to possess red sensitivity, which may be used in the color-contrast detection of flowers (Bernard 1979, Kevan 1978). Initially, I wanted to determine if AMF do utilize wavelengths beyond 600nm (red) in color-contrast detection of fruit. Studies of visual sensitivity indicated that AMF compound eyes are essentially blind to this region (Chapter V). The results of the experiments with pigmented natural fruit and fruit mimics indicate that red hues of maximum reflectance greater than 580nm are equal to attractiveness to black, suggesting that red hue *per se* is not utilized by fruit seeking flies. Thus AMF must be utilizing contrast cues other than long wavelength discrimination to detect fruits.

Intensity of reflection between 300-580nm (but not the reflectance dip at 680nm) was found to be important to AMF attraction to fruit mimics regardless of hue. Attractiveness to AMF increased with decrease in relative reflectance (Tables 5-8, Fig. 12-14,18,19). This suggests that decreases in surface intensity increase attractiveness, perhaps by enhancing the dark-object, light-background effect suggested as important in prey detection by predaceous insects (Wehner 1981). Because the effect of low intensity of fruit mimic reflectance was significant when natural host fruits were still green, the greater attractiveness of low-intensity reflecting mimics could not have been on account of such mimics appearing as though they were normal fruit. Indeed, the darkest, most attractive green shade (GREINT 3) was similar to the upper surface reflectance spectrum intensity of host leaves, not fruit (Fig. 18). On large rectangles (15 x 20cm) the attractiveness of various shades of green is the reverse of that of fruit (Chapter III), further suggesting that a shape-size interaction may be particularly important in AMF response to intensity effects. Prokopy (1968) found that preference for darker colored spheres was not affected by the color of natural fruit on the host tree. Results were the same whether the fruits were green or red.

Females were relatively more attracted than males to fruit mimics coated with light-foliage-type hues (WCL, GREINT 1,2), suggesting that some female captures may have resulted from foliage seeking behavior. Green fruit of reflected foliage-type hue, higher in intensity than surrounding vegetation, may offer a strong feeding-site-type stimulus. However, lighter pigmented fruits and mimics did not capture disproportionate numbers of immature females. The capture discrepancy between the sexes could be due, of course, to male properties only. Perhaps males have a visual system more sensitive to minor variations in reflected intensity. Our spectral sensitivity function studies, though not extensive, did not indicate sexual differences, however (Chapter V).

To an insect in nature, the intensity of fruit reflection is relative to the background against which fruits are viewed. Snodderly (1979) suggested that sometimes monkeys view nontransparent fruit in silhouette, thereby increasing contrast against a background of light filtered through or reflected from leaves. Observations of AMF orientation to green fruits indicate that AMF too may be viewing fruit in silhouette (Fig. 17). Photography under field conditions showed that green fruits contrast against a background of reflected light from foliage as fruits are more intensely reflective than leaf faces (Figs. 14-19). However, green fruit do not contrast as well against leaf backs, which are more reflective than leaf faces, unless bright light is transmitted through foliage or foliage is sufficiently sparse to provide bright background light from the sky to provide a silhouette effect (Fig.17). Studies utilizing artificially pigmented fruits and green fruit mimics suggest that dark fruit provide the most visible and attractive contrast in all situations (Tables 5,7). AMF visual mechanisms may provide enhancement of the contrast of fruits against backgrounds of either foliage or sky, as peak AMF visual sensitivity lies below 500nm (peak sky energy) for one receptor type and between 500-600nm (peak foliage energy) for a second receptor type (Chapter V). The second receptor may be the more important to fruit location, as it is both highly sensitive to foliage hue and little sensitive to the hue of red fruits. This would maximize the intensity contrast between red fruit and either reflected or transmitted energy from foliage, rendering red pigmented fruit the most easily detected in all situations. Ripe hawthorn (= the native hosts) are also the most suitable for oviposition as unripe hawthorn fruits are too firm to permit penetration by the AMF's ovipositor.

In conclusion, the results of experiments conducted on AMF fruit location suggest that AMF use intensity contrasts to detect host fruits. AMF visual mechanisms appear to have evolved to enhance these contrasts by having peak sensitivity in the spectral region of maximum energy of the background, while minimizing sensitivity to energy reflected from fruits. In addition, AMF appear to utilize behavioral means to maximize contrasts by orienting toward fruit silhouetted against a more intense background. Unlike birds, which detect ripe fruits on the basis of color-contrasts between red hued fruits and green leaves, AMF, lacking red sensitivity, appear not to utilize hue contrasts in fruit detection. The red hue of fruit probably increases attractiveness to AMF because it darkens the fruit as viewed by the fly (Figs. 19-21). Shape, the most important aspect of fruit detection and selection, is enhanced by dark pigmentation (Owens, unpublished data).

Whether or not AMF use reflectance intensity as a visual measure of fruit suitability for oviposition cannot be determined by this data. AMF females were observed attempting to oviposit into fruits of varied stages of ripeness and surface colors, particularly in apples, suggesting that additional criteria may be used by females

Figure 20. Set up as in Figure 8 photographed through a narrow band pass filter (BB450 - Corion Corp.) which filters out all light except blue (400-500nm).

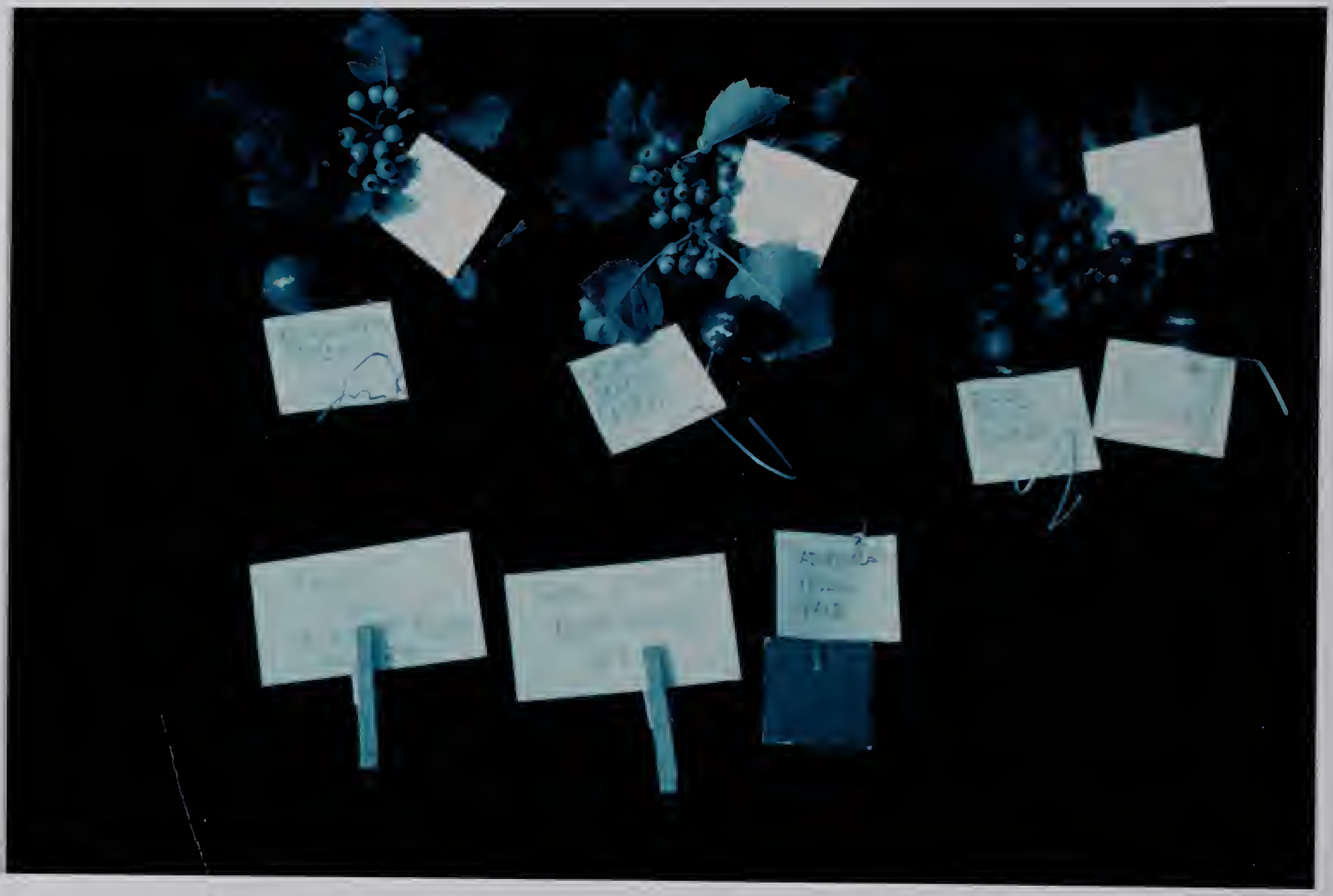
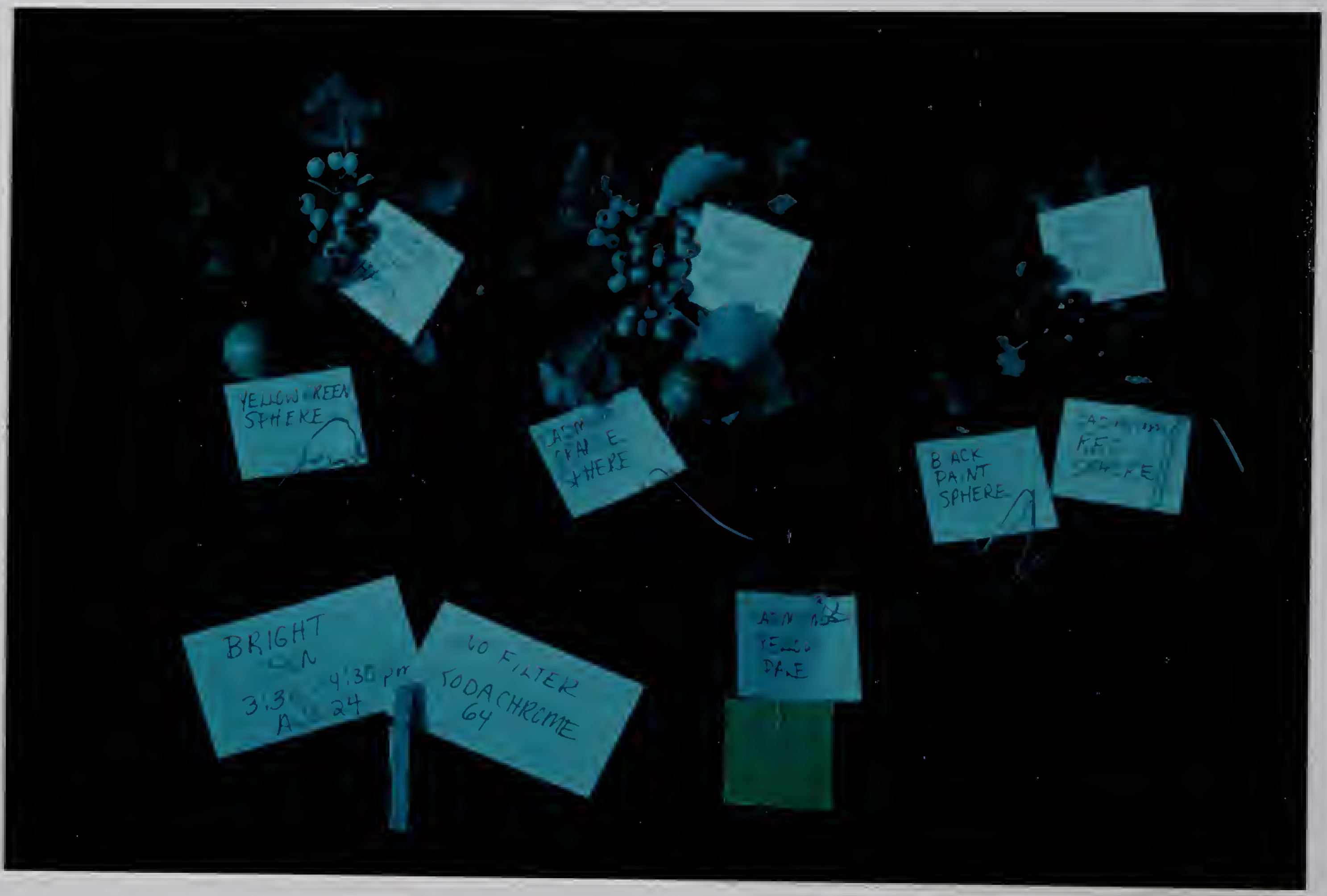


Figure 21. Set up as in Figure 8 photographed through a Kodak wratten filter (44A), the closest available approximation to the range of apple maggot visual sensitivity (360-580nm).


YELLOW GREEN SPHERE
SPHERE
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3:30 4:30 pm
24
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KODACHROME 64

in the final oviposition site selection process. Pheromone regulation of interspecific competition, fruit odor, fruit contact stimuli, and AMF physiological state factors (Prokopy 1977b) may be more important to oviposition site selection than vision. Vision's contribution may end with detection of fruit against the surrounding background.

CHAPTER V

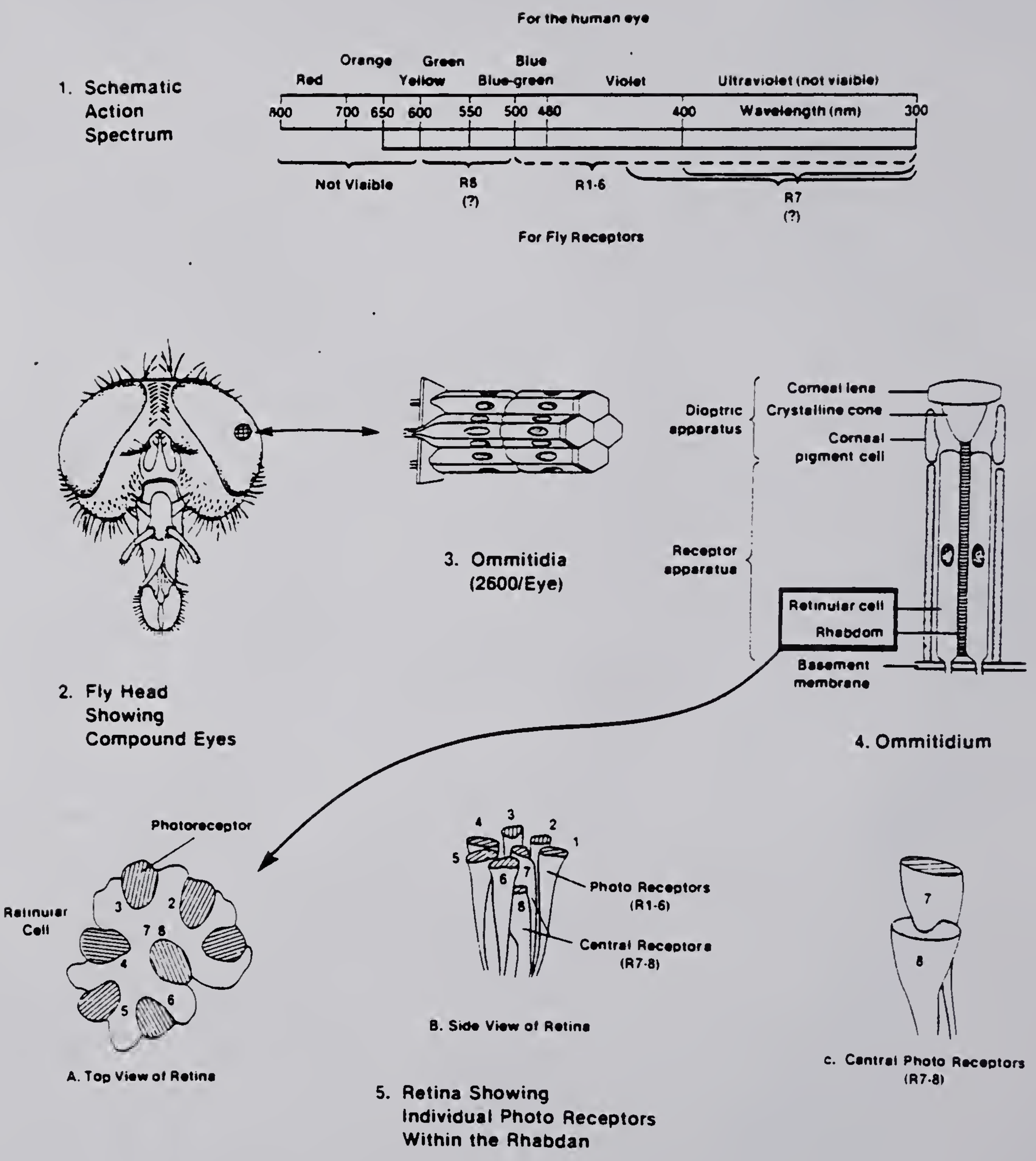
SPECTRAL SENSITIVITY OF THE APPLE MAGGOT FLY, *RHAGOLETIS POMONELLA* WALSH (DIPTERA:TEPHRITIDAE), MEASURED USING A NON-INVASIVE OPTICAL METHOD

Introduction

The apple maggot fly (AMF) is a destructive fruit pest in commercial orchards of New England. An extensive review of the known biology and control of members of the genus *Rhagoletis* was compiled by Boller and Prokopy (1976).

AMF are dirunal and are noted for their visual orientation to host structures of fruit and foliage (Boller and Prokopy 1976). Therefore, they are suspected of possessing spectral discrimination (Boller and Prokopy 1976), but little is known of the underlying mechanisms. Anatomical studies have shown that AMF compound eyes are similar to those of other dipterans (Agee et al. 1977) (Fig. 22). Each AMF compound eye is composed of approximately 260 ommatidia. Each ommatidium's retina contains 8 rhabdomeres (photoreceptors) with R1-6 arranged around R7-8. R7-8 combine into a single structure with R7

Figure 22. Schematic drawing of the action spectrum and anatomy of the compound eye in the generalized higher dipteran adult.



1. Schematic Action Spectrum

2. Fly Head Showing Compound Eyes

3. Ommitidia (2600/Eye)

4. Ommitidium

5. Retina Showing Individual Photo Receptors Within the Rhabdan

Figure 22

above R8 (Agee et al. 1977, Strausfeld and Nässel 1981). Here, the spectral sensitivity of AMF ommatidia was characterized.

Spectral sensitivity functions provide information useful for the understanding of visually oriented behavior. It is reasonable to assume that the evolution of spectral sensitivity in animals is tied to the need to locate resources and escape enemies within their environments. Therefore, a potential correlation between the range of spectral sensitivity and the spectral reflectance properties of resources exists (Dartnall 1975, Menzel 1979). Vision may function in food and mate location, sexual displays, predator avoidance, shelter location, and directional orientation. Detection of motion and polarized light, when combined with spectral discrimination, may play an important role in mediating such behavior (Menzel 1979, Waterman 1981).

Methods

Dr. Gary D. Bernard of Yale University applied his procedure for measuring the spectral sensitivity of intact, living flies to AMF using an optical method (Bernard and Stavenga, 1979). I assisted him in this work. Adult apple maggots emerging from pupae from apples collected from unsprayed Amherst, MA apple orchards were held at 22^oC, R.H. in the laboratory for 3 days prior to being used as test subjects. They were fed on a diet of yeast and sucrose with free access to water.

Adult females with an active, healthy appearance and light colored eyes were selected for spectral sensitivity measurements. They were fixed onto a platform and fed honey water to repletion prior to measurement (Bernard and Stavenga 1979). The spectral sensitivity of the peripheral retinular cells (R1-6 was determined using non-invasive, optical measurements of the increase in reflectance that accompanies the pupillary response. The technique is to chronically illuminate a localized region of the eye with a long wavelength beam, adjusted to bring pupillary scattering above threshold, and then, after stabilization, to stimulate with monochromatic flashes. A criterion increase in scattering is achieved at each wavelength by adjusting flash intensity. Measurements equal to a minimum criterion response were made from about then ommatidia in an equatorial part of an eye. Responses were recorded over a spectral range of 350-600nm. A total of 5 flies was so measured.

Results

Spectral sensitivity measurements (Fig. 23) revealed

Figure 23. Spectral sensitivity function as measured from the compound eye of an intact, living apple maggot fly.

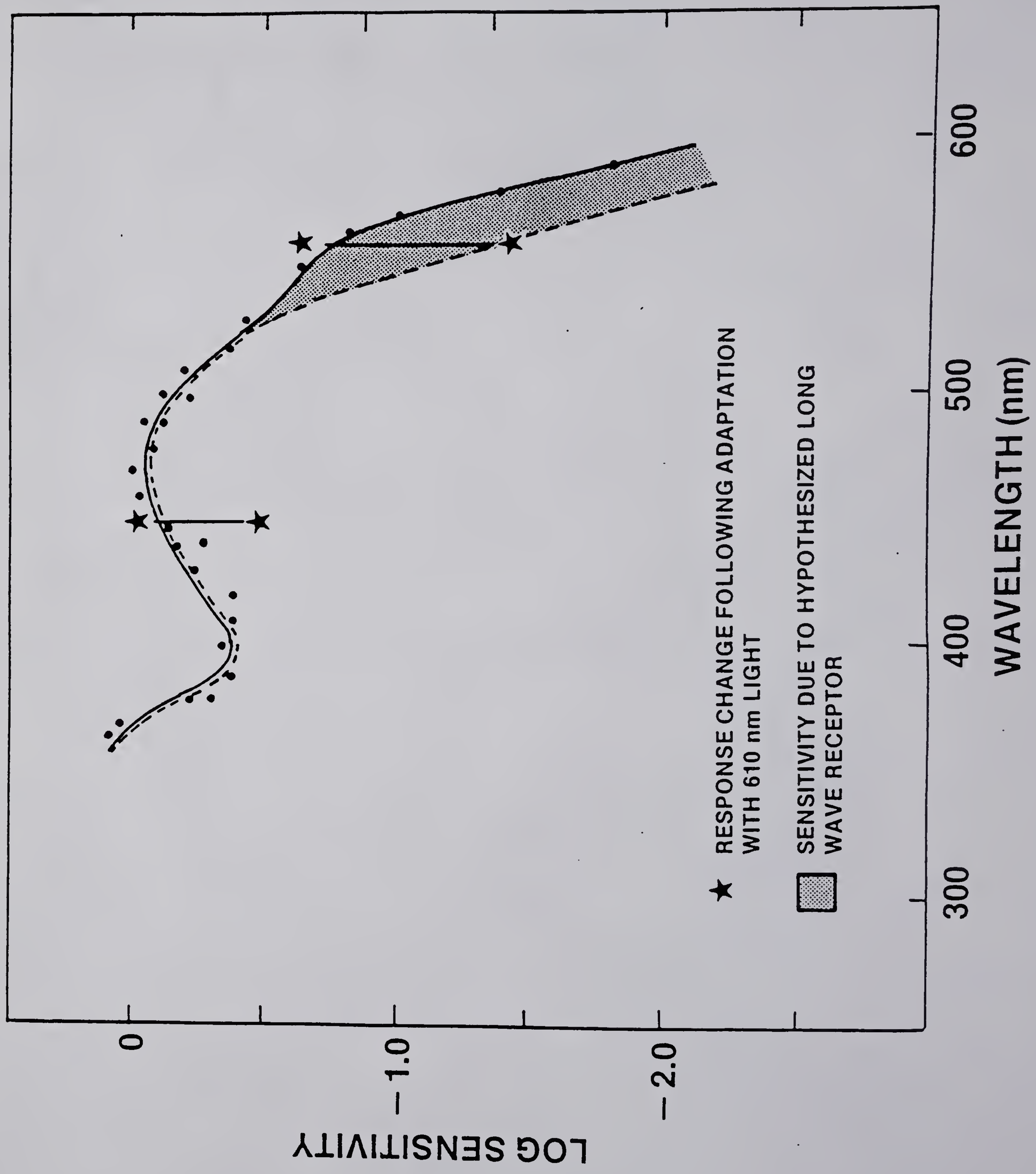

LOG SENSITIVITY
0
−1.0
−2.0
WAVELENGTH (nm)
300
400
500
600
★ RESPONSE CHANGE FOLLOWING ADAPTATION WITH 610 nm LIGHT
▨ SENSITIVITY DUE TO HYPOTHESIZED LONG WAVE RECEPTOR

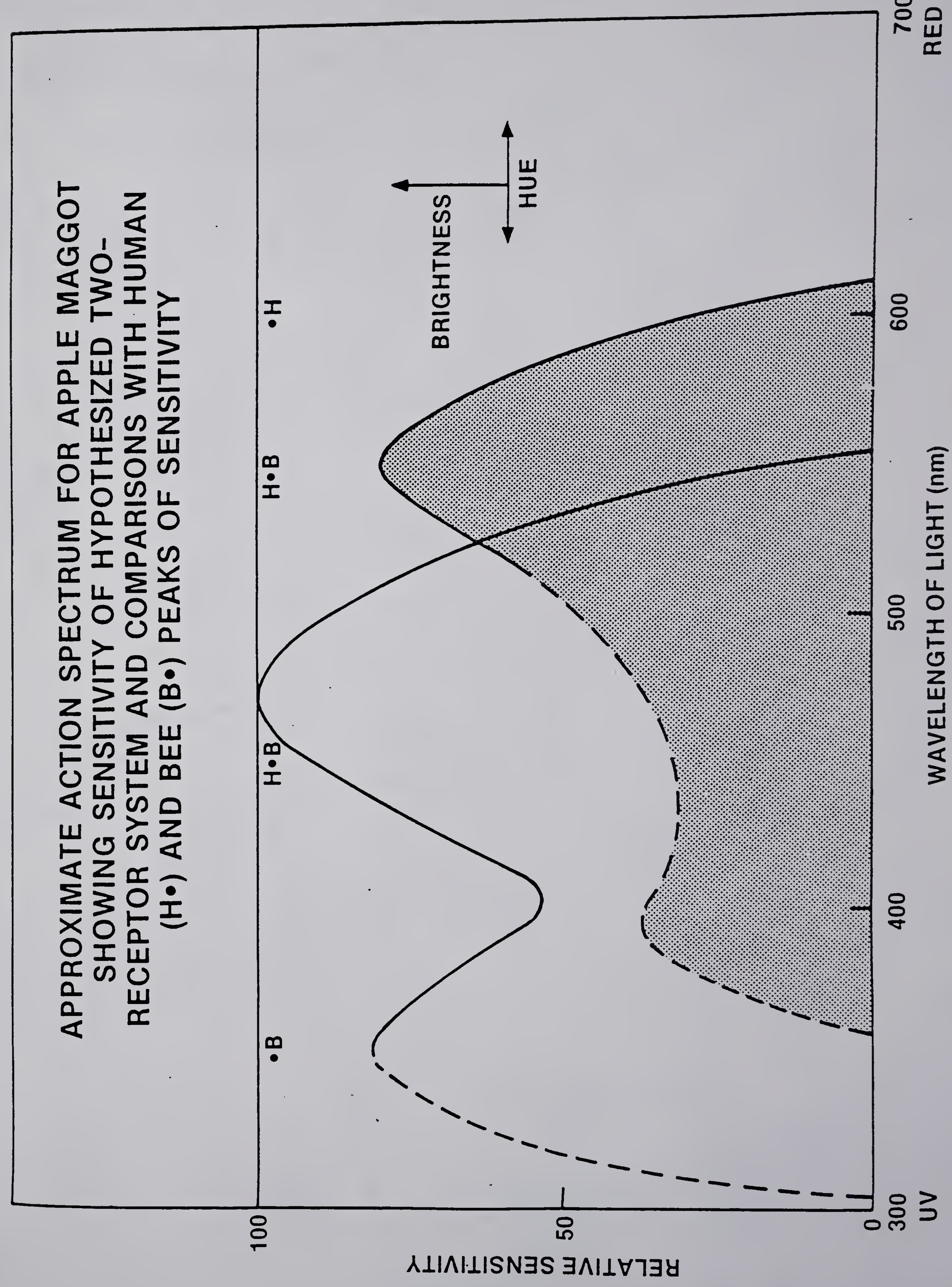
Figure 23

two broad bands of sensitivity peaking at approximately 350 and 475nm, separated by reduced sensitivity at 400nm. A third smaller band peaking between 530-560nm was indicated by adapting the entire eye with orange light (>610nm) and then measuring the change in spectral sensitivity to both 450 and 560nm monochromatic flashes. The larger drop in sensitivity to the 560nm flash indicates the possible existence of two spectral types of receptors, one more sensitive to the longer wavelength portion of the spectrum than the other. The measured variation in sensitivity indicates differential adaptation of the two receptor types.

Although the measured changes in reflectance originate primarily from R1-6 (Bernard and Stavenga, 1979), the central cells R7-8 may also contribute. The weaker response of the putative long wavelength receptor may originate from a distinct sub-population of R1-6, or may originate from one type of central receptor.

Our results indicate that AMF are sensitive to light of wavelengths ranging from the near ultraviolet (300nm) to orange-red (600nm). Within this range, we hypothesize that at least two spectral types of receptor exist: a dual peaked UV-green receptor (max. 350 and 475nm) and a yellow-green receptor (masx. 550-560nm) (Fig. 24).

Figure 24. Hypothesized sensitivity (action) spectrum of the apple maggot fly receptor visual system.



APPROXIMATE ACTION SPECTRUM FOR APPLE MAGGOT SHOWING SENSITIVITY OF HYPOTHESIZED TWO-RECEPTOR SYSTEM AND COMPARISONS WITH HUMAN (H•) AND BEE (B•) PEAKS OF SENSITIVITY

Figure 24

Discussion

The existence of photoreceptor types having different spectral properties is a necessary condition for color vision (Dartnall 1975, Menzel 1979). However, behavioral studies showing the ability of the animal to distinguish light of different wavelengths, independent of intensity, are necessary to actually prove spectral discrimination. From our results, we conclude that the potential for color discrimination in AMF does exist.

Apple maggot sensitivity is similar to that of other dipterans. All dipterans studied thus far show that R1-6 have a major sensitivity peak between 450-500nm and a secondary peak at 350nm (Bernard and Stavenga 1979, Menzel 1979, Smola and Meffert 1979). In recent studies where R7-8 cells have been selectively isolated, three other receptor types have been noted (Hardie et al. 1979, Smola and Meffert 1979). R-7 has been shown to exhibit high UV (max. 350) or UV-blue (max. 350 and 440) sensitivity, while R-8 has either blue (max. 440) or green (max 540) sensitivity. Our results show that the majority receptor (probably R1-6) has the same spectral sensitivity function as those of Drosophila. The minority receptor has its maximum at a wavelength that is 10-20nm greater than

R8 green. This study produced no data to indicate the presence or absence of additional UV, UV-blue, or blue receptor types.

The innervation of the dipteran eye suggests that R1-6 and R7-8 may be considered as two separate subsystems (Strausfield and Nässel 1981, Waterman 1981). The implications of this for fly vision have been hypothesized but not proven. It is thought that R1-6 may have more absolute sensitivity due to "neural superposition" (Strausfield and Nassel 1981). This would enhance motion detection ability. R1-6 may also function in color vision and contrast discrimination. R7-8 are thought to function at higher intensities, and have been implicated in polarization sensitivity (Hardie et al. 1979, Waterman 1981) phototactic behavior, and color vision (Hardie et al. 1979, Smola and Meffert 1979). Dartnall (1975) states that research on animal vision needs to concentrate on understanding both the visual sensitivity of the animal and the reflective patterns of life sustaining resources and their surroundings. For example, color vision may have a selective advantage for animals locating plant hosts following aerial dispersal flights. Menzel (1979) suggests that the ability to distinguish colors arose as a need to differentiate between sky (short wavelengths) and ground (long wavelengths). The putative two receptor system in AMF would enable such discrimination. AMF locate food in the form of honeydew and detritus on foliage. They find foliage initially during dispersal flights shortly following emergence from soil pupation sites (Boller and Prokopy, 1976).

In studying of within-host-tree behavior of AMF, knowledge of spectral sensitivity may provide some inslight into host structure attractiveness. Snodderly (1979) stated, from results of his studies of the relationship between visual sensitivity of monkeys and the reflectance spectrum of their preferred fruit, that animals which select ripe fruit from within vegetated canopies have less need of a red receptor for discrimination than do those which select fruit from the ground or more brown environments. He postulated that intensity contrast differences were sufficient to differentiate ripe fruit from foliage in green tree canopies.

AMF mate and oviposit on a variety of hosts: - apples, cherries, hawthorns, and rosehips. Typically of these fruits turn from green to red in color as they ripen. This is particularly true for the original host of AMF: hawthorn. Field studies of AMF attraction to host fruit mimics suggest that dark pigment shades are preferred and that AMF do not discriminate among red hues (~600nm) and black (Chapter IV). The lack of photoreceptor sensitivity above 600nm (orange-red), demonstrated by this study, may explain why AMF show no significant preference between red and black fruit mimics. It may be that the flies discriminate fruit on the basis of shape and contrast alone. On the other hand, monkey and bird species with confirmed red sensitivity behaviorally show preference for fruits of red hue (Lythgoe 1979, Snodderly 1979).

Our research approach, characterizing visual mechanisms, orientation behavior, and spectral patterns of host plants for insects, is an important contribution to the further understanding of the evolution of spectral discrimination ability. It is also probable that this understanding will contribute greatly to the design of more effective methods of insect control.

CHAPTER VI

METHODS FOR IDENTIFICATION AND QUANTIFICATION OF VISUAL PATTERN PARAMETERS OF HOST STRUCTURES ATTRACTIVE TO INSECTS

Introduction

Studies of vertebrate visual ecology have shown that quantitative measurements of environmental reflectance patterns help to explain visual sensitivity functions within the context of actual use (Dartnall 1975, McFarland and Munz 1975a,b; Snodderly 1979, Levine and MacNichol 1982). The study of insect vision can be facilitated if methods developed for the study of vertebrates are adapted to an insect scale. Object detection within an environment depends upon the perception of contrasts. Measurements of (a) the viewer's visual capacity, (b) the reflective patterns of the object to be detected, and (c) the optical background produce information on parameters providing potential visual contrasts to that specific viewer. The development of quantitative procedures to study insect visual ecology is a further step toward understanding how insect visual mechanisms have adapted to a seemingly endless diversity of habits and habitats.

Characterization of pattern parameters of host structures and optical backgrounds in a mode relevant to the insect's perceptual world provides data relevant to describing insect visual mechanisms in the context of their use (Kevan 1978). Such characterizations must include quantitative spectral measurements of the reflected energy spectrum between 300-700nm, the known region of insect visual sensitivity. Ecologists have used a variety of methods, including photography, spectrophotometry, spectral radiometry, and total incident radiometry to quantify the photic environment. The applicability of three methods - photography, spectrophotometry, and spectral radiometry - to studies of apple maggot fly host location are discussed here. Methods of quantifying color components of surface reflectance are emphasized. An appropriate combination of methods is discussed, along with suggestions on techniques and adaptation for further use in insect orientation studies.

A. Photography

Photography has been utilized as a tool to identify and describe UV-reflectance patterns not perceivable by the human eye as well as to characterize broad bands of the visible spectrum (Kevan 1979).

Silbergleid (1976) described black and white 35mm photographic methods used to identify ultraviolet reflectance patterns of butterfly wings and flower petals. Eisner et al. (1972) used video equipment with a filtered quartz lens to demonstrate UV floral patterns. Kevan (1979) quantified his studies of flower spectral reflectance by including a Kodak gray scale standard in each 35mm black and white photograph (Kevan et al. 1973). Kodak wratten filters were used to divide the spectrum into bands relevant to spectral sensitivity of bee receptor types. Snodderly (1979) used color photography to record fruit colors for his study of primate visual ecology. For comparative studies, he used Kodak gray standard as a backdrop and included Kodak standard color scales. IR photographic techniques and applications are discussed in Kodak publication No. M-28, Applied Infrared Photography (Kodak 1977). Patterns of polarized light can also be recorded using photography (Blaker 1976, Walker 1978). Here, black and white as well as color 35mm photography was used in the field to characterize apple maggot fly hosts in the near ultraviolet, visible, and near IR spectral regions. The goal was to identify patterns of broad band reflectance in nature.

Methods. A 35mm Pentax camera with a 100mm macro lens fitted with selected filters was mounted on a tripod for field use. Quartz lenses are preferable for UV photography, (Silbergleid 1976), but UV flower patterns can be detected with a glass lens (Horovitz and Cohen 1972). I chose the glass lens as it is most economical. Here Kodak wratten, Shott glass, and narrowband-pass filters (Corion Corp, Holliston, MA) were combined with Kodak Kodachrome 64, Ektachrome 200, Ektachrome IR, or Ilford HP-5 (push processed to ASA 800 in Kodak D=76 developer) to produce images of desired bands of reflected energy. To select filters, I used a publication on spectral comparisons of all available filter glasses (Dobrowolski et al. 1977), various Kodak publications, and manufacturers catalogues. A Kodak gray scale, and a card painted either half and half with Pb white pigment $(pbCO_3)_2$ and Zn white pigment (ZnO) (Mallinckrodt, Inc., Bedford, MA) or cadmium yellow pale artist oil pigment (Winsor Newton, Inc., London) were included in my photographs as reference standards. Relative reflectance spectra had been measured for each standard prior to use (Owens and Prokopy 1978) (Chapter III). Index cards bearing technical data were included near standards in photographic set ups. Information on cards was clearly visible in both filtered and unfiltered photographs, including UV. Filtered photographs were sandwiched between unfiltered reference photographs.

Exposure settings were bracketed to compensate for film and light meter variability. To optimize availability of solar UV, photography was conducted on calm, sunny, clear days at midday during June, July, and August. UV photography was conducted in the diffused light of open shade unless specular components were to be studied.

Results and discussion. Photography proved to be versatile and simple to execute, but provided little quantitative data except on geometrical shape (Chapters III, IV). The glass lens produced images of UV patterns, but these could not be quantified relative to reflection of other spectral regions. IR photographs showed that near IR reflectance increased with increasing foliage density and was prominent from fruit, but quantification was not possible. Values for surface reflection were less reliable than those obtained from spectrophotometry. Kevan (1978) was able to quantify the reflectance of petal surfaces and construct reference points within an insect color chart for variously colored artic flowers, indicating that his methods were more reliable than those described here. I found the qualitative recording of geometrical patterns and light intensities of natural host structures, as provided by photography, to be helpful in the design, conduct, and interpretation of field experiments.

Photography documented that surfaces of AMF host fruit and leaves have little reflected light compared to background sky, particularly in the UV. Spectrophotometer studies of fruit and foliage showed that <10% intensity differences were difficult to detect in photographs. Greater differences were recognizable, but were not quantitatively. Kevan (1979) suggests that only differences of 20% are biologically significant. However, 20% may be low for plant feeding insects (Moericke 1969). Photographs were useful in identifying surface features such as pubescence, glaucousness, dust, and specular reflectance which contribute to unsaturation of hue.

Photography was extremely useful for characterizing and documenting naturally occurring geometrical patterns created by relative intensity differences in reflected energy. Shape, size, surface texture, and shading differences among AMF host structures were apparent in photographs. Shape and size have both been shown to be of importance to AMF attraction (Prokopy 1968, 1977a). Isolating various spectral regions with filtered photography provided a quantitative visual image of how spectral components contribute to visual contrast in pattern formation (Chapter IV; Owens unpublished). Color contrasts have been demonstrated to be of importance to resource detection in bees (Kevan

1978) and may also contribute to within tree resource detection by AMF (Chapter III, IV). Photographs taken within AMF host trees revealed that the shape of fruit was a more consistent property than hue or intensity of fruit. However, for foliage, the hue component was the most consistent.

In conclusion, I found photography was particularly useful in: (a) identifying naturally occurring geometrical shapes, and (b) qualitative, but not in quantitative, measurements of surface spectral patterns. I agree with Snodderly (1979) that a combination of field photography and quantitative spectral measurements of resource surfaces is a viable approach to characterizing within-tree host structures. Photography is most helpful in identifying patterns not detectable to the human eye that may function in insect orientation. It's application to UV pattern detection has been clearly demonstrated. It may be equally applicable to the detection of polarized light patterns and overall characterization of visual environments. It's usefulness in all facets of visual ecology is unquestionable, but the application has barely begun.

B. Spectrophotometry

Spectrophotometric analysis is the relative measurement of spectral reflectance, spectral transmittance, or spectral emittance, as a function of wavelength. Spectrophotometers consist of a monochromator, used for the isolation of narrow portions of the light spectrum, and a photometer, which measures relative values in the visible spectrum (300-800nm) (Science of Color 1963). Photopic measurements (of surface reflectance of the monochromator beam) are made within the stable geometry of an integrating sphere. Some, but not all, spectrophotometers are equipped with filters or software that correct readings to match human sensitivity functions. These instruments are more properly called colorimeters. In both instruments, measurement values are relative to the reflective or transmissive properties of a known standard. Illumination differences are thus eliminated. Quantitative values of the effects of different illuminants can be obtained mathematically by applying correction factors calculated from spectral measurements of each illuminating source. Lythgoe (1979) considers relative reflection measurements satisfactory for visual ecology studies, as the results are the same whether it is energy or the number of photons that is measured. Values in radiometric terms must be converted to photons and/or frequency for comparison with visual sensitivity functions (Dartnall 1975).

Methods. A Shimadzu UV-210 spectrophotometer (Bausch and Lomb, Inc.) was used to study the surface reflection of apple maggot host and host mimic surfaces. Compacted powdered magnesium oxide (MgO) was used as a standard reflective surface. The non-portable instrument was capable of relative measures of diffuse reflectance from the UV (300nm) into the near IR (800nm). Unknown sample reflectance was recorded on a Houston instrument chart recorder as the % reflectance per nanometer wavelength of the known standard. Momochromator band width was set at 2nm. The reflectance of the standard was corrected to 100% across the entire spectrum. A tungsten monochromator light source was used for measurements below 500nm. Measurements were made of a 2.5 cm diam portion of the test object surface. Items too small to measure whole were made into composite mosaics by arranging them on double stick tape (3M Corp., Minneapolis, MN) such that a minimum of 90% of the surface was covered. Snodderly (1979) made optical modifications to his spectrophotometer enabling the surface measurement of single small berries.

Results and discussion. Spectral measurements can be recorded in a diversity of ways. They are often described in physiological terms which are relevant only to human vision. Units of illumination such as lux, foot candles, lumens, and color discriptions including brightness, color names, X, Y, Z values, shades, and tints are useful when describing qualitatively but not quantitative visual environmental parameters for correlations with animal visual sensitivity. Quantitative physical units, particularly microwatts and photons per wavelength or frequency, used for spectral measurements of radiance and irradiance, are best for comparisons with data from spectral sensitivity studies. In general, visual receptors are photon counters with wide spectral absorption bands. Therefore, measurements in photons are preferable for visual ecology studies. Relative measurements can be considered unitless. Therefore, relative reflectance curves may be used to represent relative photon distributions (Lythgoe 1979). Comparisons can be made between relative measurements of surfaces, provided the conditions of measurement are identical and surfaces are viewed under conditions of equal irradiance. These comparisons are useful in correlating visual sensitivity functions to color-contrast differences of host structures (Kevan 1978, Snodderly 1979). Actual numerical values taken under conditions of natural illumination are more accurate for such comparisons but also are more complex and difficult to attain (Hailman 1979).

During this study, spectrophotometry provided useful comparative data which aided not only the spectral characterization of AMF host surfaces, but also the selection and preparation of mimicking surfaces (Chapters III, IV). Exact mimics were not possible, but relative reflectance measurements enabled production of pigment mixtures which closely matched host structures in reflectance curves. This proved to be much more reliable for matching host hue reflectance than did selecting commercially prepared paints by color name or by visual inspection.

Ideally, the spectrophotometer should be used in conjunction with a portable spectral radiometer. Radiometric measurements of incident irradiance within the environment could be combined with relative reflectance curves generated by the spectrophotometer to mathematically produce photon values. The data so generated would show how incident irradiance might affect diffuse surface reflectance. However, variability due to viewing angle and surface texture (i.e., glare) would be difficult to identify. Polarization also cannot be measured by this method.

C. Spectral Radiometry

Spectral radiometry is the measurement of electromagnetic energy in physical units ($\mu W/cm^2$) per wavelength.

Radiometry measures the energy available to effect a temperature change in either the sender or the receiver (Science of Color 1963).

The radiometer, therefore, refers to a diversity of instruments. Spectral radiometers, on the other hand, are specialized instruments. Here, incoming light is divided into discrete spectral regions, and a sensor measures the light energy in individual wavelength bands. Radiometer sensitivity depends upon the wavelength range and absolute sensitivity of its energy sensor. To increase absolute sensitivity for specific spectrum regions, radiometers are frequently manufactured for a single measurement purpose. The basic instrument is very flexible and can be modified by the addition of various collection heads, sensors, scan drives, and microprocessors for specific research needs. Newer instruments, equipped with microprocessors, can make measurements in absolute or relative modes from the UV into the IR for either irradiance or radiance. Therefore, the intended purpose, the units of measurement desired, and the specific wavelength range required need to be identified prior to purchase of a radiometer for research measurements. Field use of spectral radiometers is possible (McFarland and Munz 1975a, Miller et al. 1976, Hailman 1979), though challenging.

Methods. Under both field and laboratory conditions, apple maggot host and host mimic surfaces were examined with a scanning spectral radiometer (Gamma Scientific, Inc., Palo Alto, CA) (Chapter III). The instrument was made available for use by GTE Laboratories, Inc., Waltham, MA. A glass or quartz fiber optic probe was fitted with a specially designed jig to keep the tip of the probe at a uniform distance (4cm) and geometry from measured surfaces. Data records and graphs were made by hand for measurements taken under both field and laboratory conditions in 1980. In 1981, the addition of a microprocessor capable of automatic data recording and graphing simplified measurements.

Results and discussion. Spectral radiometers of the type used here have been successfully applied in visual ecology studies (McFarland and Munz 1975a, Hailman 1979). The use of such instruments is most complex under field conditions. Lack of a solid geometry, unless provided within an integrating sphere, requires that more attention be paid to the setup and operation to insure a uniform geometry among measurements of surfaces and among conditions of illumination. Need for *in vivo* measurements may out weigh this inconvenience. Hailman (1979) cites a number of reasons for increasing the frequency of *in* vivo measurements in visual ecology studies. He suggests such measurements are the most useful source of color-contrast information on which to base inferences on how animals may use visual contrasts in resource detection.

Ideally, measurements of radiant surface energy should be made of a surface area of a size relevant to the viewer, i.e., apple maggot fly (Land 1981). This necessitates the design of an energy collector with known delineated optics, such as a fiber optic probe. The incident irradiance measurement for a general area is made using a cosign receptor which collects energy from all directions evenly. To use this measurement system accurately, one must (a) understand the animal in question, (b) make an estimation of the surface area size to be measured, and (c) finally, make spectral measurements in the field. By so doing, the resulting data will be more useful for understanding environmental visual cues in terms of the animal's behavior.

The spectral radiometer was used to measure the surface reflection of host structures and pigment covered mimics under both daylight and flight chamber lamps. This method verified that the relative reflectance pattern as measured by the spectrophotometer was reliable (Chapter III, Figs. 1,2,7). It was difficult to make measurements under field conditions due to highly variable light conditions. The manner of recording data (totally by hand) was slow and cumbersome. Thus, repeated measurements for improved reliability were not possible. Newer instruments, with automatically recording microprocessors, enable faster data collection, thereby improving measurement reliability through repeated measurements.

Measurement methods and data units are adaptable with a spectral radiometer. This instrument can be used to collect relative and absolute data under all types of illumination. Diffuse surface reflection, specular reflectance, polarized light, and transmission may be measured in field and laboratory setups. Mathematical manipulation and plotting of data is simplified when microprocessors are coupled with spectral radiometers. The spectral radiometer was the most flexible, sophisticated, portable, and expensive of the measurement instruments tested.

Conclusions

From this study of three methods for measuring reflectance of plants, I conclude that photography was most useful as a tool for initial identification and characterization of pattern parameters of apple maggot fly host plants. Photographs were powerful visual aids when explaining visual ecology to other researchers. Spectrophotometry was the easiest method for repeatable acquisition of relative surface spectral reflection data, but was not useful for obtaining numerical values of absolute energy. Relative spectrophotometric reflectance curves can be extrapolated to resemble actual field conditions through the application of correction factors for irradiance. Correction factors should, however, be derived from actual irradiance measures of natural sources made by using a spectral radiometer. Field spectral radiometry is difficult, but provides absolute values for environmental energy. This study shows that techniques should be combined in a manner adapted to the data needs of the researcher.

BIBLIOGRAPHY

Agee, H.R., W.A. Phillis, and D.L. Chambers. 1977. The compound eye of the Caribbean fruit fly and the apple maggot fly. Ann. Entomol. Soc. Amer. 70: 359-64.

Autrum, H., Ed. 1979. Handbook of Sensory Physiology. VII/6A. Springer-Verlag, N.Y., N.Y. 729p.

Autrum, H., Ed. 1981a,b. Handbook of Sensory Physiology. VII/6B,C. Springer-Verlag, N.Y., N.Y. 629p., 663p.

Bennett, M.F. 1979. Extraocular light receptors and circadian rhythms. In: Handbook of Sensory Physiology. VII/6A. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 641-64.

Bernard, G.D. 1979. Red-absorbing visual pigment of butterflies. Science 203:1125-27.

Bernard, G.D. 1981. A comparison of vertebrate and invertebrate photoreceptors. In: Springer-Verlag, Series in Optical Sciences. Vol. 23: Vertebrate Photoreceptor Optics. J.M. Enoch and F.L. Tobey, Jr., Eds. Springer-Verlag, N.Y., N.Y. pp. 433-63.

Bernard, G.D. and D.G. Stavenga. 1979. Spectral sensitivities of retinular cells measured in intact, living flies by an optical method. J. Comp. Physiol. 134: 95-107.

Blacker, A.A. 1976. Field Photography: Beginning and Advanced Techniques. W.H. Freeman and Co. San Francisco, Ca. 440p.

Boller, E.F. and R.J. Prokopy. 1976. Bionomics and management of Rhagoletis. Ann. Rev. Entomol. 21:223-45.

Burkhardt, D. 1964. Colour discrimination in insects. Adv. Insect Physiol. 2:131-203.

Burtt, E.H., Jr., Ed. 1979. The Behavioral Significance of Color. Garland STPM Press, New York. 456p.

Callahan, P.S. 1965a. Intermediate and far red infrared sensing of nocturnal insects. Part I. Evidences for a far infrared (FIR) electromagnetic theory of communication and sensing in moths and its relationship to the limiting biosphere of the corn earworm. Ann. Entomol. Soc. Amer. 58:727-45.

Callahan, P.S. 1965b. Intermediate and far infrared sensing of nocturnal insects. Part II. The compound eye of the corn earworm, Heliothis zea, and other moths as a mosaic optic-electromagnetic thermal radiometer. Ann. Entomol. Soc. Amer. 58:746-55.

Coombe, P.E. 1981. Wavelength specific behavior of the white fly Trialeurodes vaporariorum (Homoptera: Aleurodidae). J. Comp. Physiol. 144:83-90.

Dapsis, L.J. and D.N. Ferro. 1982. Trap assessment and reproductive development of adult female cabbage maggots, Hylemya brassicae (Wiedmann) (Anthomyiidae: Diptera) Entomol. Exp. and Appl. (Submitted).

Dartnall, H.J.A. 1975. Assessing the fitness of visual pigments for their photic environment. In: Vision in fishes. M.A. Ali, Ed. Plenum Press. N.Y., N.Y. pp. 543-63.

Daumer, K. 1956. Reizmetrische untersuchungen des Farbensehens der Bienen. Z. vergl. Physiol. 38:413-78.

Davson, H. 1980. Physiology of the eye. Academic Press, N.Y., N.Y. 480p.

Dickman, D.A. 1974. Color and light intensity preferences of four species of alate cereal aphids. Ph.D. thesis. South Dakota State University. 28p.

Dixon, A.F.G. 1973. Biology of Aphids. Studies in Biol. No. 44. Edward Arnold (Publ.) Ltd., London. 55p.

Dobrowolski, J.A., G.E. Marsh, D.G. Charbonneau, J. Eng, and P.D. Josephy. 1977. Colored filter glasses: an inter comparison of glasses made by different manufacturers. Applied Optics. 16:1491-1512.

Eisner, T., R.E. Silberglied, D. Aneshansley, J.E. Carrel, and H.C. Howland. 1969. Ultraviolet video-viewing: The television camera as an insect eye. Science 166:1172-74.

Evans, W.G. and J.E. Kuster. 1980. The infrared receptive fields of Melanophila acuminata (Coleoptera:Buprestidae). Can. Entomol. 112:211-16.

Finch, S. and G. Skinner. 1974. Some factors affecting the efficiency of water-traps for capturing cabbage root flies. Ann. Appl. Biol. 77:213-26.

Fox, D.L. 1979. Pigment transactions between animals and plants. Biol. Rev. 54:237-68.

Franceschini, N., R. Hardie, W. Ribi, and K. Kirschfield. 1981. Sexual dimorphism in a photoreceptor. Nature 291:241-44.

Fukushi, T. 1976. Classical conditioning to visual stimuli in the housefly, Musca domestica. J. Insect Physiol. 22:361-64.

Gates, D.M. 1980. Biophysical Ecology. Springer-Verlag, N.Y., N.Y. 611p.

Goldsmith, T.H. and G.D. Bernard. 1974. The visual system of insects. In: Physiology of Insecta, M. Rockstein, Ed., Academic Press, N.Y., N.Y. pp. 175-271.

Goodman, L.J. 1975. The neural organization of the insect dorsal ocellus. In: The compound eye and vision in insects. G.A. Horridge, Ed. Clarendon Press, Oxford, England. pp. 515-44.

Goodman, L.J. 1981. Organization and physiology of the insect dorsal ocellar system. Handbook of Sensory

Physiology. VI/6C. H. Autrum, Ed. pp. 201-86.

Greany, P.D., H.R. Agee, A.K. Burditt, and D.L. Chambers. 1977. Field studies on color preferences of the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). Entomol. Exp. and Appl. 21:63-70.

Gruber, S.H. 1979. Mechanisms of color vision: An ethologist's primer. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press, N.Y., N.Y. pp. 183-236.

Hailman, J.P. 1977. Optical Signals, Animal Communication and Light. Indiana Univ. Press. Bloomington, In. 362p.

Hailman, J.P. 1979. Environmental light and conspicuous colors. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press, N.Y., N.Y. pp. 289-354.

Hagen, K.S., W.W. Allen, and R.L. Tassan. 1981. Mediterranean fruit fly: the worst may be yet to come. California Agriculture 35:5-7.

Hamdorf, K. 1979. The physiology of invertebrate visual pigments. In: Handbook of Sensory Physiology. VII/6A. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. 1979. pp. 145-225.

Hardie, R.C. 1979. Electrophysiological analysis of fly retina. I: Comparative Properties of R1-6 and R7 and 8. J. Comp. Physiol. 129:19-33.

Hardie, R.C., N. Franceschini, and P.D. McIntyre. 1979. Electrophysiological analysis of fly retina. II. Spectral and polarization sensitivity in R7 and R8. J. Comp. Physiol. 133:23-29.

von Helversen, O. 1972. Zur Spektralen Unterschiedsempfind lich keit der Honigbiene. J. Comp. Physiol. 80:439-72.

Henderson, S.T. 1970. Daylight and its Spectrum. Hilger, London. 349p.

Horovitz, A. and Y. Cohen. 1972. Ultraviolet reflectance characteristics in flowers of crucifers. Amer. J. Bot. 59:706-13.

Horridge, G.A., Ed. 1975. The Compound Eye and Vision of Insects. 1975. Clarendon Press. Oxford, England. p. 595.

Hu, K.G. and W.S. Stark. 1977. Specific receptor input into spectral preference in Drosophila. J. Comp. Physiol. 121:241-52.

Ilse, D. 1949. Color discrimination in the Dronefly, Evistrlis tenax. Nature 163:255-56.

Ilse, D. and V. Vaidya. 1956. Spontaneous feeding response to colors in Papilio demoleus L. Proc. Indian Acad. Sci. 43:23-31.

Kennedy, J.S. 1958. Physiological condition of the host-plant and susceptibility to aphid attack. Entomol. Exp. and Appl. 1:50-65.

Kennedy, J.S., C.O. Booth, W.J.S. Kershaw. 1961. Host finding by aphids in the field. III. Visual attraction. Ann. Appl. Biol. 49:1-21.

Kennedy, J.S. and C.O. Booth. 1963a. Free flight of aphids in the laboratory. J. Exp. Biol. 40:67-85.

Kennedy, J.S. and C.O. Booth. 1963b. Coordination of successive activities in an aphid. The effect of flight on the settling responses. J. Exp. Biol. 40: 351-69.

Kevan, P.G. 1978. Floral coloration, its colorimetric analysis and significance in anthecology. In: Pollination of Flowers by Insects. A.J. Richards, Ed. Linnean Soc. Symp. Ser. 6. p. 51-78.

Kevan, P.G. 1979. Vegetation and floral colors revealed by ultraviolet light: interpretational difficulties for functional significance. Amer. J. Bot. 66: 749-51.

Kevan, P.G., N.D. Grainger, G.A. Mulligan, and A.R. Robertson. 1973. A gray-scale for measuring reflectance and color in the insect and human visual spectra. Ecology 54:924-26.

Eastman Kodak Co. 1977. Applied Infrared Photography. Publ. No. M-29. 84p.

Kretz, R. 1979. A behavioral analysis of color vision in the ant cataglyphic bicolor (Formicidae: Hymenoptera). J. Comp. Physiol. 131:217-33.

Kring, J.B. 1966. An aphid flight chamber: construction and operation. J. Econ. Entomol. 59:1518-20.

Kring, J.B. 1967. Alighting of aphids on colored cards in a flight chamber. J. Econ. Entomol. 60:12-7-10.

Kring, J.B. 1968. Trapping Hylemya spp. flies in tobacco fields on sticky colored stakes. J. Econ. Entomol. 61:1567-9.

Kring, J.B. 1969. Behavioral responses of winged bean aphids to colored fluorescent lamps. J. Econ. Entomol. 62:1450-55.

Kring, J.B. 1970. Red spheres and yellow panels combined to attract apple maggot flies. J. Econ. Entomol. 63:466-9.

Kring, J.B. 1972. Flight behavior of aphids. Ann. Rev. Entomol. 17:461-92.

Kring, J.B. 1977. Structure of the eyes of the pea aphid, Acyrthosiphon pisum. Ann. Entomol. Soc. Amer. 70: 855-60.

Kunze, P. 1979. Apposition and superposition eyes. In: Handbook of Sensory Physiology. VII/6A. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 411-502.

Land, M.F. 1981. Optics and vision in invertebrates. In: Handbook of Sensory Physiology VII/6B. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 471-594.

Laughlin, S.B. 1981. Neural principles in the visual system. In: Handbook of Sensory Physiology. VII/6B. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 133-280.

Levine, J.S. and E.F. MacNichol, Jr. 1982. Color vision in fishes. Scientific American 246:140-42.

Lythgoe, J.N. 1979. The Ecology of Vision. Clarendon Press. Oxford, England. 244p.

MacDowall, F.D.H. 1972. Photactic action spectrum for whitefly and the question of colour vision. Canad. Entomol. 104:299-307.

Mazokhin-Porshnyakov, G.A. 1969. Insect Vision. Plenum Press, N.Y., N.Y. 306p.

Mazokhin-Porshnyakov, G.A. and V.I. Kazyakina. 1979. Eye structure in winged aphids (Homoptera:Aphididae). Entomol. Rev. 58:20-7.

McFarland, W.N. and F.W. Munz. 1975a. Part II: The photic environment of clear tropical seas during the day.

Vision Res. 15:1063-70.

McFarland, W.N. and F.W. Munz. 1975b. Part III: The evolution of photopic visual pigments in fishes. Vision Res. 15:1071-80.

Menzel, R. 1967. Untersuchungen zum Erlernen von Spektralfarben durch die Honig biene, Apis mellifica. Z. vergl. Physiol. 56:22-62.

Menzel, R. 1975. Colour receptors in insects. In: The Compound Eye and Vision of Insects. G.A. Horridge, Ed. Clarendon Press, Oxford, England. pp. 121-49.

Menzel, R. 1979. Spectral sensitivity and colour vision in invertebrates. In: Handbook of Sensory Physiology. VII/6A. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 503-80.

Meyer, J.R. 1976. Positive phototaxis of adult alfalfa weevils to visible and near-infrared radiation. Ann. Entomol. Soc. Amer. 69:21-5.

Meyer, J.R. 1977. Head capsule transmission of long-wavelength light in the Curculionidae. Science 196: 524-25.

Miller, L.D., R.L. Pearson, C.J. Tucker. 1976. A mobile field spectrometer laboratory. Photogram. Eng. and Remote Sens. 42:569-72.

Moericke, V. 1955. Uber die Vebensgewohnheiter der Geflugelten Blattlause unter Besonderer Berucksichtigung des Verhaltens beim Landen. Z. Agnew. Entomol. 37:29-91.

Moericke, V. 1962. About the optical orientation of aphids. Z. Agnew. Entomol. 50:70-4.

Moericke. V. 1969. Host plant specific colour behavior by *Hyalopterus pruni* (Aphididae). Entomol. Exp. and Appl. 13:503-

Moericke, V. 1976. Response to colour stimuli (in Tephritidae). In: Studies in biological control. V.L. Delucchi, Ed. Cambridge Univ. Press, Cambridge, England. pp. 23-27.

Moericke, V., H. Schneiders, B. Vogt. 1966. Flughemmung and Fall reflexhaltung als Reaktion auf Gelbreiz bei *Trialeurodes vaporariorum*. Z. Pflanzenkr. Pflanzenschutz. 73:6-14.

Moore, D., J. Penikas, M.A. Rankin. 1981. Regional specialization for an optomotor response in the honeybee compound eye. Physiol. Entomol. 6:61-9.

Mote, M.I. and R. Wehner. 1980. Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. J. Comp. Physiol. 137:63-71.

Mound, L.A. 1962. Studies on the olfaction and colour sensitivity of *Bemishia tabaci* (Genn.) (Homoptera: Aleyrodidae). Entomol. Exp. and Appl. 5:99-104.

Mulroy, T.W. 1979. Spectral properties of heavily glaucous and non-glaucous leaves of a succulent rossete-plant. Oecologia (Berl.) 38:349-57.

Munz, F.W. and W.N. McFarland, 1977. Evolutionary adaptations of fishes to the photic environment. In: Handbook of Sensory Physiology. VII/5. F. Crescitelli. Ed. Springer-Verlag, N.Y., N.Y. pp. 193-274.

Neumeyer, C. 1980. Simultaneous color contrast in the honeybee. J. Comp. Physiol. 139:165-76.

Neumeyer, C. 1981. Chromatic adaptation in the honeybee: Successive color contrast and color constancy. J. Comp. Physiol. 144:543-53.

Owens, E.D. and R.J. Prokopy. 1978. Visual monitoring traps for European apple sawfly. J. Econ. Entomol. 71:576-8.

van der Pijl, L. 1972. Principles of Dispersal in Higher Plants. Springer-Verlag, N.Y., N.Y. 161p.

Prokopy, R.J. 1968. Visual responses of apple maggot flies, <u>Rhagoletis</u> <u>pomonella</u> (Diptera:Tephritidae): Orchard Studies. Entomol. Exp. and Appl. 11:403-22.

Prokopy, R.J. 1969. Visual responses of European cherry fruit flies, <u>Rhagoletis</u> <u>cerasi</u> L. (Diptera:Trypetidae). Polskie Pismo Entomol. 39:539-66.

Prokopy, R.J. 1972. Response of apple maggot flies to rectangles of different colors and shades. Environ.

Entomol. 1:720-26.

Prokopy, R.J. 1975. Selective new trap for Rhagoletis cingulata and R. pomonella flies. Environ. Entomol. 4:420-24.

Prokopy, R.J. 1975b. Apple maggot control by sticky red spheres. J. Econ. Entomol. 68:197-8.

Prokopy, R.J. 1976. Feeding, mating, and oviposition activities of Rhagoletis fausta flies in nature. Ann. Entomol. Soc. Amer. 69:899-904.

Prokopy, R.J. 1977a. Attraction of Rhagoletis flies (Diptera:Tephritidae) to red spheres of different sizes. Can. Entomol. 109:593-96.

Prokopy, R.J. 1977b. Stimuli influencing tropic relations in Tephritidae. Int. Symp. on Tropic Relations in Insects. Tours, France Coll. Int. CNRS: 265:305-36.

Prokopy, R.J., E.W. Bennett, and G.L. Bush. 1971. Mating behavior in Rhagoletis pomonella. I. Site of Assembly. Can. Entomol. 102:1405-9.

Prokopy, R.J., F.W. Bennett, and G.L. Bush. 1972. Mating behavior in Rhagoletis pomonella II. Temporal organization. Can. Entomol. 104:97-104.

Prokopy, R.J. and E.F. Boller. 1971. Response of European cherry fruit flies to colored rectangles. J. Econ. Entomol. 64:1444-47.

Prokopy, R.J. and G.L. Bush. 1973. Mating behavior in Rhagoletis pomonella. IV. Courtship. Can. Entomol. 105:873-91.

Prokopy, R.J., A.P. Economopoulos, and M.W. McFadden. 1975. Attraction of wild and laboratory-cultured Dacus oleae flies to small rectangles of different hues, shades, and tints. Entomol. Exp. and Appl. 18:141-52.

Prokopy, R.J. and A.P. Economopoulos. 1976. Color responses of Ceratitis capitata flies. Z. Angew Entomol. 80:434-37.

Prokopy, R.J. and G.E. Haniotakis. 1976. Host detection by wild and lab-cultured olive flies. Symp. Biol. Hung. 16:209-14.

Prokopy, R.J. and K.I. Hauschild. 1979. Comparative effectiveness of sticky red spheres and Pherocon® AM standard traps for monitoring apple maggot flies in commercial orchards. Environ. Entomol. 8:696-700.

Prokopy, R.J. and E.D. Owens. 1978. Visual generalist - visual specialist phytophagous insects: host selection behavior and application to management. Entomol. Exp. and Appl. 24:609-20.

Prokopy, R.J. and D.C. Smith. 1980. Mating behavior of Rhagoletis pomonella (Diptera:Tephritidae) VI. Site of early-season encounters. Can. Entomol. 112:585-90.

Rausher, M.D. 1978. Search image for leaf shape in a butterfly. Science 200:1971-73.

Reichardt, W. and T. Poggio. 1979. Figure-ground discrimination by relative movement in the visual system of the fly. Biol. Cybernetics. 35:81-100.

Roitberg, B.D., J.C. van Lenteren, J.J.M. Alphe, F. Galis, and R.J. Prokopy. 1982. Foraging behavior of Rhagoletis pomonella, a parasite of hawthorn (Crataegus), in nature. J. Animal Ecol. 52: (In Press).

Rose, R. and R. Menzel. 1981. Luminance dependence of pigment color discrimination in bees. J. Comp. Physiol. 141:379-88.

Röttger, V.V. 1979. Undersuchungen zur Wirtswahl der Rübenfliege Pegomya betae Curt. (Diptera:Anthomyidae) II. Optische Orientierung zur Wirtspflanze. Z. Ang. Entomol. 88:97-107.

Rowland, W.J. 1979. The use of color in intraspecific communication. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press, N.Y., N.Y. pp. 379-421.

Saxena, K.N. and S. Goyal. 1978. Host-plant relations of the citrus butterfly Papilio demoleus L.: Orientation and ovipositional responses. Entomol. Exp. and Appl. 24:1-10.

The Science of Color. 1963. Optical Soc. of Amer. Washington, D.C. 385p.

Silbergleid, R.E. 1966. Visualization and recording of longwave ultraviolet reflection from natural objects. Parts 1 and 2. Functional Photography. 11:20-33.

Smola, V. and P. Meffert. 1979. The spectral sensitivity of the visual cells R7 and R8 in the eye of the blowfly *Calliphora erythrocephala.* J. Comp. Physiol. 133:41-52.

Snodderly, D. Max. 1979. Visual discriminations encountered in food foraging by a neotropical primate: Implications for the evolution of color vision. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press. N.Y., N.Y. pp. 237-79.

Strausfeld, N.J. and D.R. Nassel. 1981. Neuroarchitecture of brain regions that subserve the compound eyes of crystacea and insects. In: Handbook of Sensory Physiology. VII/6B. H. Autrum, Ed., Springer-Verlag. N.Y., N.Y. pp. 49-132.

Sustare, B.D. 1979. Physics of light: An introduction for light-minded ethologists. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press, N.Y., N.Y. pp. 3-27.

Swihart, C.A. and S.L. Swihart. 1970. Colour selection and learned feeding preferences in the butterfly, Heliconius charitonius Linn. Anim. Behav. 18:60-4.

Tinbergen, N. 1951. The Study of Instinct. Chapman and Hall Publ. Oxford, England. pp. 16.

Truman, J.W. 1976. Extra retinal photoreception in insects. Photochem. Photobiol. 23:215-25.

Underwood, H. 1979. Extraretinal photoreception. In: The Behavioral Significance of Color. E.H. Burtt, Jr., Ed. Garland STPM Press. N.Y., N.Y. pp. 127-78.

Vaishampayan, S.M., M. Kogan, G.P. Walbauer, and J.T. Woolley. 1975a. Spectral specific responses in the visual behavior of the greenhouse whitefly. Entomol. Exp. and Appl. 18:344-56.

Vaishampayan, S.M., G.P. Waldbauer, and M. Kogan. 1975b. Visual and olfactory responses in orientation to plants by the greenhouse whitefly, Trialeurodes vaporariorum (Homoptera:Aleyrodidae). Entomol. Exp. and Appl. 18:412-22.

Walker, J. 1972. Amateur scientist: more about polarizers and how to use them, particularly for studying polarized skylight. Scientific American. 238:132-36.

Waterman, T.H. 1981. Polarization sensitivity. In: Handbook of Sensory Physiology. VII/6B. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 281-470.

Wehner, R. 1976. Polarized-light navigation by insects. Sci. Amer. 235:106-15.

Wehner, R. 1981. Spacial vision in arthropods. In: Handbook of Sensory Physiology. VII/6C. H. Autrum, Ed. pp. 287-616.

Wehner, R. and F. Toggweiler. 1972. Verhaltensphysiologischer Nachweis des Farbensehens bei Cataglyphis bicolor (Formicidae:Hymenoptera). J. Comp. Physiol. 77:239-55.

Weiss, H.B. 1943. The group behavior of 14,000 insects to colours. Entomol. News 54:152-56.

Wolken, J. 1975. Photoprocesses, Photoreceptors, and Evolution. Academic Press, N.Y., N.Y. 317p.

Woolley, J.T. 1971. Reflectance and transmittance of light by leaves. Plant Physiol. 47:656-62.

Wyszecki, G. and W.S. Stiles. 1967. Color Science: Concepts and Methods, Quantitative Data and Formulas. Wiley, N.Y., N.Y. 462p.

Yoshida, M. 1979. Extraocular photoreception. In: Handbook of Sensory Physiol. VII/6A. H. Autrum, Ed. Springer-Verlag, N.Y., N.Y. pp. 581-640.