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DISTANCE OF DETECTION OF HOST TREE VISUAL AND OLFACTORY STIMULI BY THE APPLE MAGGOT FLY, *RHAGOLETIS POMONELLA* (WALSH) (DIPTERA: TEPHRITIDAE)

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by
THOMAS A. GREEN

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DISTANCE OF DETECTION OF HOST TREE VISUAL AND OLFACTORY STIMULI BY THE APPLE MAGGOT FLY, *RHAGOLETIS POMONELLA* (WALSH) (DIPTERA: TEPHRITIDAE)

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To Brook and Justin Green who have beared with me throughout, and to Erin Mackesey, who took me on knowing I still wasn't done!

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ABSTRACT

DISTANCE OF DETECTION OF HOST TREE VISUAL AND OLFACTORY STIMULI BY THE APPLE MAGGOT FLY, *RHAGOLETIS POMONELLA* (WALSH) (DIPTERA: TEPHRITIDAE)

SEPTEMBER 1992

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Mature female apple maggot flies, *Rhagoletis pomonella* (Walsh) were released individually onto a single fruitless hawthorne tree in the center of an open field. This tree was surrounded by four 1 m^2 plywood host tree models painted green or white, with or without synthetic host fruit odor (butyl hexanoate), placed at one of several distances from the release tree. Each fly was permitted to forage freely on the release tree for up to 1 hour, or until it left the tree. Flies left the tree significantly sooner when green models with host fruit odor were present at 0.5 m, 1.5, or 2.5 m distance from the release tree than when these models were placed at a greater distance (4.5 m) from the release tree or when no models were present. These results suggest that female apple maggot flies did not detect green $1 m^2$ models with odor 4.5 m away or models without odor 2.5 m or more away.

Increasing model size to 2 m^2 increased the distance at which flies responded to green models without odor. Decreasing model size to 0.5 m^2 reduced fly responsiveness. The presence of host fruit odor alone did not influence residence time on the release tree.

Rate of movement and upwind orientation ($\pm 22.5^{o}$) of individually-caged *R. pomonella* flies increased significantly over no-odor conditions in the presence of a stationary point source of butyl hexanoate at a distance of 12 m ($P \leq 0.03$) in an open grassy field, but not at 24 m. Increasing the rate of butyl hexanoate release from ca. 500 ug per hour to ca. 6000 ug per hour did not significantly increase distance of response.

Take-off direction of *R. pomonella* from a platform in the center of a large open field was random with respect to wind direction when no host odor stimulus was present. Take-off direction was significantly biased upwind ($\pm 67.5^{o}$) when 8 evenly spaced butyl hexanoate-filled vials surrounded the release platform in a circle with a radius 6 m ($P \leq 0.03$), and downwind ($\pm 67.5^{o}$) when the same number of vials encircled the platform at 12 m ($P \leq 0.01$). Similarly, take-off direction tended towards upwind when 16 evenly spaced butyl hexanoate-filled vials surrounded *R. pomonella* at 12 m ($P \leq 0.10$), and was significantly biased downwind at 24 m ($P \leq 0.01$).

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CHAPTER 1

LONG-DISTANCE RESPONSE TO RESOURCES BY INSECTS

> "Studies dealing with only one modality inaccurately portray the mechanism used to locate resources and underestimate the real amount of information available." Bell (1990)

Introduction

The survival and reproductive success of an organism is dependent upon its ability to locate essential resources, including food, moisture, mates, and oviposition sites. The behavior of insects foraging for these resources has attracted considerable attention over the past 20 years (reviewed in Kennedy 1977, Hassel and Southwood 1978, Finch 1980, Stephens and Krebs 1986, Visser 1988, Bell 1990), both as a basic research question and a pest management concern. The foraging behavior of tephritid fruit flies for host plant resources has been investigated quite extensively, perhaps as thoroughly as any other family of insects (reviewed in Prokopy & Roitberg 1989). More may be known about the foraging behavior of the apple maggot fly, *Rhagoletis pomonella* (Walsh) (=AMF), than any other tephritid species. The goal of this dissertation (Chapters 2 and 3) was to determine the maximum distance at which apple maggot flies respond to the odor cues provided by host fruit and to visual stimuli provided by the host tree.

To introduce this study, it is essential to review terms and definitions, mechanisms of detection and response, sources of variation in response, and the few previous studies of maximum distance of response. A thorough understanding of these issues and events is critical to choosing appropriate stimuli and experimental design, anticipating measurable responses, and interpreting results. While not an exhaustive review, this chapter is intended to describe at least some examples of all known mechanisms and sources of variability in long distance response to resource cues by insects.

Definition Of Terms

A framework of concepts and a specific vocabulary has been proposed and debated to describe the foraging process. Foraging, *sensu* Kennedy (1985) is movement that is "readily interrupted" by encounter with the resource in need. Foraging in a broader sense would include information gathering by stationary animals such as visual scanning. Searching is often used interchangeably with foraging, but its teleological implications probably make foraging a more desirable term.

Foraging activities can be placed within a hierarchy of levels: the habitat, patch, and individual resource unit (Hassel & Southwood 1978). Movement and foraging may occur between habitats (= migration, but see Kennedy 1985), between patches (= ranging), and within patches (= local search) (Jander 1975). The insect in nature best defines these levels through changes in behavior, such as switching from extensive to area-concentrated search. Alternative models have been proposed to describe variations in this system including non-patchy habitats, and insects which feed while moving through rather than within patches (Arditi and Dacorogna 1988).

Foraging behavior has been described as the product of 3 types of influences: (1) external environmental constraints including resource availability, apparency, and distribution, and interference from predators or abiotic factors, (2) the inherent biology of the organism which dictates sensory and locomotory ability, and (3) internal, physiological state variables such as egg load or degree of deprivation (Bell 1990).

Responses to cues can be categorized as kineses, or changes in rate of locomotion or turning, or taxes, directed movement towards or away from the stimulus (Fraenkel and Gunn 1940, Kennedy 1977, 1978). Behavioral response may be under allothetic control, initiated and modulated by information from sources external to the insect, and/or ideothetic control, generated internally from stored information or proprioceptors (Visser 1988).

Long-Distance Response To Resources

The maximum distance over which an insect can respond to resource cues has been determined for only a very few species (Miller and Strickler 1984). Other issues have been the focus of most foraging research, possibly in part because determining the maximum distance of response can be a very difficult question to address. It is testimony to the paucity of research on this topic that this review can be undertaken without narrowing its focus to some subset of Insecta, such as herbivorous or parasitic insects. Restricting a review to this Class may still be too parochial. Foraging studies of organisms outside the Insecta hold much information that is of much value to entomologists (Dethier 1986).

Long range response occurs at a distance greater than that at which chemotaxis (= directed movement in response to an odor gradient) is possible, generally thought to be at least several millimeters or centimeters from the source (Kennedy 1977). Visual cues associated with the host may operate over a shorter range in comparison to airborne odor cues, which may travel many meters. Visual cues not associated with the resource itself influence flight speed and direction through the optomotor response. Orientation to odors may also involve mechanoreception through detection of wind direction by crawling insects, and by flying insects prior to take-off. Auditory cues are also important for resource detection in some species, particularly for mate location (Ewing 1984), but are not considered here.

Assays of response to visual and odor cues include trapping studies, direct measurement of movement parameters under conditions ranging from completely natural settings to tightly controlled laboratory arenas, and electrophysiological measurements at the receptor organ and cell level. Specific behavioral responses to resource cues include increased movement, directed movement, take-off, upwind flight, and arrival at a source.

Visual Response

Mechanisms

Prokopy and Owens (1983) describe a process whereby an insect more than a few meters from a plant can detect only the dark silhouette against a brighter sky. Within a very few meters or less, characteristics common to most plants such as spectral hue (dominant wavelength) and intensity (brightness, or total reflected energy) may become apparent, and within a meter or less, discrimination between host and non-hosts plants may be possible based on fine dimensional or pattern cues provided by the plant.

Few examples of response to exclusively visual cues from a distance are available. Most foraging studies fail to dissect response into visual and olfactory components. This discrimination is most readily accomplished by carefully constructing unidimensional resource mimics containing only the visual or olfactory aspects of the actual resource.

Host plant finding by *Pieris rapae* (L.) (Lepidoptera: Pieridae) is mediated by unknown mechanisms, but landing is elicited by a specific plant hue (Renwick & Radke 1988). Plant odor, and leaf size and shape are not important. Alightment by *Delia radicum* (L.) (Diptera: Anthomyiidae) is also influenced primarily by plant hue, at least within patches of closely spaced plants (Prokopy *et al.* 1983a). Todd *et al.* (1990b) reported a highly specific response by host-seeking *Dalbulus maidis* (DeLong and Wolcott) (Homoptera: Cicadellidae) to reflected light within a narrow wavelength band around 560 nm. Response was reduced by more than half at wavelengths of 500 and 580 nm.

In addition to color, structure or shape of the resource can also provide important visual cues. Several tephritid species including *Anastrepha fraterculus* (Wiedemann) (Cytrynowicz *et al.* 1982), *Ceratitis capitata* (Wiedemann) (Nakagawa *et al.* 1978), and *R. pomonella* (Walsh) (Prokopy 1968, Prokopy *et al.* 1973, Moericke *et al.* 1975) preferentially respond to fruit and foliage mimics of various sizes and shapes. Response to specific shapes can be enhanced by increasing contrast against background (Owens and Prokopy 1984, 1986, Allen and Stoffolano 1986).

Visual Discrimination Of Distance

Experimental demonstration of the maximum distance of insect visual response to resources is sparse. Two formicid (Hymenoptera) species for which visual discrimination of distant resources has been studied are apparently not able to judge absolute distance to objects of variable size solely by visual cues (*Myrmecia gulosa* F., Via 1977; *Cataglyphis bicolor* , Wehner 1981, 1987). It is likely that they possess specific limited abilities to process critical stimuli, such as determining when a prey object of "expected" size is within striking range. Their compound eyes contain localized arrays of ommatidia or "visual streaks" which focus on a visual field at a set distance on the horizon. Stimulation of a specific number of these ommatidia, directly related to the size of the object entering the visual field, triggers the appropriate response (Via 1977, Wehner 1981, 1987, Schiff *et al.* 1985).

Distance to stationary objects further than a few centimeters from an insect may be judged by motion parallax. In this process, the insect moves its head from side to side and nearby objects appear to move more rapidly than faraway objects (Collett 1978, Eriksson 1980, Goulet *et al.* 1981, Wehner 1981). True binocular triangulation of size and distance is possible only at distances of a few centimeters at most.

In laboratory tests in an artificial arena and in field experiments within host trees, Roitberg (1985) measured distance of AMF response to a 6 cm dia. cluster of host fruit. The resulting reactive envelope wherein ca. 50% of flies responded to fruit, was assymetrical, reaching a maximum of 16-22 cm directly in front of the fly and decreasing as the eye to fruit cluster angle increased. Although odor was not eliminated as a possible influence on fly response, later work (Aluja-Schunemann 1989, Aluja *et al.* 1989) suggests that visual cues predominate under conditions of plentiful and readily apparent fruit.

Sources Of Variability In Response To Visual Cues

Comprehensively reviewed in Prokopy and Owens (1983), insect visual detection of resources is a function of a combination of environmental variables including the spectrum and intensity of natural illumination, contrast against background, and resource size, form, and spectral characteristics of reflected light. Inherent biological factors such as the sensitivity of ocular receptors to a limited range of wavelengths of light, the size of the eye and of the visual field, and the arrangement of ommatidia also determine insect visual ability (Wehner 1981, Wehner and Srinivasan 1984, Wehner 1987). An insect may be able to enhance its perception of a host resource by eye movement, and by controlling its precise position within the habitat, such as its angle of approach. Finally, variable physiological factors such as age (Campan and Gautier 1975), mating status, and degree of satiation may influence insect visual ability and receptivity.

In the following experiments reported in this dissertation, visual cues were standardized by using artificial host trees of consistent size and shape, closely mimicing spectral characteristics of real trees, and against a uniform background. Experiments were conducted in the field under naturally varying levels of illumination, temperature, humidity and wind speed. Experimental animals were of uniform age, sex, and mating status, and were pre-tested for propensity to oviposit by being offered a host fruit immediately prior to testing. Individuals which rejected this fruit were not used in the experiments.

Olfactory Response

Mechanisms

While many issues regarding odor movement and variables influencing response have received attention in sex pheromone communication, most have yet to be as fully addressed with regard to host odors. Characteristics of host odors and insect herbivore or predator/parasite response to host odors may be markedly different than sex pheromone cues and responses to mates (Cardé 1986). Evolution has probably favored rapid, accurate response to the presence of sex pheromone, as the first male arriving at a calling female may have the highest probability of mating and reproducing. Response to host odors may not suffer the same time constraints: host odors are typically present over a longer period, and hosts may not be limited to use by the first arriver. Differences in the sizes and spatial distribution between sex pheromone sources and host odor sources may also be important factors in the evolution of response mechanisms to these two types of resources.

Arrival of males at a calling female is typically accomplished by odor-mediated, optomotor anemotaxis during flight. Males respond to pheromone stimulation by taking flight, and in flight by moving in an upwind direction in a pattern of self-steered counterturns or zigzags, coupled with an optomotor response to wind-induced drift, and concentration-modulated changes in course angle and airspeed (Baker 1986, Baker and Haynes 1987, 1989). Flight direction, speed and height are maintained by reference to visual image flow across specialized regions of the compound eye (David 1986). This description of the typical moth mate-finding process represents years of experimentation, reevaluation, and debate (reviewed in Farkas and Shorey 1974, Roelofs and Cardé 1977, Kennedy 1983, Murlis *et al.* 1992).

This typical pattern, however, is not characteristic of male potato tuberworm moths, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) which reach calling females through a series of short flights or hops less than 1 m in length (Ono and Ito 1989), suggesting mechano-anemotaxis. In this process, wind direction is determined by mechanoreceptor input while the odor-stimulated insect is on the ground. Orientation of several dipteran species to host odor is also by mechano-anemotaxis and short flights, or an "aim then shoot" strategy (Hawkes and Coaker 1976, Dindonis and Miller 1980, Aluja-Schunemann 1989, Brady *et al.* 1990). Upon landing, the fly may wait for odor stimulation and then immediately take off in an upwind direction. A combination of mechano-anemotaxis and optomotor anemotaxis has also been observed in dipterans (Nottingham and Coaker 1985, 1987, Nottingham 1988, Gibson and Brady 1988). Optomotor anemotaxis in response to an oviposition attractant is suggested by preliminary experiments with female *Culex quinquefasciatus* Say (Diptera: Culicidae) (Pile *et al.* 1991).

Only one study to date has directly compared the response of males to female pheromone, and that of females of the same species, *Amyelois transitella* (Walker) (Lepidoptera: Pyralidae), to host odor (almond oil) (Haynes and Baker 1989). Results indicate gross similarity of upwind flight parameters of both sexes, with no evidence of zigzag flight by either sex.

Direct chemo-orientation to chemical stimuli in still air has been demonstrated over a distance of 16-18 cm by walking *Ips paraconfusus* Lanier (Coleoptera: Scolytidae) (Akers 1989, Akers and Wood 1989) and by *Trogoderma variable* Ballion (Coleoptera: Dermestidae) (Tobin and Bell 1986) in an artificial pheromone corridor.

Extrinsic Sources Of Variability In Response To Odor Cues

Unlike photons, odor molecules travel at a rate primarily dependent upon wind-caused air movement. External environmental factors such as wind speed (Nottingham 1987a, Salom and McLean 1991, Brady *et al.* 1990) and directional consistency, temperature (Linn *et al.* 1987), humidity (Nottingham 1987a), topography and ground cover (Wallbank and Wheatley 1979) can all profoundly influence movement of odor molecules from the source, and/or insect response (Aylor *et al.* 1976, Cardé 1984; Elkinton and Cardé 1984, Perry and Wall 1986, Visser 1986, Elkinton *et al.* 1987, Judd and Borden 1988, Murlis *et al.* 1992). Prolonged exposure to low relative humidity can decrease the receptivity of contact chemoreceptor cells (Stadler *et al.* 1987), and could conceivably affect other olfactory receptors.

While an odor gradient may exist within millimeters or at most a few centimeters of a source, it disappears beyond this distance

(Murlis *et al.* 1992). An insect at a distance downwind from the source is exposed to intermittent contact with varying concentrations of odor carried in a discontinuous plume whose size and shape varies widely depending on the degree of turbulence. Turbulence is determined by wind speed, temperature gradients, and habitat vegetation.

Response to odor can also be affected by factors associated with the cue itself. These factors include: release pattern (pulsed vs. continuous, Willis and Baker 1984, Baker *et al.* 1985; diffuse vs. discrete plume, Nottingham and Coaker 1985, 1987), release rates (Baker and Roelofs 1981, Dindonis and Miller 1981, Reissig *et al.* 1982, Tilden *et al.* 1983, Dickens 1986, Charlton *et al.* 1992, Linn *et al.* 1987, Baker and Haynes 1989, Leonhardt *et al.* 1990), ratio of component compounds (Linn *et al.* 1987, Willis and Baker 1988), presence of non-resource odors (Thiery and Visser 1986, Nottingham 1987b), and height of the source (Cuthbert and Peacock 1975, Ono and Ito 1989).

A pulsed pattern of release may result in a greater distance of response than continuous release of the same amount of odor stimulus, assuming that an insect needs only a momentary exposure to concentrations of odor molecules above threshold to respond (Dusenbery 1989). The directional consistency of wind and pheromone puffs over short periods of time may be more important than linearity of the trajectories of the individual puffs (Elkinton *et al.* 1987). Higher release rates of odor molecules may result in a greater distance of response (Baker and Haynes 1989), but may not increase the number of individuals arriving at the source due to inconsistent directionality and cohesiveness of the plume at long distances (Elkinton *et al.* 1987), and/or because of the deterrent effect of high concentrations closer to the source (Baker and Roelofs 1981, Dickens 1986, Charlton *et al.* 1992).

Interactions between different types of odors can influence response. Green leaf volatiles enhance response of boll weevils *Anthonomus grandis* Boh. (Coleoptera: Curculionidae) to aggregation pheromone (Dickens 1989), while host volatiles synergize response to pheromone of dried fruit beetle *Carpophils hemipterus* (L.) (Coleoptera: Nitidulidae) (Dowd and Bartelt 1991). Microbial products from decomposition of host and non-host material play a role in *Delia antiqua* host location and acceptance (Hausmann and Miller 1989), and may be feeding and sex attractants to female and male *Dacus* spp. (Drew 1987). Non-host odors hinder location of hosts in *Psila rosae* F. (Diptera: Psilidae) (Nottingham 1987b), and Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) (Thiery and Visser 1986).

Insect density can also influence response to resources. The foraging behavior of gypsy moth males is typically by optomotor anemotaxis. In high density populations, many matings occur prior to calling by the female, apparently a result of random search by males of tree trunks (Cardé and Hagaman 1984).

An insect may undertake active behaviors to increase the probability of encounter with odor cues. The question of whether downwind, upwind or crosswind flight is optimal for insects foraging for an odor plume is a matter of some controversy (Sabelis and Schippers 1984, Dusenbery 1989, 1990, Murlis *et al.* 1992).

Intrinsic Sources of Variability In Response To Odor Cues

Internal sources of variability both between individuals and in the same individual at different times include experience, genetic and maternal effects, degree of satiation or deprivation, sex, mating status and temporal and age related parameters (Klowden and Lea 1979, Papaj and Rausher 1983, Prokopy 1986, Landolt and Heath 1988, Roitberg 1990, Bell 1990). Endogenous periodicity in male response to female-emitted pheromone has been demonstrated repeatedly (reviewed in Cardé and Webster 1981).

A well-developed picture of individual variation in bark beetle response to pheromone and host odor cues is reviewed in Borden *et al.* (1986). Prior flight or walking activity, lipid content, weight, or generation and/or season of emergence greatly influence response to pheromone and host-odor cues in species within a number of different scolytid genera.

Reproductive maturity is apparently a prerequisite for directional response and positive anemotaxis in the onion fly, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae). In fields devoid of host odor, onion flies disperse at random with respect to wind direction. When grass fields are permeated with a component of onion odor, mature virgin flies respond directionally while immature and mated flies do not (Judd and Borden 1988). Mated, gravid *D. radicum* respond to host plant odors, but males and unmated females are unresponsive (Hawkes and Coaker 1976). Similarly, only mated female navel orangeworm, *Amyelois transitella* Walker (Lepidoptera: Pyralidae), respond to almond odors (Phelan *et al.* 1991). Oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae) males increase in responsiveness to methyl eugenol as they approach sexual maturity (Wong *et al.* 1989). Initiation of foraging behavior in honey bees, *Apis mellifera* L. (Hymenoptera: Apidae) is also age-dependent and can be manipulated by topical, oral or injection application of juvenile hormone (Robinson and Ratnieks 1987).

Sustained flight response to host cues of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) depends upon prior exposure to components and combinations of components of the plant-host complex including damaged leaves, host larvae and larval feces (Drost *et al.* 1986). Experience also influences response of *Trichogramma maidis* Pint. et Voeg. (Hymenoptera: Trichogrammatidae) (Kaiser *et al.* 1989) to a mixture of host and plant odors. Individual *M. croceipes* may inherit differential responsiveness to airborne allelochemicals (Prevost and Lewis 1990). The heritable variation of pink bollworm *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) response to pheromone is sufficiently high to suggest the potential for rapid selection under pressure from mating disruptants used for control of this pest (Collins and Cardé 1989a).

Degree of starvation of desert locusts *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae) influences response to grass odor

(Kennedy and Moorhouse 1969). Sex, age and degree of starvation of *Leptinotarsa decemlineata* alter responsiveness to host odor (reviewed in Mitchell 1988).

It is important that studies of long-distance resource detection attempt to anticipate and standardize or otherwise treat these sources of variation in a conscious, formal manner to insure repeatable results. In the following studies reported in this dissertation, odor cues were standardized by using artificial host odor released at a known, constant rate, with and without visual stimuli present. Variable wind speed, temperature and humidity were measured and considered in the analysis and interpretation.

Interaction Between Visual And Olfactory Cues

Early speculation that different cues played distinct roles in separate phases of the mate/host location and acceptance process has been countered by subsequent demonstration of the importance of the entire menu of resource characteristics acting as a whole to elicit optimum response in some systems (Linn *et al.* 1987, Sweeney *et al.* 1990, Harris and Miller 1991). Similarly, visual and olfactory modalities have been discussed as playing distinct roles in short vs. long range resource detection. Yet examples exist of all possible combinations of cues acting at all levels of resource foraging. Most studies directly addressing the interaction between visual and odor cues make no effort to determine distances at which these interactions occur, nor to define the boundaries at which a change in modality might be made.

Visual cues not associated with the resource operate in optomotor control of odor-initiated upwind flight. These visual cues are not limited to image formation and horizontal orientation, but can include light discrimination and vertical orientation, and possibly involve receptors other than compound eyes (Choudhury and Kennedy 1980). Visual optomotor response can be turned off by the loss of odor stimulation, or by contact with inhibitory chemicals (Preiss and Kramer 1983).

As demonstrated in a recent review of host finding by moths (Ramaswamy 1988), little attention has been paid to the complex of modalities and mechanisms of host and host habitat recognition and location in this group. The few examples cited, however, support the role of vision and/or olfaction in both long and short range host location behavior.

Male gypsy moths *Lymantria dispar* L. (Lepidoptera: Lymantriidae) respond to female sex pheromone by upwind flight, orienting to and alighting on the vertical silhouette of the tree bole from which the pheromone is released, and commencing a zig-zag crawling pattern to contact the female. Despite a high degree of apparency of female visual cues, these cues did not influence the landing site of the male, nor the speed and path linearity with which males arrived at the pheromone source (Charlton and Cardé 1990). Even when extremely short distances (< 5 cm) separated the stimuli, males oriented to the pheromone source alone rather than to female visual cues alone.

The converse occurs with tsetse fly (*Glossina* spp., Diptera: Glossinidae). Flies responding to host odor cues are diverted away from the odor source by visual host mimics placed 1.5 m from the odor source (Torr 1989). The presence of host odor increases the number of flights per minute and rate of alightment on visual models (Warnes 1989).

Dalbulus maidis response to green light is synergized by maize odor over a distance of at least 26 cm (Todd *et al.* 1990a). Alfalfa seed chalcids (Hymenoptera: Eurytomidae) apparently lose their ability to locate host-plant-odor baited targets when deprived of polarized sky light (Kamm 1990). Host color, shape, size and odor all significantly influenced acceptance of host surrogates by *Delia antiqua* , and act in a synergistic manner to elicit oviposition (Harris and Miller 1982, 1983, 1984). Host odor influences each step in the sequence of behaviors from alightment through oviposition (Harris and Miller 1991). The combination of host odor and a vertical silhouette greatly enhance response of black cutworm larvae, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) to traps in the field (Whitford and Showers 1984).

The southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae), may land at random on vertical objects, including host trees (Payne 1986). Whether or not the beetle remains depends on the quantity of host odor encountered upon landing. Once attack is initiated, the beetle releases pheromone which in addition to host odors from the freshly wounded tree, stimulates other individuals to join in the attack. Variations on this theme, including beetle attraction from a distance to hosts possessing particular odor profiles, have been demonstrated or proposed for several other bark beetle species (Borden *et al.* 1986).

The spatial distribution of host plants can influence the interaction between visual and olfactory cues. With artificial plants spaced 100 cm apart, twice as many *Delia radicum* landed on odor-baited plants as on unbaited plants (Prokopy *et al.* 1983b). This difference disappeared when plants were 25 cm apart. These results suggest that flies may choose the most visually stimulating plant for alightment when faced with an odor source emanating from an array of closely spaced plants.

While dissection of the resource seeking process into visual and olfactory components is often experimentally possible and desirable in interaction studies, a complete response can only be determined by integration of the typical blend of cues found in nature into the experimental design. Sources of variability must be recognized and can often be controlled experimentally, but the true, full picture of response measures these variables and their effects on response over the range of variability experienced in nature.

Determining Distance Of Detection Of Resource Cues

Despite the emergence of foraging behavior as an important area of research, little information is available about the maximum distance insects are able to detect resources. This lack of information may be due at least in part to the difficulty in identifying when an insect actually begins to perceive the resource cue that results in eventual arrival at the resource. Small, free-ranging, fast-moving insects can be extremely difficult if not impossible to follow for any length of time. Attempts to confine such animals to restricted areas which permit easy observation risk altering their behavior in such a way as to invalidate the results obtained, and limits the distance over which behaviors can be observed.

Even in the case of a distinct, observable response such as wing fanning by male moths in the presence of pheromone, the complexity of the question of maximum distance of response to odor cues defies easy demonstration. An above-threshold dose of odor molecules may elicit a response at whatever distance from the source this dose is encountered. The maximum distance of detection may then be the maximum distance over which this dose can be delivered. The question which naturally follows may then be with what frequency and directional consistency does this dose have to be encountered to promote eventual arrival at the source? Simply because an odor stimulus is detectable at a distance downwind of the source does not insure that an insect can successfully navigate to the source of that stimulus.

In addition to the myriad environmental, biological and physiological state parameters influencing foraging behavior, variation associated with the resource cue can be an obstacle to success. It is often difficult to identify the precise resource cue which elicits a response and to standardize cue quality and quantity over a number of replicates and experiments. Researchers have turned to use of artificial, limited components of the resource cue to overcome this obstacle, unfortunately often resulting in misleading results (Linn *et al.* 1987). Especially with odor cues, it can be difficult to pinpoint the location of the odor stimulus at any distance downwind from the source.

Most theoretical predictions of the distribution of above-threshold concentrations of odor molecules (i. e. size of the "active space" of the odor stimulus) have used Gaussian plume models which average odor concentrations over some interval of time (Sower *et al.* 1973, Shapas and Burkholder 1978, Stanley *et al.* 1985). These models have failed validation tests because above-threshold instantaneous odor concentrations persist at greater distances than those predicted for time-averaged, above-threshold concentrations (Elkinton and Cardé 1984, Elkinton *et al.* 1984). Mathematical expression of instantaneous concentrations of odor molecules have not yet proven accurate or very useful (Murlis *et al.* 1992). Practical solutions such as approximating plume location with smoke (Baker and Roelofs 1981, Brady *et al.* 1990), bubbles (Linn *et al.* 1987, 1988), or unipolar ions (Murlis and Jones 1981) have better served studies of maximum response distance.

Direct Assessment Of Maximum Distance Of Response

Despite these difficulties, direct determination of at least distance of detection if not distance of successful response (=arrival at the source) has been achieved in several studies. One method has been to observe flight of caged insects in response to a resource or resource cues placed at a distance upwind of the cage. Hawkes (1974) found that a higher proportion of caged gravid female cabbage root fly, *Delia radicum* flew to the upwind side of the cage when brassica plants were 1-15 m away than when plants were more distant or when no plants were present. A subsequent experiment provided evidence that cabbage root flies fly upwind irrespective of the presence or absence of host odor (Finch and Skinner 1982), but this report has been contradicted by several more recent studies (Nottingham and Coaker 1987, Nottingham 1987a, 1988, Banks *et al.* 1988).

Exposure of caged, female Mexican fruit flies, *Anastrepha ludens* (Loew) (Diptera: Tephritidae) to 100 male-equivalents of pheromone in an indoor hallway resulted in increased flight activity and upwind movement to a maximum distance of 8 m (Robacker and Moreno 1988). A lesser distance of response was observed at lower pheromone concentrations.

Eisemann (1988) measured response of caged blowflies, *Lucilia cuprina* (Weidemann) (Diptera: Calliphoridae) to sheep and found that significantly more flies responded to a caged flystruck sheep at 20 m downwind, and to a caged unstruck sheep at 10 m than to an empty control cage.

Males of many moth species wing fan when they encounter an above-threshold dose of pheromone, providing a clear demonstration of odor detection (Baker and Roelofs 1981, Elkinton *et al.* 1984, 1987, Linn *et al.* 1987, Collins and Cardé 1989b). To determine maximum response distance, a pheromone source has been provided upwind of male moths held in stationary cages at several distances from the source (Elkinton *et al.* 1987), or in cages carried upwind along the pheromone plume (Baker and Roelofs 1981, Linn *et al.* 1987, 1991). Oriental fruit moths, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae) respond to a three-component pheromone blend at different distances downwind of the source depending upon release rate, with a ten-fold increase in rate resulting in ca. doubling of response distance to a maximum of ca. 80 m at 1000 µg per septum (Baker and Roelofs 1981). *Grapholita molesta* males responded to the same blend at 60 m (100 µg/septum) when temperatures were within 25-28° C, but responded only at shorter distances (5-30 m) to incomplete blends, single components, or at lower temperatures (19-21° C). *Lymantria dispar* respond to pheromone by wing fanning at distances greater than 120 m from the source, but very few arrive at the source from this distance (Elkinton *et al.* 1984, 1987).

As part of what is perhaps the most complete work to date on long distance response of any insect to host plant visual and olfactory cues, sexually mature, virgin female *Delia antiqua* were released in the center of an arena surrounded by dipropyl-disulphide baited traps at 25, 50, or 100 m (Judd 1986, Judd and Borden 1988, 1989). Control releases indicated random takeoff with respect to wind direction. A positive anemotactic response was recorded when the odor sources were located at all three distances, giving the longest distance of response recorded for any insect to host plant odor to date. A positive response was not exhibited by mated female *D. antiqua*, suggesting that in this case, host plant odor may have been used to locate males and mating sites.

An important caveat to this work is that Judd used flies from a 10 yr old lab colony. Results may not be comparable to wild fly response. Significant differences in response of wild flies vs. flies reared under semi-natural conditions vs. flies under continuous laboratory culture have been noted in studies of *D. radicum* distance of response to allylisothiocyanate (Finch and Skinner 1982), *Dacus dorsalis* response to methyl eugenol (Wong *et al.* 1989), and spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) response to sex pheromone (Sweeney and McLean 1990).

Indirect Assessment of Maximum Distance of Response

Several indirect approaches have been suggested for determining distance of response in the absence of a marked behavioral change when an insect is presented with a stimulus. These approaches, including mark-recapture and trap competition studies, yield measurements which may have a positive relationship to distance of response, but do not represent the actual distance at which the response occurred.

Mark-recapture trapping experiments have been used to speculate on distance of response for a number of species with many different attractants and trap types (Maxwell and Parsons 1968, Hawkes 1974, Coyne *et al.* 1987, Wall and Perry 1987,. Mason *et al.* 1990). These studies at most determine a sampling range, or the distance over which an insect may move within a specified amount of time. With this approach, it is not possible to determine the actual distance at which the insect perceived and responded to the stimulus. Perception and response may have occurred, if at all, at any point along the path the insect followed to reach the recapture point.

Mark-recapture data have been fit to random movement models to compare expected arrival at a resource patch with observed arrival of insects released at varying distances from the patch (Banks *et al.* 1988, Harrison 1989). Significantly higher observed arrival has been interpreted as indicative of orientation. This approach is fraught with possibility for error including disturbance of marked insects, incomplete calculation of true arrival, distance-dependent mortality, inaccurate model parameters, and a likely asymmetrical "absorption" zone within which individuals respond to the patch stimuli. This approach cannot determine the distance at which the insect responded to cues provided by the patch and can only offer a rough estimate of the maximum limit of any possible orientation.

The dimensions of the absorption zone are the true representation of distance of response.

Byers *et al.* (1989) have proposed an effective attraction radius (EAR) to represent the average distance of response to attractive traps, computed from the ratio of attractant-baited trap captures to passive (no attractant) trap catches, and the longitudinal cross section (or effective trapping area) of the passive trap. These authors failed to consider possible visual responses to the passive traps, or odor-mediated visual responses to the odor-batied trap. The greatest limitation to this approach in general is that theoretically all insects encountering the passive trap are captured, yet only those insects which are of the appropriate physiological state (age, maturity, degree of deprivation or satiety) to respond to the attractant may be captured by the baited trap. Variable environmental conditions such as wind speed may also influence attractant trap catches disproportionately to passive traps. The ratio may be useful primarily as an index to compare relative distance of attraction between different times, areas, attractants, and insect species.

Cunningham and Couey (1986) developed distance/response curves for *Ceratitis capitata* response to trimedlure. They released marked flies at different distances and directions from a central baited trap. The proportion of flies captured was plotted against distance of release to determine a probability of recapture. From their model, they were able to predict the efficiency of different trap densities used in detection programs, but not actual distance of response.

Trap competition studies have also been used to suggest a range of attraction, by determining the maximum distance between traps at which competition can be detected. Howell (1983) examined competition between traps containing 10 live virgin codling moths, *Cydia pomonella* L. (Lepidoptera: Tortricidae) and blacklight traps. Blacklight traps typically catch more male than female codling moths. When a blacklight trap was surrounded by 8 traps containing virgin females, the ratio changed in favor of females. This competitive effect disappeared when the 8 surrounding virgin female-baited traps were more than 75-91 m from the blacklight trap. Distance of response to the blacklight trap was estimated at 27-40 m from previous tests, leaving an estimated 35 to 64 m drawing range of virgin female baited traps containing 10 females.

A study of *Cydia nigricana* (F.) (Lepidoptera: Tortricidae) indicated competition among traps when placed in a linear array or in a circle around a center trap were 100 m apart (Wall and Perry 1978, 1980, 1987). The authors suggest a range of attraction equal to at least this distance and possibly to 400 m based on these results, anecdotal observations of individual moths, and results of timed mark-recapture experiments. In a similar study using pine beauty moth, *Panolis flammea* (Denis and Schiffermuller) (Lepidoptera: Noctuidae), Bradshaw *et al.* (1989) placed traps releasing pheromone at two different rates in linear arrays with inter-trap distances of 1, 5, 20, 50 and 100 m. Apparent competition or interference by low-dose and high-dose traps disappeared between 20 and 50 m.

Dransfield (1984) suggests a maximum distance of response of 15-20 m for *Glossina pallidipes* Westwood (Diptera: Glossinidae) to biconical visual traps, based on a trap competition study. Dransfield also compared captures of flies in traps placed in an open field at various distances from a forest edge. The capture of flies in these traps was compared to captures expected of flies naturally active in the grassland, and captures expected if no flies were active there (all coming from the woodland, attracted by the trap). This comparison was used to suggest which traps lay within the range of attraction, and which were beyond this range, and corroborated results of the trap competition study. Tsetse flies have also been shown to respond to 0.75 x 0.75 m visual targets from a distance of at least 5 m in a separate study which did not examine responses at greater distances (Torr 1988).

Finally, interception trapping of AMF may provide indirect evidence of distance of response to artificial host fruit odor. Red, spherical traps baited with butyl hexanoate and placed around the perimeter of orchard blocks have been used successfully in small-scale tests (3 acres or less) to intercept AMF entering commercial orchard blocks. These flies originate from unsprayed trees at some distance outside the blocks. Effective control, equivalent to that obtained with pesticide, has been achieved with traps placed 5 m apart in trees around the entire orchard perimeter, but this control breaks down when the inter-trap distance is increased to 10 m (Prokopy *et al.* 1990).

Response of AMF to Host Plant Cues

AMF is a serious pest of commercial apples in North America. Females oviposit into and larvae develop within the fruit. Pupation occurs in the soil. An emerging adult can be faced with a long-range search for oviposition sites if (1) it has emerged some distance from host trees because the fruit within which it completed larval development was carried away from the tree, (2) host trees are not fruiting due to a biennial fruiting habit or lack of fruit set due to frost or other injury, or (3) fruit is already occupied by conspecifics.

A mark-recapture experiment has indicated that AMF may travel at least 1572 m from a release site to apple orchards (Maxwell and Parsons 1968). A dispersal study using radio-labeled AMF indicated that most AMF released within an abandoned orchard were recaptured there, although some flies were recaptured ca. 45 m from the marking site (Neilson 1971).

AMF respond to visual stimuli associated with apple fruit. AMF foraging within a host tree find red spheres more frequently and more rapidly than green or clear spheres of identical size (Aluja-Schunemann 1989). More AMF are trapped on dark-colored spheres than on lighter-colored spheres, or on rectangles, cylinders, or cubes

(Prokopy 1968). Contrast of fruit against background has a substantial effect on fruit apparency, more substantial than fruit hue (Owens and Prokopy 1984, 1986).

AMF have been shown to respond to hue, size, form and orientation of host-tree model silhouettes in field studies (Prokopy *et al.* 1973, Moericke *et al.* 1975). AMF also respond to the spectral reflectance characteristics of host tree foliage both from outside and within host trees (Prokopy 1968, Prokopy *et al.* 1973, Owens 1982, Owens and Prokopy 1986),

AMF respond to certain volatile compounds given off by ripening fruit. In laboratory electro-antennogram and wind tunnel studies, fruit volatiles elicited significant EAG responses, directed upwind movement, and arrival at the odor source (Fein *et al.* 1982, Averill *et al.* 1988). In field trapping assays, 2-5 times more AMF are captured on traps baited with real (Prokopy *et al.* 1973, Reissig 1974) or artificial host fruit odor (Reissig *et al.* 1982, 1985). Under direct observation in a patch of fruitless host trees permeated with artificial host fruit odor, AMF make more upwind flights, leave trees sooner, visit more trees per minute, arrive at the edge of the patch, and leave the patch sooner than when no host fruit odor is present (Aluja and Prokopy 1992). Within a host tree, host fruit odor significantly enhances the ability of AMF to find host fruit only when fruit are present at very low density or when the visual stimulus is weak (e.g. green fruit) (Aluja-Schunemann 1989, Aluja *et al.* 1989).

In the following chapters, I report on the maximum distance of response of female apple maggot flies to host tree visual and odor stimuli. Also examined are several factors which influence this distance, including environmental conditions (wind speed and direction, temperature, relative humidity), and stimulus characteristics (size and color of visual stimuli and release rate of odor stimuli). This project was conducted in as natural a setting as possible, to mimic the processes occurring in nature.

CHAPTER 2

INTERACTION OF VISUAL AND OLFACTORY STIMULI IN DISTANCE OF RESPONSE TO HOST TREE MODELS BY FEMALE APPLE MAGGOT FLIES

Abstract

Mature female apple maggot flies, *Rhagoletis pomonella* (Walsh) were released individually onto a single potted, fruitless hawthorne tree in the center of an open field. This tree was surrounded by four 1 m^2 plywood host tree models painted green or white, with or without synthetic host fruit odor (butyl hexanoate), and placed at one of several distances from the release tree. Each fly was permitted to forage freely on the release tree for up to 1 hour, or until it left the tree. Flies left the tree significantly sooner when green models with host fruit odor were present at 0.5 m, 1.5, or 2.5 m distance from the release tree than when these models were placed at a greater distance (4.5 m) from the release tree or when no models were present. Flies responded detectably to 1m^2 models without odor up to a maximum distance of 1.5 m. These results suggest that female apple maggot flies did not detect green 1m^2 models with odor 4.5 m away or models without odor 2.5 m or more away. Flies responded to white models with and without odor to a much lesser extent, both in terms of response distance and flight to and alightment upon models.

Increasing model size to 2 m^2 increased the distance at which flies responded to green models without odor. Decreasing model size to 0.5 m^2 reduced fly responsiveness to green or white models. The presence of host fruit odor alone, without the visual stimulus of a green model, did not influence residence time on the release tree.

Introduction

Over the past 20 years, intensive study of the foraging behavior of insects for food and water, shelter, mates and oviposition sites has illuminated basic behavioral mechanisms and improved pest management strategies. Information sources, tactics, orientation mechanisms, resource assessment and utilization, individual and environmental variability, and the role of experience have been the dominant topics in basic foraging research (reviewed in Hassell and Southwood 1978, Finch 1980, Papaj and Rausher 1983, Visser 1988, Papaj and Prokopy 1989, Bell 1990). Efforts to describe, model and test foraging strategies maximizing proximal success and reproductive fitness of the forager have demanded a rigorous, comprehensive and quantitative assessment of foraging behavior (Pyke 1984, Stephens and Krebs 1986, Houston *et al.* 1988).

Pest management techniques have benefited from foraging research through proposal and application of efficient trap and attractant combinations (Coli *et al.* 1985, Chenier and Philogene 1989, Leonhardt *et al.* 1990, Salom and McLean 1990, Prokopy *et al.* 1990, Colvin and Gibson 1992), disruptants and deterrents (Bartell 1982, Van Steenwyk and Barnett 1987, Miller and Cowles 1990), aggregants and attractants (Dickens 1989, Gray and Borden 1989, Lewis and Martin 1990), planting schemes designed to foil foraging strategies (Perrin and Phillips 1978, Cromartie 1981, Thiery and Visser 1986, Nottingham 1987b), and resource characteristics artificially altered to disguise quality (Boller *et al.* 1987).

Despite the attention these issues have received, the maximum distance at which resources are detected by foraging insects has remained largely undetermined, except for a very few species. Distance of response to a pheromone source has been demonstrated in convincing fashion for lepidopterans *Lymantria dispar* (Elkinton *et al.* 1987) and *Grapholita molesta* (Baker and Roelofs 1981, Linn *et al.* 1987, 1991), to host odor for dipterans *Lucilia cuprina* (Eisemann 1988), *Delia antiqua* (Judd and Borden 1989), and *Delia radicum* (Hawkes 1974), and to male-produced pheromone for female tephritid *Anastrepha ludens* (Robacker and Moreno 1988).

Most theoretical predictions of the distribution of above-threshold concentrations of odor molecules have used Gaussian plume models which average odor concentrations over some interval of time (Sower *et al.* 1973, Shapas and Burkholder 1978, Stanley *et al.* 1985). These models have failed validation tests because above-threshold instantaneous odor concentrations persist at greater distances than those predicted for time-averaged, above-threshold concentrations (Elkinton and Cardé 1984, Elkinton *et al.* 1984). Mathematical expression of instantaneous concentrations of odor molecules have not yet proven accurate or very useful (Murlis *et al.* 1992).

Speculation about maximum response distance has been generated from absolute density estimates based on trap catches (Howell 1983, Dransfield 1984), survey-trap optimum density analysis (Cunningham and Couey 1986), trap competition experiments (Wall and Perry 1978, 1980, 1987, Tilden *et al.* 1983, Bradshaw *et al.* 1989, Byers *et al.* 1989), mark-recapture dispersal studies (Maxwell and Parsons 1968, Coyne *et al.* 1987, Mason *et al.* 1990, Martinson *et al.* 1989, Harrison 1989), and probability estimates for colonization of new crop plantings (Martinson *et al.* 1988). These studies have yielded measurements which may be positively correlated with distance of response, but do not definitively determine the distance at which response occurred.

The variety of potential mechanisms of detection and response available to insects in locating resources requires examination of multiple modalities to draw meaningful conclusions from foraging studies (Dethier 1947, Kennedy 1978, Bell 1990). Specifically, the interaction of visual and olfactory cues has been reviewed (Prokopy 1986) and reported in subsequent studies (Green 1986, Prokopy *et al.* 1987, Nottingham 1988, Tuttle *et al.* 1988, Torr 1989, Warnes 1989, Charlton and Cardé 1990, Todd *et al.* 1990a). Variable resource and environmental factors affecting stimulus apparency, and external and endogenous influences on insect response, demand careful consideration in experimental design, interpretation and analysis (Mitchell 1988).

Tephritid fruit fly foraging behavior (reviewed in Prokopy and Roitberg 1989, Fletcher and Prokopy 1991) and in particular the behavior of the apple maggot fly, *Rhagoletis pomonella* (Walsh) (= AMF) have been frequent subjects of research (Roitberg *et al.* 1982, Roitberg and Prokopy 1982, 1984, Prokopy and Roitberg 1984, Aluja-Schunemann 1989). The economic importance of this major pest of commercial apple in North America, and the relative ease of rearing and handling individual AMF in both field and laboratory settings have contributed to its popularity as a model organism.

Roitberg and Prokopy (1982) found that foraging AMF departed from host trees sooner when neighboring non-fruiting trees were nearby than when trees were further away or absent. This relationship was used to determine when neighboring trees were beyond the maximum distance of detection, i. e. AMF foraged on a host tree as if no trees were nearby. Visual and olfactory cues, air temperature, relative humidity, and wind speed were examined for influence on the maximum distance of detection of host tree models by mature, host-seeking female AMF.

Materials And Methods

All experiments were conducted during the summer months of 1986, 1987 and 1988 in an open 80 x 200 m field surrounded by non-host trees in Amherst, Massachusetts, USA. Artificial host tree mimics and synthetic host fruit odor were used as test stimuli. This eliminated natural variability in canopy size, structure, and spectral characteristics of reflected and transmitted light of real trees, and in release rate and ratio of component compounds of real host fruit. These aspects vary both between individual trees and host fruit, and within trees and fruit over time, potentially contributing substantial error variation to assays using real trees and fruit (Averill *et al.* 1988).

A fruitless potted hawthorne (*Crataegus mollis* var *toba* , pruned to ca. 1.5 m height, 0.75 m dia. canopy with ca. 125 leaves) was placed in the center of the open field. This tree was surrounded by green or white two-dimensional host tree models, with or without synthetic host fruit odor, at one of several distances from the tree (Figure 1). White models served as a control for any influence of a green model on air movement. Distance to the models was measured from the outer branch tips of the tree canopy. A no-model treatment served as an additional control and consisted of a vertical 1 cm dia. stake with a wire cross-piece at 1.5 m height from which empty or odor-filled vials were suspended.

Tree models were 1 cm thick plywood panels, 0.5, 1, or 2 m^2, painted with a mixture of oil pigments (83% cadmium yellow, 12% Winsor green, and 5% mars black, Winsor and Newton, London) to closely match the spectral reflectance pattern of apple foliage (Owens 1982). The reverse side was painted with a non-UV reflecting white paint (675 White, Kyanize, Everett, Massachusetts). Each panel was perforated with 144, 4-cm-dia. holes per m^2 to approximate light and air penetration through real trees. Panels were nailed vertically to an upright white post mounted on a movable base such that the center of each panel was 1.5 m above ground.

Two clear polyethelene vials (Andler Israel & Son, Boston, Massachusetts) were partially filled with synthetic apple odor, and hung at 1.5 m height at the sides of each model. Odor was released at a rate of ca. 500 ug per hour, equivalent to about 35,000 unripe or

330 ripe McIntosh apples (Carle *et al.* 1987). In 1986, this odor consisted of 6 components of the behaviorally active fraction of the volatile blend given off by apples after harvest (Fein *et al.* 1982, Reissig *et al.* 1985). A subsequent study showed that at least one of these components was not present in apples before harvest (Carle *et al.* 1987). Therefore, after 1986, butyl hexanoate, the major behaviorally-active component of the volatile blend given off by fresh apple and hawthorne fruit, was used alone (Carle *et al.* 1987). Empty vials were used in the no-odor treatments.

Preliminary tests using artificial "smoke" ($TiCl_4$) confirmed that wind moved at least some air across the release tree from vial positions regardless of wind direction. The proportion of time this was so appeared to decline with increasing distance between the models and the release tree.

Test flies were 14-21 day old females, reared from fruit collected in nature and maintained in the laboratory according to methods reported in Roitberg *et al.* (1982). To insure uniformity of fly physiological state as much as possible and thus minimize error variability in test results, all pre-test experience with fruit was standardized. Beginning 48 hours before transport to the field, flies were permitted free access to *C. mollis* fruit for a period of 24 hours. Immediately prior to testing, each fly was assayed for propensity to oviposit (and presumably affirm a host-seeking mode) by being offered a single *C. mollis* fruit. Only those flies which oviposited in these assay fruit were used. Each fly was tested only once. Treatments were replicated an average of 20 times for a total of 800 trials. Tests were conducted between 0800 to 2000 h (Table 1), and the daily sequence of treatments was randomized throughout the course of the experiment.

During test days, flies were maintained with food and water in a shaded spot 40 m from the test arena. To begin a test, a single fly was carefully moved to the release tree while ovipositing in the assay fruit and transferred to a leaf at the lower center of the canopy as soon as oviposition was complete. For each test, 4 models of the same size, color and odor condition were present around the release tree at one of the treatment distances (or no models = control).

Each fly was allowed to move freely within the release tree for up to one hour. During this time, 2 observers tracked its movement, recording number of leaves visited, time elapsed before departure, direction of departure over the first ca. 50 cm after leaving the tree, and whether or not the departing AMF alighted on a model. Wind direction at time of departure was noted by observing wind-caused displacement of a feather suspended from a thread within the tree canopy. Average wind speed was measured with a cup anemometer (Wind-Minder Indicator, Weathermeasure Model W200-SI, Qualimetrics Inc., Sacramento, CA), mounted at 1.5 m height. Temperature and humidity were recorded at the beginning and end of each trial. All data were collected using a Radio Shack 100 portable computer (Tandy Corp., Fort Worth, Texas), and later transferred to a Control Data Corp. Cyber 175/730 mainframe at the University of Massachusetts Computing Center for statistical analyses. Analyses were performed using BMDP (BMDP Statistical Software Inc., Los Angeles).

Because the data were incomplete or censored (i. e. 10.4 % of flies remained on the tree for the full 60 minutes permitted), a survival-type regression analysis was performed using BMDP2L (Dixon 1985). The effects of covariates model color, distance to model, model size, temperature, humidity, and wind speed on residence time on the release tree were fit using a Cox proportional hazards model. Proportions of AMF flying to and landing on the models were compared using logistic regression analysis (BMDPLR). Multiple regression (BMDP1R) analysis was applied to analysis of take-off flight direction when leaving the release tree in relation to wind direction at the time of departure.

Results

Environmental parameters air temperature, relative humidity and wind speed were highly variable (Table 1), and represented the wide range of conditions experienced by foraging AMF in nature. Seventy-three per cent of all tests were conducted after noon.

When no tree models were present, flies remained on the release tree for ca. 31 min, regardless of the presence or absence of synthetic host fruit odor (Figure 2). Flies left the tree significantly sooner when (1) 1 m^2 green models with odor were present at 0.5 m, 1.5 m, or 2.5 m from the release tree, or without odor at 0.5 or 1.5

m, (2) 0.5 m^2 green models with odor were present at 0.5 or 2.5 m, or without odor at 0.5 m, (3) 2 m^2 green models with or without odor were present at 2.5 m, and (4) 1 m^2 white models with or without odor were present at 0.5 m.

Regression analysis indicated that model color and size, the presence of odor, and the distance between models and the release tree were very highly significant covariates influencing residence time on the tree ($P \leq 0.001$, Table 2). Air temperature was highly significant ($P \leq 0.01$), while relative humidity and wind speed were not significant. Interactions between odor and color, and between distance and size were also tested and found to be insignificant. The regression model predicted that an AMF would leave the tree (1) 1.03 times sooner for each 1 degree increase in air temperature, (2) 1.39 times sooner when odor was present than when odor was absent, (3) 1.59 times sooner when green models were present than when white models of the same size were present at the same distance, (4) 1.33 times sooner for each 1 m^2 increase in model size, and (5) 0.80 times sooner (will remain longer) for each 1 m increase in distance between the release tree and the models.

The proportion of AMF landing on models approached 100% when green 1 m^2 models with or without odor were present at 0.5 m, and declined to less than 35% when these models were at 2.5 m distance (Figure 3). Lesser proportions of AMF landed on white models at these distances. Regression analysis indicated that model color, size and distance were very highly significant factors influencing flight to and alightment on models (Table 3). The influence of odor was significant ($P \leq 0.05$).

Wind direction at the time AMF left the tree significantly influenced the direction AMF left the tree ($P \leq 0.001$, Table 4). Model color and distance from the release tree and time of day (pre- or post-noon) were also significant covariates.

The number of leaves visited was significantly positively correlated with residence time on the tree ($r = 0.38$ for 550 observations, $P \leq 0.001$). Total time on the tree, wind speed, relative humidity, and model size were significant or very highly significant covariates affecting number of leaves visited (Table 5).

Discussion

AMF foraging on host trees were apparently unable to detect or respond to neighboring host tree models beyond 2.5 m distance, regardless of size, color, or the presence or absence of synthetic host fruit odor. This is a relatively short distance in comparison to results of other studies of insect response to odor cues alone. Response distance maxima have been reported as at least 100 m for *Delia antiqua* to dipropyl-disulphide baited traps (Judd and Borden 1989), 15 m for *Delia radicum* to brassica plants (Hawkes 1974), 8 m for *Anastrepha ludens* to male produced pheromone (Robacker and Moreno 1988), and 20 m for *Lucilia cuprina* to flystruck sheep (Eisemann 1988). Response of Lepidoptera to pheromone has been demonstrated up to 80 m for *Lymantria dispar* (Elkinton *et al.* 1987) and *Grapholitha molesta* (Baker and Roelofs 1981, Linn *et al.* 1987, 1991).

Results here were remarkably similar to those of Roitberg and Prokopy (1982) who found that AMF foraged on a fruitless host tree for 32 min when no alternate host trees were nearby (vs. 31 min here). They reported a mean within-tree foraging time of 16.4 min when fruitless hosts trees (ca. 2 m tall) were 1.6 m distant (vs. 14.9 min. for 1 m^2 green models with odor at 1.5 m distance here), and 22.1 min when fruitless host trees were 3.2 m distant (vs. 16.6 and 26.7 min for green 1 m^2 models with odor at 2.5 and 4.5 m, respectively, here). Roitberg and Prokopy used real trees for neighboring hosts, and counted time AMF spent actively foraging and not time spent motionless. Here all time on the release tree was counted. They did not consider the influence of host fruit odor on their results, although their experiments were conducted within a fruiting apple orchard with neighboring trees with fruit ca. 15 m distant.

Results here were also similar to those obtained by Aluja and Prokopy (1992) who observed AMF foraging in a patch of real fruitless host trees spaced 0.6 m apart from one canopy edge to the next. They found that on average, AMF left host trees within 5.3 min when odor was present, and 8.8 min when odor was absent (vs. 8.9 min with odor and 11.8 min with no odor associated with 1m models at 0.5 m distance here, Figure 2).

Roitberg and Prokopy (1982) clearly demonstrated that AMF invested less search effort within a tree when alternate foraging sites were nearby. Their results fulfilled a prediction of optimal foraging theory that foragers should remain in a patch longer as travel costs between patches increase (Pyke 1984). Results here indicated that in addition to distance from nearby host trees, search effort is highly dependent on specific characteristics of nearby host trees, including size, color, and the presence of host fruit odor. Differences in these characteristics apparently affected the ability of AMF to detect the host tree models, and may have also imparted information about the potential quality of the nearby host mimic. Differences in perceived quality may account for some of the differences in response observed here. Expected benefits from higher quality resources (e. g. larger size models, fruit odor present) may have counterbalanced costs and risks associated with travel from the release tree.

For nearly all models of the same size, color and odor condition, response was graduated at distances between 0.5 and 2.5 m (Figure 2), not simply one residence time when models were apparent, and a different residence time equal to the no-model control when models were beyond the maximum distance of detection. This graduation may have resulted from individual variation among flies in perceptual ability or responsiveness. Individual variation in various phases of foraging behavior due to genotype, environment, or experience has been demonstrated repeatedly (reviewed in Chapter 1, Papaj and Rausher 1983, Roitberg 1990). By standardizing adult

AMF pre-test environment and experience, these two sources of individual variation were hopefully minimized.

Alternatively or in addition, the relationship between the benefits of remaining within a patch and the cost of travel to nearby patches may have been continuous rather than discrete. Neighboring host tree models of the same type may have presented perceptible levels of difference in travel distance and associated risks and costs, creating or contributing to the graduated response evident here.

Interaction of odor and visual stimuli. In assays here, host fruit odor and host tree visual stimuli acted synergistically. AMF did not respond to green 0.5 m^2 or 1 m^2 models without odor at 2. 5 m distance, nor to odor alone at 1.5 m (no model treatment, Figure 2). However, the combination of odor and 0.5 m^2 or 1 m^2 models at 2.5 m distance elicited a significant response. Synergism between visual and odor cues in response to host plant cues has been reported for another Dipteran, *Delia antiqua* (Harris and Miller 1982), and for a leafhopper, *Dalbulus maidis* (Todd *et al.* 1990a).

The fact that AMF did not detectably respond to host odor in the absence of visual stimuli was an unexpected result. Subsequent work (Chapter 3, Aluja and Prokopy 1992) has indicated that AMF were able to detect and respond to host fruit odor at a much greater distance than found here. Presumably AMF foraging in the presence of the no model + odor treatment were able to detect host fruit odor, but did not exhibit a discernable response. This lack of response clearly demonstrates the limitation of the current work as a definitive assay for distance of host tree stimulus detection. Rather, this set of experiments represented Giving Up Time (GUT) assays for the maximum distance of response of foraging AMF to nearby host tree stimuli. The physiological state of AMF foraging among non-host plants for host cues may be one of heightened sensitivity to host tree stimuli, and detect and respond to such stimuli at a greater distance. Odor cues in particular may be more discernable from a distance than visual cues of host vs. non-host trees.

Other studies have demonstrated that AMF foraging within a patch of fruitless host trees leave trees sooner, reach the edge of the patch sooner, and make more straight flights when host fruit odor is present at the edge of the patch than when odor is absent (Aluja and Prokopy 1992). The fact that host odor did not generate a detectable response in the absence of any visual stimuli here suggested that the costs and risks of travel over large open spaces remained high and outweighed any influence of odor cues indicating the presence of host fruit somewhere in the vicinity.

A factor not considered in the design of experiments here was the distance between odor vials, which varied according to model size and distance from the release tree. Additional experiments (Chapter 3) have shown distance between odor sources surrounding AMF to be critical in determining response distance. In any case, two discrete odor sources per model was not representative of a natural situation where a tree may have several hundred point sources scattered over its entire silhouette, providing a vertically and horizontally diffuse odor plume. Height of odor sources (held constant at 1.5 m here) has been shown to influence response in several studies (Cuthbert and Peacock 1975, Ono and Ito 1989).

Influence of color on response. White models were intended as a control for the effect of green tree models on air movement between the models and the release tree. The significant effect of white 1m^2 models at 0.5 m distance on fly residence time indicated that air movement or some other aspect of the white models did influence AMF foraging behavior, albeit to a much lesser degree than did green models. From most positions within the release tree canopy, the background behind all models was dark (woods or grass). White models perforated with holes (144, 4 cm dia. holes per m^2) may have represented sparsely foliated trees (i. e. the inverse image of green models). Several studies have confirmed the importance of contrast against background in resource location (Owens and Prokopy 1984, Allen and Stoffolano 1986).

Alternatively, perceptible white models may have simply offered a landing and perching site for AMF. The availability of such a perch may have reduced the costs and risks of travel between patches, especially given that AMF do not travel readily across open, grassy areas. In previous studies, numbers of AMF captured on sticky-coated white tree models were ca. 50% of captures on green models (Moericke *et. al.* 1975), roughly comparable to proportions of AMF landing on white vs. green models here (Figure 3). Large white rectangles (1.2 x 2.4 m^2) with apples captured twice as many AMF as white rectangles without apples (Prokopy *et al.* 1973), but only 20% as many as yellow rectangles with apples.

Interaction of Stimulus Size and Distance.The 2 m^2 model at 2.5 m, the 1 m^2 model at 1.5 m, and the 0.5 m^2 model at 0.5 m were selected to occupy an approximately equivalent area in the visual field of AMF foraging within the release tree canopy (Figure 4). AMF responded as if these size/distance combinations were nearly equivalent when green models were used with odor. These size and distance combinations elicited different responses when odor was absent. It is unclear why these disparate results were obtained. The experimental design permitted AMF to view the models from many vantage points within the release tree, including during occasional brief circling or looping flights just outside the canopy diameter. Perhaps as foraging time on the tree increased when odor was absent, AMF were able to obtain more information and judge the size/distance relationship more accurately.

In previous studies, increasing the size of sticky-coated red or yellow rectangles placed in open fields resulted in a proportional increase in the numbers of AMF captured per rectangle, but the numbers of AMF captured per cm^2 decreased with increasing size of yellow but not red rectangles (Moericke *et al.* 1975). Increases in ox-mimic size resulted in much greater than proportional increases in response by tsetse flies (Hargrove 1980b). An increase, not always proportional, in AMF alighting on models with increasing model size was noted here for green models with odor at 0.5, 1.5 and 2.5 m distance, and without odor at 0.5 and 1.5 m (Figure 3).

Alightment on Tree Models. The proportion of flies landing on models after leaving the release tree did not give accurate information about the distance of detection of the model, because no information was available as to whether the fly detected the model while on the release tree or sometime after leaving it. The substantial proportion of AMF alighting on white models (though much less than for green models, Figure 3), and the significant influence of 1 m^2 white models at 0.5 m distance on residence time (Figure 2), support the possibility that white models may have at least provided intermediate perching sites for AMF if in fact they did not elicit a response due to a resemblance to sparsely foliated trees.

Takeoff Direction and Wind Direction at Time of Departure. In this study, the presence or absence of synthetic host fruit odor did not significantly influence direction of departure from the release tree. These result were in contrast to those obtained in subsequent studies where takeoff direction of AMF from a platform was random in the absence of odor stimuli, but directional in the presence of synthetic host fruit odor (Chapter 3, Aluja and Prokopy 1992). *Glossina* spp. (Bursell 1987), *Lucilia cuprina* (Eisemann 1988), *Delia antiqua* (Judd and Borden 1988), *Psila rosae* (Nottingham 1987b) and *D. radicum* (Hawkes 1974, Nottingham and Coaker 1987) also made more upwind flights in the presence than in the absence of host odors.

Results here were more influenced by other variables. The position of the sun in the morning vs. the afternoon (75% of tests were conducted after noon) may have created more or less apparent silhouettes for certain model positions. The fact that model color, distance to models, and time of day had a greater impact on departure direction than did wind direction (Table 4) suggested that this may have been the case. Significant deviation from odor-mediated upwind flight in the presence of visual targets at different distances and orientations has been demonstrated for tsetse flies (Torr 1989, Gibson *et al.* 1991).

Effect of Wind Speed, Temperature, and Relative Humidity. It was surprising that wind speed was not a significant determinant of departure time from the tree, especially given the wide range and sometimes very high wind speeds experienced over the course of this study (Table 1). AMF were often observed crouching low on leaf surfaces during wind gusts, and increasing wind speeds resulted in significantly fewer leaf visits (Table 5). It was expected that this "down time" would be reflected in higher residence times for trials during high winds. This finding may have represented (1) continued assessment of the release tree and surroundings by AMF during wind-caused "down time", (2) an internal, fixed-time GUT clock (Roitberg and Prokopy 1984, Prokopy and Roitberg 1989), set upon release on the tree and continuing to run during this time, or (3) GUT set by an energy expenditure clock rather than a fixed-time clock and continuing expenditure of energy during this "down time" to maintain position during strong wind gusts, or possibly greater energy expenditure per unit time when foraging under higher wind speed conditions. High wind speeds significantly slowed rate of departure of alate aphids from host plants in the field or from artificial substrates or host plants in the laboratory (Walters and Dixon 1984, Bottenberg and Irwin 1991). Departure was delayed but not prevented at wind speeds as high as 10 m s^{-1}.

The significant effect of increasing temperatures, reducing residence time (Table 2), was in agreement with non-significant trends reported for AMF by Roitberg and Prokopy (1984). However, temperature was not significantly correlated with foraging speed measured in number of leaves visited per second (r= .00791, NS), nor was temperature a significant influence on the total number of leaves visited (Table 5). Temperature may have (1) increased foraging rates and/or energy expenditure in a way undetected by this assay and so speeded up the GUT clock, (2) acted in some other way to increase perception of surrounding host tree stimuli, or (3) caused AMF to leave the release tree sooner to seek shelter and cooler temperatures. Studies of other systems have provided evidence that one or more of these possibilities may have occurred. Tsetse fly wing beat frequency increased with increasing temperatures from 20 to 32 ^{o}C (Hargrove 1980a), and a bimodal behavioral response resulted. With increasing temperatures, a greater proportion of flies became active, but duration of flights decreased due to more rapid oxidation of metabolite reserves. Oriental fruit moth males responded to an equivalent release rate of pheromone blend at twice the distance when temperatures were 25-28 ^{o}C vs. 19-21 ^{o}C, and male specificity of response increased at the lower temperature range (Linn *et al.* 1987). These authors hypothesized that higher temperatures may have increased release rates of pheromone, increased body temperatures permitting greater levels of sustained flight, and/or altered interactions between chemical stimuli and receptors at the peripheral sensory level, optimizing response spectra or rates of disadaptation.

The small but significant influence of relative humidity on number of leaves visited (coefficient = -0.23, P (F) $\leq$ 0.04) is the first reported evidence of an effect of moderate humidity levels on AMF foraging. The regression model predicted a slight decrease in the number of leaves visited with an increase in humidity. Nottingham (1987a) demonstrated significantly greater than expected trap captures of *Delia radicum* at 65-70% relative humidity, and trap catch increased linearly with increasing humidity.

Dispersal studies have indicated that marked AMF can travel at least 1572 m from a release site to apple orchards (Maxwell and Parsons 1968), and marked AMF have been captured up to 45 m from a release site within an abandoned orchard (Neilson 1971). Although results here in no way rule out directed movement over long distances, especially to odor cues, AMF foraging on host trees exhibit a very limited distance of response (maximum of between 2.5 and 4.5 m) to neighboring host trees of up to 2 m^2 in canopy size.

For AMF, color, size, distance of nearby tree models and the presence or absence of host fruit odor may act alone and/or in combination to affect stimulus apparency, and significantly impact

GUT and alightment decisions in a continuous fashion. Environmental variables temperature, relative humidity, and wind speed and direction also affect AMF behavior in quantifiable ways. In light of these findings, models of AMF foraging may be improved to increase predictability of AMF movements under a broader range of resource and environmental conditions.

CHAPTER 3

DISTANCE OF DETECTION OF SYNTHETIC HOST FRUIT ODOR BY FEMALE APPLE MAGGOT FLIES

Abstract

Distance of detection of a synthetic host fruit odor (butyl hexanoate) by mature, wild-origin, female apple maggot flies, *Rhagoletis pomonella* (Walsh), was assessed by measuring rate of fly movement and within-cage orientation in 3 experiments, and time until take-off and take-off direction in a fourth experiment. Rate of movement and upwind orientation (± 22.5^0) of individually-caged *R. pomonella* flies increased significantly over no-odor conditions in the presence of a stationary point source of butyl hexanoate at a distance of 12 m ($P \leq 0.03$) in an open grassy field, but not at 24 m. Increasing the rate of butyl hexanoate release from ca. 500 ug per hour to ca. 6000 ug per hour did not significantly increase distance of response or proportion of flies responding. .

Take-off direction of *R. pomonella* from a platform in the center of a large open field was random with respect to wind direction when no host odor stimulus was present. Take-off direction was significantly biased upwind (± 67.5^0) when 8 evenly spaced butyl

hexanoate-filled vials surrounded the release platform in a circle with a radius 6 m ($P \leq 0.03$), and downwind (± 67.5°) when the same number of vials encircled the platform at 12 m ($P \leq 0.01$). Similarly, take-off direction tended towards upwind when 16 evenly spaced butyl hexanoate-filled vials surrounded *R. pomonella* at a distance of 12 m ($P \leq 0.10$), and was significantly biased downwind at 24 m ($P \leq 0.01$). Time between emerging from a release jar and take-off was significantly longer when *R. pomonella* were surrounded by the treatments which elicited downwind flight than when no butyl hexanoate was present or when treatments which elicited upwind flight were present.

These results suggest that *R. pomonella* flies use mechano-anemotaxis to orient towards sources of host fruit odor, and are the first indication that *R. pomonella* may fly downwind when stimulated by directionally non-specific, low amounts of butyl hexanoate. Air temperatures and wind speeds typically experienced by AMF in nature significantly influenced rate of movement ($P \leq 0.006$). Relative humidity influenced rate of movement in one experiment and upwind orientation in another ($P \leq 0.003$).

Introduction

Insects following odor cues to distant resources have developed a following of their own, as evidenced by the frequency of reviews and theoretical examinations on this topic over the past 20 years (Farkas and Shorey 1974, Kennedy 1977, 1986, Finch 1980, Murlis and Jones 1981, Bell and Tobin 1982, David *et al.* 1982, Bell 1984, Cardé 1984, Sabelis and Schippers 1984, Visser 1986, Murlis *et al.* 1992). The strongest attraction in both basic and applied insect olfaction research appears to have been towards male response to female-produced pheromone in the Lepidoptera (reviewed in Roelofs and Cardé 1977, Cardé and Webster 1981, Bartell 1982, Kennedy 1983, Baker 1986, Perry and Wall 1986, Ramaswamy 1988, Ridgway *et. al.* 1990). Research on insect response to distant host odor sources has been less frequent (reviewed in Finch 1980, Visser 1986). Much of what has been learned has been gained from studies of Coleoptera (Borden *et al.* 1986, Dickens 1986, 1989, Jermy *et al.* 1988, Mitchell 1988, Chenier and Philogene 1989, Dowd and Bartelt 1991), Lepidoptera (Landolt 1989, Tingle *et al.* 1989, Phelan *et al.* 1991, Mitchell *et al.* 1991), and Diptera to both animal (Colvin and Gibson 1992) and plant host cues (Nottingham 1988, Judd and Borden 1989, Prokopy and Roitberg 1989, Fletcher and Prokopy 1991).

Issues pursued in the study of olfactory detection of distant resources include the size, shape and behavior of the signal plume (Murlis *et al.* 1992), influence of stimulus, environmental, and physiological state variables on odor movement and insect response

(Baker and Haynes 1987, 1989, Brady *et al.* 1990), mechanisms of detection and response on the organism and receptor cell level (Cardé 1986, Bell 1990), the interaction of odor cues with other stimuli (Prokopy 1986, Aluja-Schunemann 1989, Judd 1986), and applications to pest management (Bartell 1982, Gray and Borden 1989, Lewis and Martin 1990, Prokopy *et al.* 1990, Colvin and Gibson 1992). Proposed optimal strategies for insects locating and following odor plumes have generated some controversy, which still awaits full resolution (Sabelis and Schippers 1984, Dusenbery 1989, 1990, Murlis *et al.* 1992).

The maximum distance of detection of resource odor cues has received comparatively little attention. Convincing evidence of distance of detection maxima has been reported for male lepidopterans *Lymantria dispar* (Elkinton *et al.* 1984, 1987) and *Grapholita molesta* to a pheromone source (Baker and Roelofs 1981, Linn *et al.* 1987, 1991), for dipterans *Lucilia cuprina* (Eisemann 1988), *Delia antiqua* (Judd and Borden 1989), and *D. radicum* to host odor (Hawkes 1974), and for female *Anastrepha ludens* to male-produced pheromone (Robacker and Moreno 1988). Mark-recapture and trap competition studies have yielded measurements which may be positively correlated with distance of detection, but do not definitively determine the distance at which detection occurred (Finch and Skinner 1982, Howell 1983, Dransfield 1984, Wall and Perry 1987, Martinson *et al.* 1989, Harrison 1989, Mason *et al.* 1990).

An above-threshold dose of odor molecules may elicit a detectable response at whatever distance from the source this dose is encountered. The maximum distance of detection may then be the maximum distance over which this dose can be delivered. A second, more difficult question to answer is with what frequency and directional consistency does this dose have to be encountered to promote eventual arrival at the source?

A large part of the challenge in determining distance of detection is to identify when an insect actually begins to perceive a resource cue. Small, free-ranging, fast-moving insects are extremely difficult if not impossible to follow for any length of time or over any distance. Confining such animals to restricted areas to permit easy observation risks confounding results by altering their behavior, and limits the distance over which behaviors can be observed.

Long and short-range behavioral and electroantennogram responses to volatile components of ripening fruit have been reported for a number of tephritids (Metcalf *et al.* 1983, Robacker and Garcia 1990, and references in Prokopy and Roitberg 1989, Fletcher and Prokopy 1991). These studies have described behavioral responses to host fruit chemical cues including changes in rate of movement and flight, oriented movement and flight, sustained progress towards and eventual arrival and/or landing at the source, and feeding at the source.

The apple maggot fly, *Rhagoletis pomonella* (Walsh) (AMF), is a major pest of commercial apples in North America and a model organism for basic research on host race formation, foraging behavior, learning, visual ecology, and female-produced host marking pheromone. A female AMF in nature may be faced with a long-distance search for host trees and fruit beyond the range of visual detection when (a) it has been carried some distance away from a fruiting host as a larva within its fruit of origin, (b) its tree of origin has not fruited due to a biennial habit, frost or disease, (c) fruit in its tree of origin were previously parasitized by conspecifics. AMF have been reported to travel at least 1572 m to host trees (Maxwell and Parsons 1968).

AMF response to host fruit odor has been demonstrated repeatedly. Trap captures of AMF increased due to the presence of real fruit odor (Prokopy *et al.* 1973, Reissig 1974) or synthetic fruit odor (Fein *et al.* 1982, Reissig *et al.* 1982, 1985, Averill *et al.* 1988). EAG and/or wind tunnel flight responses of AMF have been demonstrated to several esters present in ripening or ripe fruit (Fein *et al.* 1982, Averill *et al.* 1988). Within host trees, when the visual stimulus was weak (fruit present at low densities or green), AMF found fruit models more rapidly when host odor was present than when it was absent (Aluja *et al.* 1989). Within a patch of fruitless host trees permeated with synthetic fruit odor, AMF moved faster, left trees sooner, visited more trees per minute, and arrived at the edge of the patch sooner than when synthetic host odor was absent (Aluja and Prokopy 1992). When the same patch was bordered by a single point source of odor, AMF made more upwind flights and arrived at or near the tree harboring the point source with much greater frequency than when no odor was present. Distance of detection of non-fruiting host trees (Roitberg and Prokopy 1982) or host tree models 2-2.5 m in height with or without synthetic host fruit odor (Chapter 1) was limited to 2.5-3 m, and of small fruit clusters to 40 cm (Roitberg 1985).

The objectives of the following study were to develop an assay for detection of host odor by mature, female AMF in the absence of host visual stimuli, determine the maximum distance of detection, and examine the effects of environmental variables and varying amounts of host odor on response.

Materials And Methods

All experiments were conducted at the University of Massachusetts during summer months from June of 1986 (experiment 1) through August of 1989 (experiment 4). Test flies were 14-21 day-old females, reared from fruit collected in nature and maintained according to methods reported in Roitberg *et al.* (1982). Forty-eight hours prior to testing, AMF were permitted free access to *Crataegus mollis* fruit for oviposition, until 24 hours before the test at which time fruit were removed. In experiments 1-3, each test fly was offered a single *C. mollis* fruit immediately prior to and after testing. Only those flies which oviposited in both these fruit were used. This standardized physiological state by affirming that flies were in an oviposition and ideally a host-seeking mode. Experiments 2-4 were designed in response to results of the preceeding experiments. Therefore the rationale behind the designs is more fully reported in the results section.

Experiment 1 was designed to detect changes in rate of movement or orientation by caged AMF in response to synthetic host odor. At one end of an empty, whitewashed, ca. 10 x 20 m greenhouse, a 0.75 m dia. box fan was placed such that the center of the fan was 1 m above ground (Figure 5A). Several thicknesses of white cheesecloth were suspended in front of the fan to obscure any visual stimulus provided by the fan, and to diffuse the air stream emanating from the fan. A polyethelene vial (Andler Israel & Son, Boston, MA), empty (control) or containing the Fein blend (Fein *et al.* 1982) of synthetic host fruit volatiles releasing at ca. 500 ug/hr (equivalent to about 35,000 unripe or 330 ripe McIntosh apples, Carle *et al.* 1987) was hung directly in front of the cheesecloth. Prior to testing, flies were maintained in a shaded location outside the greenhouse.

For each test, a single female AMF was placed in the center of each of two 15 cm dia. spherical wire screen cages, positioned at 1 m height 1, 2 or 3 m downwind of the fan. Treatments were still clean air, moving clean air, or moving odor-filled air at each of the three distances. At 5 s intervals over a period of 20 min, two observers recorded the position of the fly in the cage (divided into 8 sections of equal size) and whether the fly was moving (= displacement of over one body length per second) or stationary.

Temperature and relative humidity (RH) were recorded at the beginning and end of each test. Wind speeds at the cages with the fan on (moving air treatments) were 0.4, 0.2, and 0.125 m s^{-1} at 1, 2, and 3 m from the fan, respectively. Two exhaust fans were run continuously at the far end of the greenhouse to provide ventilation. In between replicates, the greenhouse was fully vented for at least 10 min to clear out BH remaining from the previous treatment.

Experiments 2, 3 and 4 were conducted in an open ca. 300 x 600 m field of short grass. Prior to testing, flies were maintained in a shaded spot 100 m from the test arena. Results of studies available after experiment 1 was completed showed that at least one of the components of the Fein blend was not present in apples before harvest (Carle *et al.* 1987), and that butyl hexanoate (a component of the Fein blend) was the major behaviorally-active component of the volatile blend given off by fresh apple and hawthorne fruit (Averill *et al.* 1988). Butyl hexanoate elicited a similar trap catch to that of the Fein blend in field studies (Averill *et al.* 1988). Therefore, in experiments 2-4, butyl hexanoate was used alone.

The design of experiment 2 provided for continuous or near continuous exposure of flies to odor at distances to 5.5 m under naturally varying wind speeds and directions. A 4-arm horizontal wind vane was constructed with aluminum tubing which rotated freely with the wind such that one arm was maintained upwind of a central cage continuously (Figure 5B). The cylindrical cage, 1 m height x 1 m dia., was constructed with screen side walls and wooden floor and ceiling. One or 12 empty or BH-filled vials were mounted on a 50 x 50 cm wire screen and suspended from the upwind arm at a 1.5, 3.5, or 5.5 m distance from the outer edge of the cage. Screens containing identical numbers of empty vials were suspended at the same distance from the other other 3 arms to control for any visual response to the screens and vials.

At the start of each test, a single AMF was released into the center of the cage and allowed to acclimate for 5 minutes before the treatment screens were put in place. Every 5 s for a total of 15 min, an observer recorded the position of the fly within the cage (divided into 8 wedge-shaped sections), whether the fly was moving or stationary, and the location of the upwind arm relative to the cage (i. e. which cage section faced upwind). Wind speed was measured continuously with a cup anemometer (Wind-Minder Indicator, Weathermeasure Model W200-SI, Qualimetrics Inc., Sacramento, CA). Temperature and RH were recorded at the beginning and end of each test.

The design of experiment 3 permitted testing of response at greater distances than in the preceeding experiments, using a stationary BH source (Figure 5C). At the start of each test, a single AMF was placed in the center of each of two cages identical to the cage used in experiment 2 and allowed to acclimate for 5 min. A screen (1.5 m height x 2 m width) holding 1 or 12 BH-filled vials was then positioned 6, 12 or 24 m upwind of the cages (based on the prevailing wind direction over the previous 15 minutes). The bottoms of both the screen and cages were mounted 0.5 m above ground. Twelve empty vials at 6 m upwind served as a control. Fly behavior and environmental parameters were recorded as in experiment 2.

Finally, in experiment 4, take-off direction of individual flies released from a central platform surrounded by BH-filled vials or no vials (control) was assayed (Figure 5D). Vials were suspended at 1.5 m height from metal stakes arranged in a circular array around the release platform such that regardless of wind direction, odor would have been carried across the platform with a higher frequency than if a single source had been used. The actual frequency would have been largely dependent upon number of and distance to BH-filled vials. Eight stakes and vials were used at 6 or 12 m, 16 at 12 or 24 m, or 24 at 18 m, maintaining a 4.7 or 9.4 m distance between vials along the circumference of the circle.

On the morning of each test day, 10 female AMF were pre-tested as in experiments 1-3 and placed in a 275 ml glass jar fitted with a screen top. At the start of a test, the screen top was replaced with a paper one with a 2.5 cm dia. hole in the center. The jar was then placed on a wooden platform 1.5 m in height in the center of the field. Flies were allowed to emerge from the hole until all 10 had emerged or for a maximum of 15 minutes. Time of emergence from the jar, time and direction of take-off, and wind speed and direction at the platform at time of take-off were recorded for each fly. Take-off direction was defined as the heading within the first 50 cm of flight. Wind speed was measured with a hot-wire anemometer (AVM 502, Prosser Scientific Instruments, Hadleigh UK). Wind direction at time of take off was determined by checking a bird feather wind-vane, mounted horizontally just below the release platform on a vertical wire through its shaft. This feather was very sensitive to directional shifts of even light winds. AMF which emerged from the jar and failed to take-off (< 2%) were not included in the analysis. Temperature and relative humidity were recorded at the beginning and end of each release.

Data from each experiment were recorded on a Radio Shack 100 portable computer (Tandy Corp., Fort Worth, Texas, USA), and later transferred to a Control Data Corp. Cyber 175/730 mainframe at the University of Massachusetts Computing Center. Statistical analyses were performed using BMDP (BMDP Statistical Software Inc., Los Angeles, Dixon 1985). Analysis of variance and covariance (BMDP P2V) and single degree of freedom contrasts for mean separation (BMDP P4V or P7D) were applied to data from experiments 1-4. Direction of take-off (experiment 4) was analyzed using logistic regression (BMDP PLR).

Results

Mean air temperatures, RH, and wind speeds for experiments 2-4 were similar for all 3 experiments, and represent the range of conditions experienced by AMF in nature (Table 6). In all experiments using caged AMF (experiments 1-3), AMF spent nearly all of the time walking along the cage wall, and very little time in flight, although this observation was not quantified.

In experiment 1, a pre-experiment test in which artificial "smoke" ($TiCl_4$) was used in place of host odor indicated that the smoke plume moved in a straight trajectory from the fan to a distance of ca. 2.5 m. Beyond 2.5 m, the plume became greatly diffused and turned upwards and to one side, precluding tests much beyond this distance.

When the Fein blend of synthetic apple odor was present, AMF within the 15 cm dia. cages were moving a significantly greater number of times at all three distances than in still air or moving clean air (Figure 6A, Table 7). Differences in time AMF were in the upwind vs. downwind half of the cages due to treatment were not significant, differences between cages were significant for orientation only (Figure 6B, Table 7). Temperature and RH had no significant effect on movement or position. AMF were in the upper half of the cages during 80.3% (± 1.7% S. E.) of all observations, regardless of treatment.

Experiment 2 was designed to test the possibility that the lack of an orientation response in experiment 1 may have been influenced by cage size, and to test for response at greater distances than possible within the greenhouse. Rate of movement was not influenced significantly by the presence of BH at any distance (Fig. 7A, Table 7). Temperature, RH, and wind speed did have a significant effect on rate of movement. Overall, AMF were observed moving 23.8% of the time, less than the 37.9% for AMF in clean air and 55.8% for AMF in odor-laden air in experiment 1. AMF were observed a significantly greater number of times in the upwind 1/8 of the 1 m height x 1 m dia. cylindrical cage when 1 or 12 BH-filled vials were continuously upwind than when empty vials were used (Figure 7B).

Distance to the vials (1, 3.5, or 5.5 m), number of BH-filled vials (1 vs. 12), temperature, RH and wind speed had no effect on AMF position within the cage (Table 7).

In experiment 2, the visual distraction of wind-caused motion of the screens and cross-arms may have influenced rate of movement of AMF, possibly confounding any effect of treatment. Therefore, both within-cage orientation and rate of movement were assayed in experiment 3 with a stationary odor source. The stationary odor source more closely represented conditions experienced by AMF in nature and permitted testing at greater distances, desirable due to lack of distance effects on orientation in experiment 2.

Differences in both rate of movement and upwind orientation within the cage in the presence vs. absence of BH were detectable and significant to 12 m from the stationary odor source (Figure 8). No significant response to BH was detected at 24 m. Cage effects, cage by treatment interaction, and temperature and wind speed significantly influenced rate of movement (Table 7). Differences in rate of movement due to the number of BH-filled vials (1 vs. 12) were significant for cage 1 only. AMF were moving 19.0% of the time when odor was absent, and 30.3% when 1 vial was present at 6 m, about the same proportionate increase in rate of movement observed in experiment 1.

The effect of RH on time in the 1/8 of the cage facing the odor source was significant ($P \leq 0.001$). Effects of cage, temperature and wind speed were not. The 1/8 of the cage facing the stationary odor source was directly downwind (± 22.5°) of the odor source 60% of the time, or near to downwind (± 67.5°) 87% of the time. The proportion of time that this was so was not a significant determinant of movement, nor of upwind orientation ($P \leq 0.09$).

Finally, experiment 4 was designed to determine if fly response could be found at distances greater than detected in experiment 3 by increasing the probability of odor contacting test flies through spatial arrangement of the odor sources.

Overall, 43% of AMF loaded into the jars left the jar during the 15 minutes allowed for each test. Take-off direction of AMF in relation to wind direction at time of take-off was significantly biased upwind (± 67.5°) when 8 BH-filled vials were present at 6 m (Figure 9), with a non-significant trend ($P \leq 0.10$) towards upwind when 16 vials were present at 12 m. Take-off was significantly biased downwind (± 67.5°) when 8 BH-filled vials were present at 12 m or 16 vials were present at 24 m. The proportion of upwind or downwind take-offs within a narrower range (± 22.5°), comparable to the specificity of within-cage upwind orientation in experiments 2 and 3, was not significantly different among treatments ($P \leq 0.08$ for 8 vials at 6 m). Logistic regression analysis yielded odds ratios for upwind take-off of 1.14 for each additional BH-filled vial used and 0.84 for each 1 m increase in distance to the odor source, over no odor controls (Table 8). The odds ratio of 1.14 means approximately that with every increase in BH-filled vials used, an AMF is 1.14 times more likely to move in an upwind direction. The odds ratio for downwind take-off was 0.91 for each additional BH-filled vial used, and 1.13 for each 1 m increase in distance to the odor sourcerelative to no-odor controls. Take-off direction became progressively less directed upwind as distance to the vials increased, even when the number of vials was increased to maintain a 4.7 m distance between vials (16 at 12 m, or 24 at 18 m).

Time between emergence from the release jar and take-off from the top of the jar was significantly longer when the release jar was surrounded by 8 vials at 12 m ($P \leq 0.003$), 16 vials at 24 m ($P \leq 0.03$), or 24 vials at 18 m ($P \leq 0.001$) vs. time when no odor was present (Figure 9). Time until take-off for 8 vials at 6 m, or 16 vials at 12 m was not significantly different than the no odor control. Temperature and wind speed were significant covariates (Table 7).

Discussion

The significant response to 16 vials of butyl hexanoate at 24 m is the greatest distance of detection of synthetic host fruit volatiles by AMF reported to date, and is the first experimental evidence of downwind flight of AMF in response to low rates of synthetic host odor. This distance of detection compares to distance maxima of at least 100 m for *D. antiqua* to dipropyl-disulphide (DPDS) baited traps (Judd and Borden 1989), 15 m for *D. radicum* to brassica plants (Hawkes 1974), 8 m for *A.ludens* to male produced pheromone (Robacker and Moreno 1988), and 20 m for *L. cuprina* to flystruck sheep (Eisemann 1988). Response of Lepidoptera to pheromone has been demonstrated to 120 m for *L. dispar* (Elkinton *et* *al.* 1984, 1987) and *G. molesta* (Baker and Roelofs 1981, Linn *et al.* 1987, 1991).

Kinetic response. Increased movement of AMF in the presence of synthetic host fruit odor was evident in two settings of this study: in experiment 1, in which the Fein blend was artificially blown past caged AMF continuously at a constant speed and from a constant direction for 20 minutes; and in experiment 3, where naturally varying wind direction and speed provided intermittent odor stimuli to caged AMF over a period of 15 minutes. A greater rate of movement for AMF exposed to synthetic host fruit odor was consistent with results of previous studies which showed an increase in total time spent moving and a greater number of landings per min in a wind tunnel in the presence of the Fein blend (Aluja-Schunemann 1989), and a greater number of trees visited per minute in a patch of fruitless host tress permeated by synthetic host fruit odor (Aluja and Prokopy 1992). These authors suggested that activation may serve to increase the liklihood of response and shorten response time of AMF to odor cues during brief moments of time when wind speed and direction are favorable for response. In the Diptera, activation in response to host odor has been reported for *D. radicum* (Hawkes and Coaker 1976), *Glossina* spp. (Bursell 1984) and to trimedlure for *C. capitata* (Jones *et al.* 1981).

Orientation response. AMF oriented towards the BH source in 3 settings: experiment 2, in which the odor source was always coincident with an upwind direction; experiment 3, in which the odor source was coincident with an upwind direction (±22.5^{o}) 60% of the time or a more broadly defined upwind direction (± 67.5°) 87% of the time; and in experiment 4, when 8 vials were present at 6 m and the odor source was coincident with an upwind direction a variable and undetermined amount of time. Upwind orientation of AMF in response to host fruit odor was consistent with previous wind tunnel and field trapping studies with the Fein blend (Fein *et al.* 1982, Averill *et al.* 1988, Aluja-Schunemann 1989, Aluja and Prokopy 1992), and 5 individual esters including butyl hexanoate (Averill *et al.* 1988).

In all three situations, AMF were assayed for a response generated almost exclusively (experiments 2 and 3) or exclusively (experiment 4) while walking or stationary, providing a strong indication that AMF used mechano-anemotaxis to identify the instantaneous wind direction and orient towards the source of BH. Distances tested here were too great for orientation by monitoring distance-related changes in concentration (Murlis and Jones 1981). Use of mechano-anemotaxis and upwind take-off in the presence of nearby synthetic host odor in experiment 4 support the possibility of an "aim then shoot", or "series of steps" mechanism of host odor source location proposed for AMF by Aluja and Prokopy (1992), for *D. antiqua* by Dindonis and Miller (1980), for *D. floralis* by Havukkala (1987), and for the potato tuberworm moth *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) by Ono and Ito (1989). This hypothesis describes a process whereby a foraging insect lands frequently, turns upwind when stimulated by resource odor, and takes off in that direction. Evidence here in no way rules out use by AMF of anemotaxis in flight in addition to mechano-anemotaxis from a perch, as has been proposed for *D. radicum* (Nottingham and Coaker 1985, 1987, Nottingham 1988) and *Glossina* spp. (Gibson and Brady 1988).

The failure of AMF in small cages (15 cm dia., experiment 1) to orient upwind as was observed within larger cages (1 m dia x 1 m height, experiments 2 and 3) was consistent with observations of *D. radicum* by Hawkes and Coaker (1976). These authors reported an increased rate of movement without upwind orientation by *D. radicum* exposed to host odor in small cages (40 x 30 x 30 cm). Upwind orientation was detected in a large wind tunnel (6 x 2.3 x 1.8 m), and in field experiments using larger, 1 m^3 cages (Hawkes 1974).

Orientation by AMF towards host odor sources demonstrated in this study and in previous studies (Fein *et al.* 1982, Averill *et al.* 1988, Aluja-Schunemann 1989, Aluja and Prokopy 1992) appears to be subject to much greater variability than male moth response to pheromone. In pheromone-response studies, nearly all males exposed to a sufficient concentration exhibit a response (Baker and Roelofs 1981, Elkinton *et. al.* 1984, 1987, Linn *et. al.* 1987, 1991). The limitation of orientation response of AMF to host odor to a smaller proportion of the test populations may reflect different evolutionary pressures on host odor response vs. response to pheromone (Cardé 1986). Evolution has probably favored rapid, accurate response to the presence of sex pheromone, as the first male arriving at a calling female may have the highest probability of mating and reproducing. Host odors are typically present over a longer period, and hosts may not be limited to use by the first arriver.

Random take-off with respect to wind direction when no odor stimulus was present (experiment 4) was consistent with previous results for AMF (Aluja and Prokopy 1992), *D. antiqua* (Judd and Borden 1988), *D. floralis* (Havukkala 1987), and *D. radicum* (Nottingham and Coaker 1985). *Glossina* spp. take-off in a downwind direction in the absence of host odor (Bursell 1987).

A greater frequency of upwind take-offs when AMF were surrounded by a large number of nearby odor sources (8 vials at 6 m) was consistent with results obtained in a field permeated with the Fein blend (24 vials, 1.3 m apart in a 8 x 8 m square array, Aluja and Prokopy 1992). The decline in upwind take-offs beyond 6 m was in contrast to response of *D. antiqua*, which maintain upwind take-off when surrounded by 8 dipropyl-disulphide (≥0.01 concentration) sources at 25, 50 or 100 m.

Downwind take-off in the presence of lesser numbers of vials indicates AMF may use a plume-location strategy suggested as optimum for insects under variable wind-direction conditions by Sabelis and Schippers (1984, but see Murlis *et al.* 1992). According to these authors, a variation in wind direction of 30° or more will favor downwind searching due to minimization of energy expenditure per unit distance travelled and a higher probability of contact with an odor plume at a location closer to the source. Why AMF took flight in a random direction in the absence of any odor stimulus, and downwind only under conditions of lesser amounts of odor is unknown. A concentration effect on take-off direction has also been noted for *D.antiqua.* which take-off in an upwind direction when surrounded by 0.01 - 10.0 % concentrations of DPDS released from 8 evenly spaced sources, but cross-wind when at a concentration of 0.001%. Development of realistic, comprehensive models of optimum insect behavior for odor plume location has been hindered by a lack of good field evidence (Murlis *et al.* 1992).

Latency Response. The significantly increased time between emergence from the release jar and take-off when exposed to low concentrations of BH in experiment 4 might be termed an arrestment response. It is doubtful that AMF were arrested in the typical sense, that is a decline or cessation of activity and/or change in rate of turning which serves to maintain position within a limited area (Kennedy 1978). Perhaps the delay in departure represents extended processing time, due to insufficient stimulus for a rapid, conclusive response. Increased latencies have also been recorded for male *L. dispar* at lower doses of synthetic pheromone (Cardé and Hagaman 1979).

Dose Response. An increase in response to increasing doses of resource odor has been demonstrated within the range of biologically relevant dosages for a number of insects in several different orders (Dickens 1986, Landolt 1989, Mitchell *et al.* 1991, Phelan *et al.* 1991). Among Diptera, responses to increasing doses of resource odor include a progressive increase in frequency of flights per minute over a 50-fold, 4-step increase in trimedlure concentration for lab-cultured *C. capitata* (Jones *et al.* 1981), an increase in upwind flights over a 50-fold, 3 step increase in number of brassica plants for *D. radicum* (Nottingham and Coaker 1985), a linear increase in log number of flies caught and log weight of livestock attractant for *Glossina* spp. (Hargrove and Vale 1978, Colvin and Gibson 1992), and a non-significant trend towards greater trap captures with a 10,000 fold, 5-step increase in DPDS for *D. antiqua*. (Dindonis and Miller 1981). A leveling off of increases in response has been reported for higher doses of DPDS for *D. antiqua* (Dindonis and Miller 1981). Repellance by higher dosages of host plant compounds have been reported for allyl isothiocyanate in *D. radicum* (Wallbank and Wheatley 1979). EAG, peripheral olfactory receptor neuron, and behavioral responses to increasing concentrations of resource odor plotted for a number of Lepidoptera exhibited common characteristics suggesting that the relationship between dose and these responses may operate under some principles applicable to insects in general (Mayer *et al.* 1987).

Dose-response effects have been reported for AMF and fruit volatiles, including apparent decreases in effects at higher rates. Red spherical traps baited with 50 or 100 mg of Fein blend captured significantly greater numbers of AMF than unbaited spheres or baited spheres with 300 mg of blend (Reissig *et al.* 1982). Information on release rates of these doses was not provided. EAG response by AMF increased steadily with increasing concentrations of propyl hexanoate, a behaviorally-active ester found in the headspace of host fruit and a component of the Fein blend (serial dilutions from 10^3 to 10^{-3} ug, Averill *et al.* 1988). No significant differences in number of landings by AMF within a wind tunnel were found between doses of 18 ug/h and 500 ug/h (Aluja-Schunemann 1989).

The only detectable, significant effect of 1 vs. 12 vials here was a lack of increased movement by AMF in cage 1 when 12 BH-filled vials were used at 6 or 12 m in experiment 3 (Figure 8). The odor plume may have been carried into cage 1 with lower frequency vs. cage 2. However, the variability in wind direction was much the same for both 1 and 12 vial treatments (source directly upwind of the cages 58 vs. 62% of the total time), and no difference in response between cages was apparent for the 1 vial dose. Another possibility was that the odor plume may have been carried into cage 1 with greater frequency vs. cage 2, and the decrease in response over cage 2 represents habituation due to the greater amounts of odor when 12 vials were present. This hypothesis is supported by a lack of upwind fly orientation suggesting possible repellence by 12 vials at 6 m for cage 1, and is worthy of further investigation. However, rate of movement of AMF within the canopy of a single tree did not suggest habituation when Fein blend was released at 8000 ug/ h (16 vials) vs. no odor, and rates of movement under low and high release rates of Fein blend (8 and 500 ug/h) declined over time at the same rate in wind tunnel experiments (Aluja-Schunemann 1989).

In experiment 4, increasing the total number of vials from 8 to 16 at 12 m, and thus increasing the total release of volatiles, resulted in an upwind trend to take-off direction. Given results of the previous experiments, in which no dose response was evident, the additional vials almost certainly had a greater effect due to physical distribution decreasing intermittency (= time stimulus is absent) at the release platform than to dose or total release rate.

Environmental variables. In tests here, wind speed caused a significant decrease in rate of movement in both experiments 2 and 3, and a significant increase in time until take-off in experiment 4. In wind tunnel assays, an increase in wind speed from 0 or 8 m s^{-1} to 1.6 m s^{-1} resulted in significant downwind movement of AMF, and a significant decrease in time spent moving (Aluja-Schunemann 1989). AMF foraging in fruitless hosts visited significantly fewer leaves with increasing wind speeds (Chapter 1), and were often observed crouching low on leaves during gusts and crawling under leaves during periods of high winds (Chapter 1, Aluja and Prokopy 1992). High wind speeds have also been reported to slow rate of departure of alate aphids from host plants in the field or from artificial substrates or host plants in the laboratory (Walters and Dixon 1984, Bottenberg and Irwin 1991). Departure was delayed but not prevented at wind speeds as high as 10 m s^{-1}.

Wind speed effects on orientation were not detected under the range of wind speeds experienced here, although wind speeds can greatly influence directional consistency of plume trajectories (David *et al.* 1982, Brady *et al.* 1990), and odor concentration (Elkinton and Cardé 1984). AMF may have avoided movement and flight during periods of high wind to avoid being blown from a perch, facilitate control of flight direction, and as protection from the desiccating effects of wind. The absence of a significant effect of wind speed on orientation in all experiments indicated AMF could accomplish directed movement, probably by taking advantage of moments of relative calm during windy periods. Wind speeds during tests here (max. of 4.5 m s^{-1}) were never sufficiently high to preclude all movement during any one replicate.

Very highly significant temperature effects on rate of movement (experiments 2 and 3) and time to take-off (experiment 4) are in agreement with previous reports (Chapter 1). As discussed by Linn *et al.* (1991), higher temperatures may have increased release rates of the stimulus, increased body temperatures permitting greater levels of sustained movement, and/or altered interactions between chemical stimuli and receptors at the peripheral sensory level, optimizing response spectra or rates of disadaptation.

Very highly significant and positive relative humidity effects on rate of movement (experiment 2) compare to previous reports in which numbers of leaves visited decreased slightly with increased humidity (Chapter 1). Very highly significant effects of RH on orientation (experiment 3) are the first indication of such an effect for AMF. *D. radicum* captures on visual traps in the vicinity of host plants increased linearly with increasing humidity levels (Nottingham 1987a).

Odor dispersion and distance of response. Odor plumes vary widely in large-scale, small-scale and time-averaged structural characteristics, including size, shape, intermittency, and concentration (Murlis *et al.* 1992). These characteristics are determined by wind speed, temperature gradients, habitat, and the size, position, release pattern and rate, and the chemistry of the odor stimulus. The main result of increasing distance to the odor source may be to increase intermittency, primarily due the relatively slow expansion of the instantaneous plume as it is transported downwind. Any fixed point at greater distances from the odor source has a declining probability of lying within the plume with greater distance from the source. Murlis *et al.* (1990) reported a systematic increase in intermittency from > 60% at 2.5 m to over 90% at 20 m. Pockets of high concentration of odor are maintained well beyond that distance. By using a directionally-controlled odor source in an enclosed space in experiment 1, and by maintaining the odor source continuously upwind of the cage in experiment 2, intermittency due to plume movement may have been greatly reduced. In these experiments, no distance effect on response to odor was observed, although distances may have been insufficient for such an effect to be apparent. Intermittency may have been correlated with the number of times the cages were not directly downwind of the odor source in experiment 3, and with distance between vials and distance to vials in experiment 4.

Intermittency may be effectively achieved when concentration drops below threshold. The EAG threshold of AMF response to propyl hexanoate (another behaviorally-active ester found in the headspace of host fruit and a component of the Fein blend) is apparently very small. A 10^{-3} ug concentration elicited a response which increased through at least 10^3 ug (Averill *et al.* 1988). The behavioral threshold is unknown, but AMF within a wind tunnel spent significantly more time moving when exposed to 18 ug/h of Fein blend, the lowest release rate tested, over no odor (Aluja-Schunemann 1989).

Mechanism of location of host trees. In an open field here, AMF detected and oriented to a single BH source 12 m upwind, and detected BH emanating from multiple, surrounding sources 24 m distant. The question of the maximum distance AMF can follow and successfully arrive at a host odor source remains unanswered. In another study, however, Aluja and Prokopy (1992) showed that ca. 40% of AMF released singly in the center of a 25 m^2 patch of host trees and observed for up to 1 h located and arrived at a Fein-blend-baited host tree positioned 1 m from the edge of the patch. This baited tree was positioned without regard to prevailing wind direction, in a random direction 3.5 m from the initial fly release point, and was 1-5 m from the fly throughout each test. No AMF arrived at a similarly positioned non-baited tree.

The mechanisms by which a particular insect successfully responds to odor cues provided by a distant resource are presumably dictated by selection for those behaviors most appropriate to the characteristics and conditions associated with that resource cue, and presumably, the variability of those characteristics and conditions. AMF foraging behavior in relation to location of distant host trees may have been selected in habitats occupied by grasses and a variety of densities of shrubs, and also possibly through intervening forest. The native host of AMF is the hawthorne, *Crataegus* spp., an intermediate succession plant in northeastern North America often accompanied by blackberry, dogwood, chokecherry and other plants of densely branched woody structure and low height. Because of the profound effect of habitat on odor plume movement (Elkinton *et al.* 1984, 1987, Brady *et al.* 1990), variability in ancestral habitats may have preadapted AMF to exploit the even wider variety of habitats within which host trees are now found. Untended apple trees are often located within new-growth forests. Commercial orchards can be surrounded by forest, shrub or grasslands, or urban or suburban development. AMF manage to locate these orchards in large numbers, even when sources of immigrating flies are greater than 200 m away (Prokopy *et al.* 1990).

Hawthorne apparently does not produce attractive volatiles until fruit are ripe (August-September), whereas certain apple cultivars emit highly attractive compounds 1-2 months prior to ripening (Carle *et al.* 1987). The premature attractiveness of certain apple cultivars may have facilitated the initial shift of AMF from hawthorne to apple.

Results here demonstrate that a broad array of closely spaced odor sources elicits greater AMF response than a less closely spaced array at the same distance. Large acreages of closely spaced commercial apple trees may act to provide a wide front of continuous odor over a large area downwind of the orchard. The practical importance of regulating distance between odor sources has been demonstrated by the effectiveness of interception traps (red, spherical traps baited with butyl hexanoate) spaced 5 m apart along the perimeters of commercial orchards in controlling crop damage due to immigrating AMF, and failure of control when inter-trap distances are 10 m or more (Prokopy *et al.* 1990).

The significant response to a single synthetic component of host fruit odor demonstrated here may support the contention of Judd and Borden (1989) that host finding is not necessarily dependent upon high release rates of complex mixtures of host volatiles, contrary to hypotheses of Miller and Strickler (1984) and Finch (1986). However, responses measured here were not directly compared to AMF response to a more complete blend. A greater rate or distance of response may be obtained by the addition of other volatiles, or other types of odor. Prokopy (pers. comm.) reports greater trap captures of AMF when ammonium carbonate (a food odor) is used in addition to butyl hexanoate.

Finally, most of the behaviors assayed in this study may relate best to AMF perched on or walking within a tree. Additional experiments examining the response of AMF in flight to host odor vs. clean air would be helpful to complete the picture of AMF response presented here.

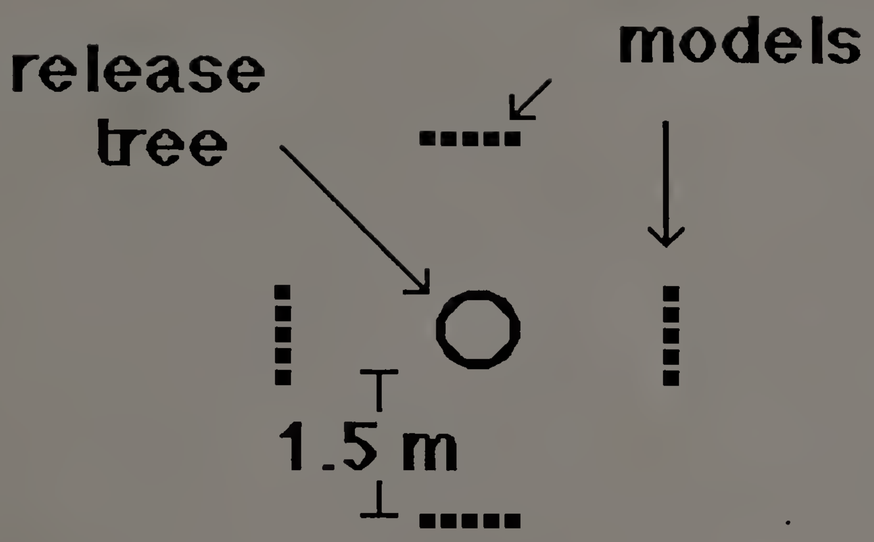


Figure 1. Experimental design and overhead view of one treatment: 1 m^2 models at 1.5 m distance from the release tree. For each test, a single fly was released onto the fruitless hawthorne tree and exposed to a treatment consisting of four tree models of one size (0.5, 1, or $2m^2$, or no models = control), color (white or green), and synthetic host fruit odor condition (present or absent) surrounding the release tree at one distance (0.5, 1.5, 2.5, or 4.5 m). N=800 flies tested.

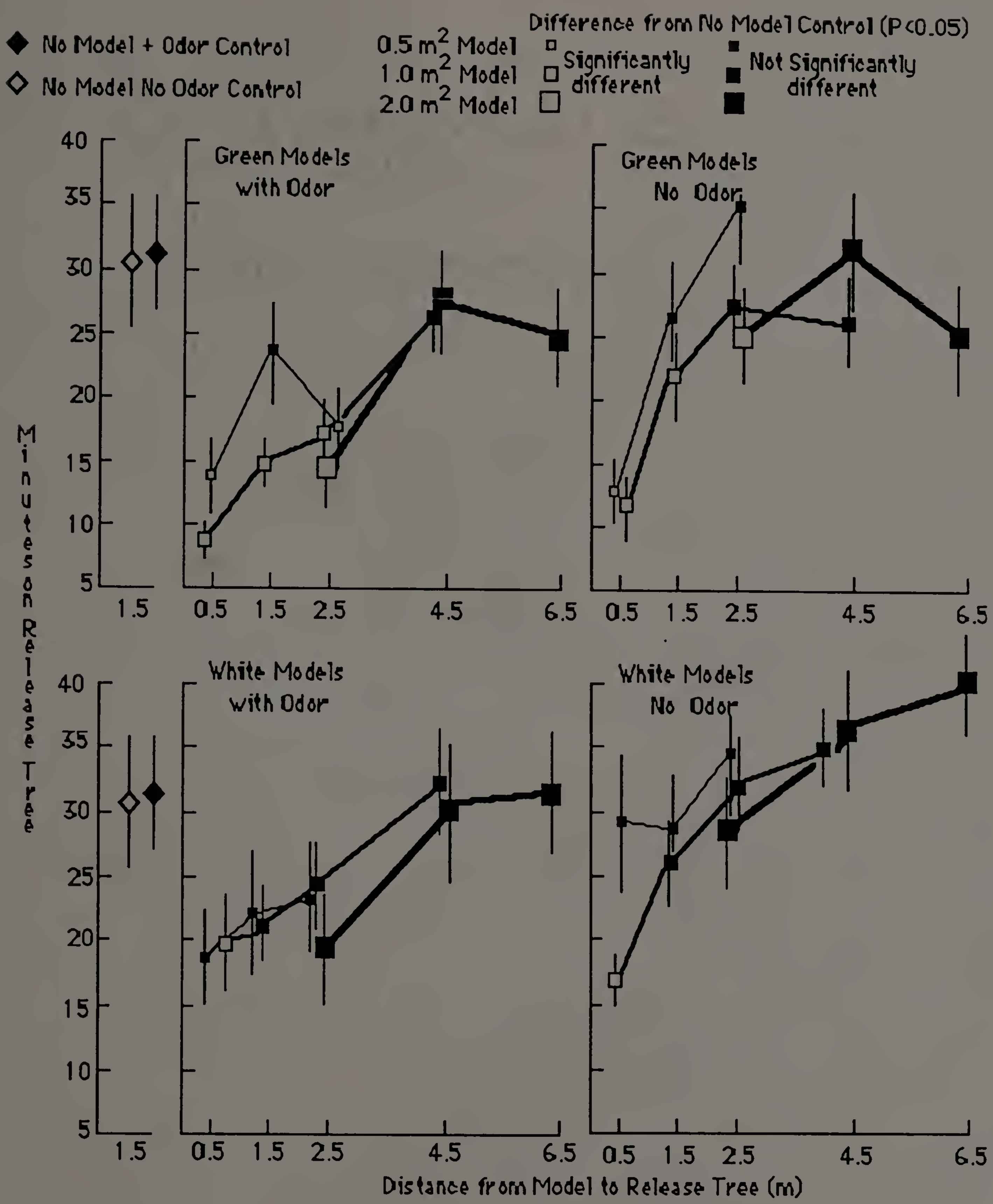


Figure 2. Mean residence time of AMF on a fruitless hawthorne tree surrounded by four green or white tree models of various sizes, with or without synthetic host fruit odor, and placed at one of several distances from the tree (or no models = control). Single degree of freedom contrasts were used to compare treatment means to those of the no model control.

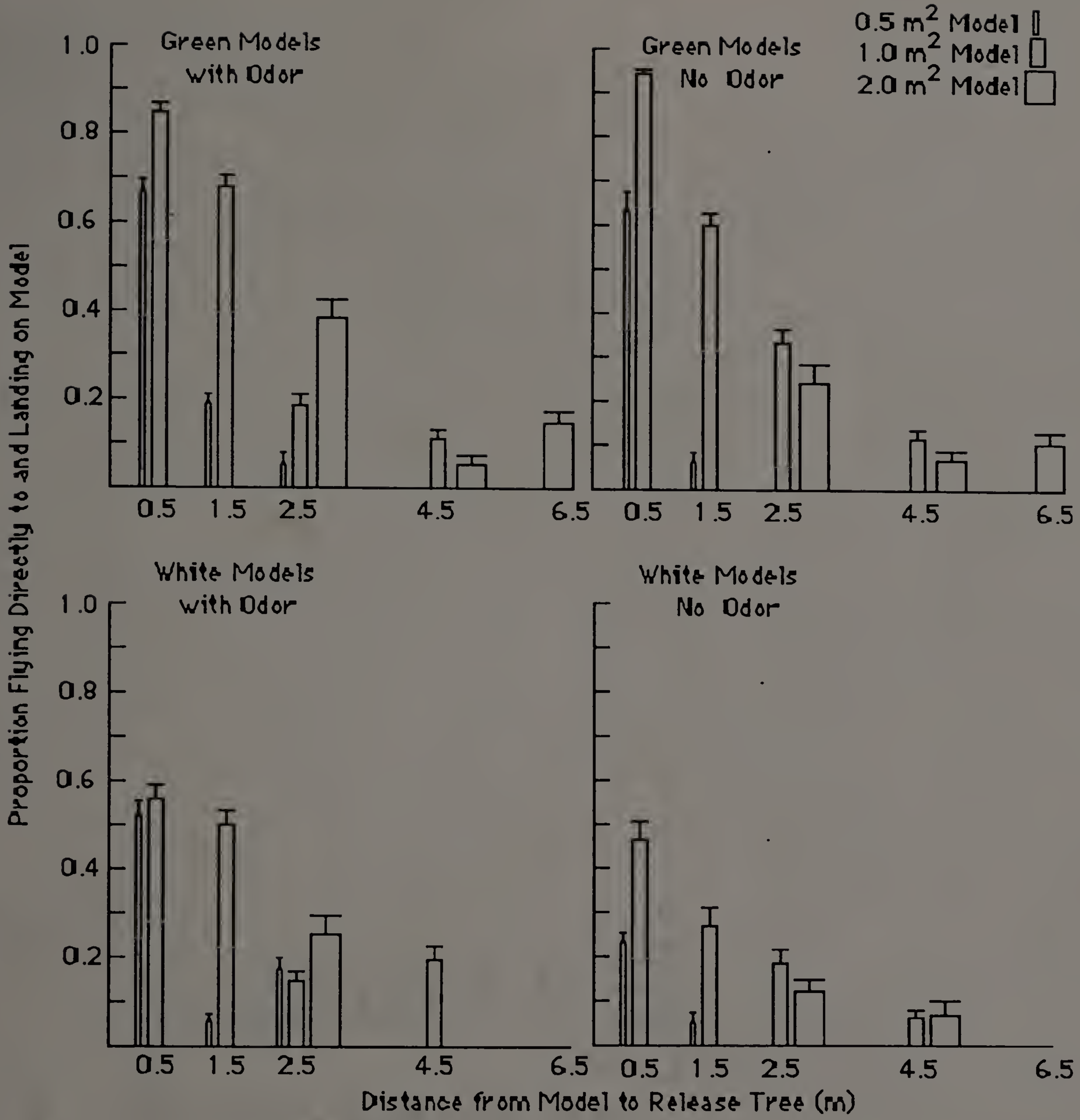


Figure 3. Proportion of AMF (± S. E.) leaving the release tree and flying directly to and landing on the surface of a tree model. The 0.5 m^2 models were present at 0.5, 1.5 or 2.5 m, 1 m^2 models at 0.5, 1.5, 2.5 or 4.5 m, and 2 m^2 models at 2.5, 4.5 or 6.5 m. N = 528 flies.

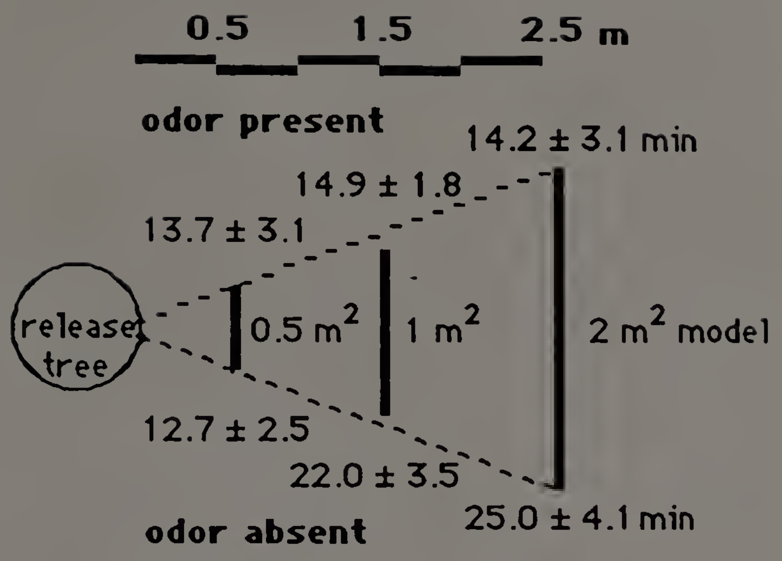


Figure 4. Average residence time (± S. E.) on the release tree for AMF when 0.5 m^2 green models were 0.5 m from the release tree or 1 m^2 green models were 1.5 m from the release tree, hypothetically creating an image occupying the same area in the visual field of AMF foraging on the release tree.

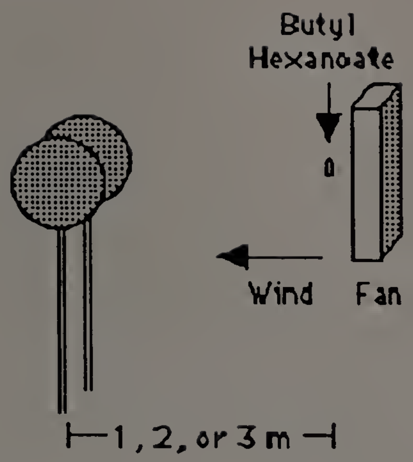
Figure 5. Experimental designs (A) Experiment 1. Two 15 cm dia. cages were placed 1, 2 or 3 m from a fan within a greenhouse. For each test, a single female AMF was placed in each of the cages. The location of each AMF and whether it was moving or stationary were recorded every 5 s for 20 min per test. Treatments were fan off and butyl hexanoate (BH) absent, fan on and BH absent, and fan on and BH present.

(B) Experiment 2. A wind-vane-driven outdoor olfactometer was operated in the center of an open field. The wind vane rotated with wind, maintaining 12 empty or 1 or 12 BH-filled polyethelene vials at end of cross-arm continuously upwind of the single AMF in the central cage. Three other cross-arms held empty vials. The central cage was divided into 8 equal wedge-shaped sections. Wind direction, AMF location and whether the AMF was moving or stationary were recorded every 5 s for 15 min per test.

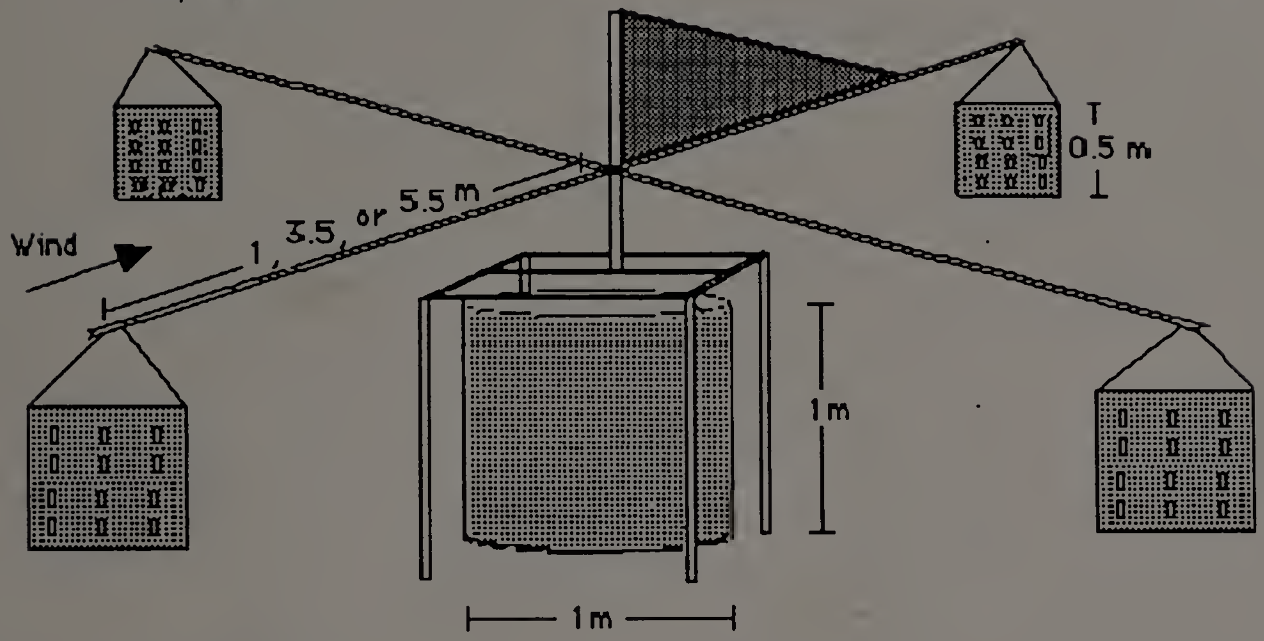
(C) Experiment 3. Two 1 m height by 1 m dia. cages were positioned 0.5 m above ground in the middle of an open field. For each test, a single female AMF was placed in each cage. Wind direction, AMF location and whether the AMF was moving or stationary were recorded every 5 s for 15 min per test. One or 12 empty or BH-filled vials, mounted on a stationary screen, were positioned upwind of the cages. Wind direction was determined by observation of flags atop the cages during the 15 min immediately preceeding each test.

(D) Experiment 4. AMF were released from a glass jar and allowed to take off from a platform in the middle of an open field. The platform was surrounded at 6, 12, 18, or 24 m by 8, 16, or 24 BH-filled vials or no vials (control). Direction of take-off and wind direction at time of take-off were recorded for each fly.

A. Experiment 1



B. Experiment 2



C. Experiment 3

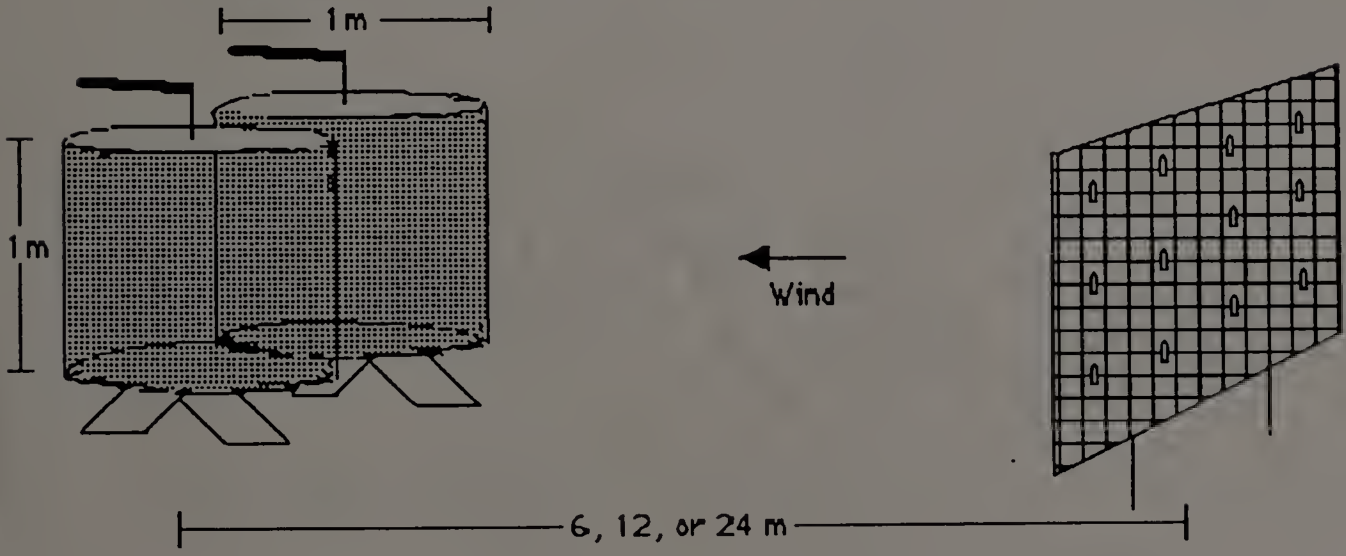


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Figure 5. Continued

D. Experiment 4

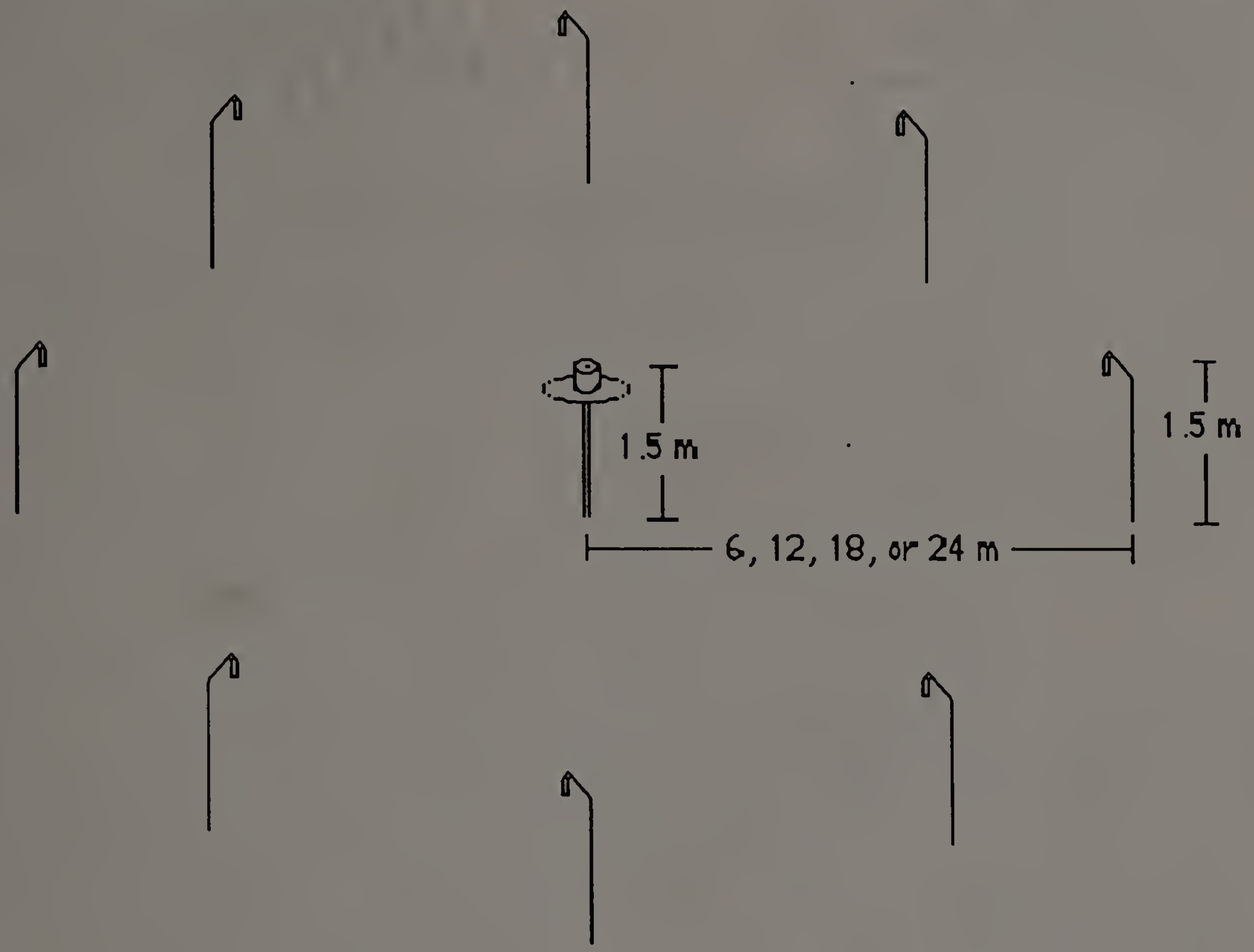

Figure 6. Results, experiment 1. Of 240 total observations per fly (one every 5 s for 20 min per replicate), mean number (± S. E.) when AMF were (A) moving vs. stationary, and (B) in the upwind half of the cage. For each 20 min test, two 15 cm dia. wire screen cages each containing a single AMF were positioned 1, 2, or 3 m from a fan and a polyethelene vial empty or filled with the Fein blend of synthetic host fruit volatiles, within a greenhouse. Treatments were fan off and odor absent, fan on and odor absent, or fan on and odor present. Repeated measures analysis of variance indicated for (A) effects of treatment were significant ($P \leq 0.01$)(treatment means not followed by the same letter significantly different, single degree of freedom contrast test, $P \leq 0.05$), effects of distance and differences between cages were not significant ($P > 0.05$), and for (B) effects of treatment and distance were not significant, differences between cages were significant ($P \leq 0.04$). N = 16 flies per treatment at each distance. Because of the large number of measurements (240 per fly), counts were analyzed rather than proportions.

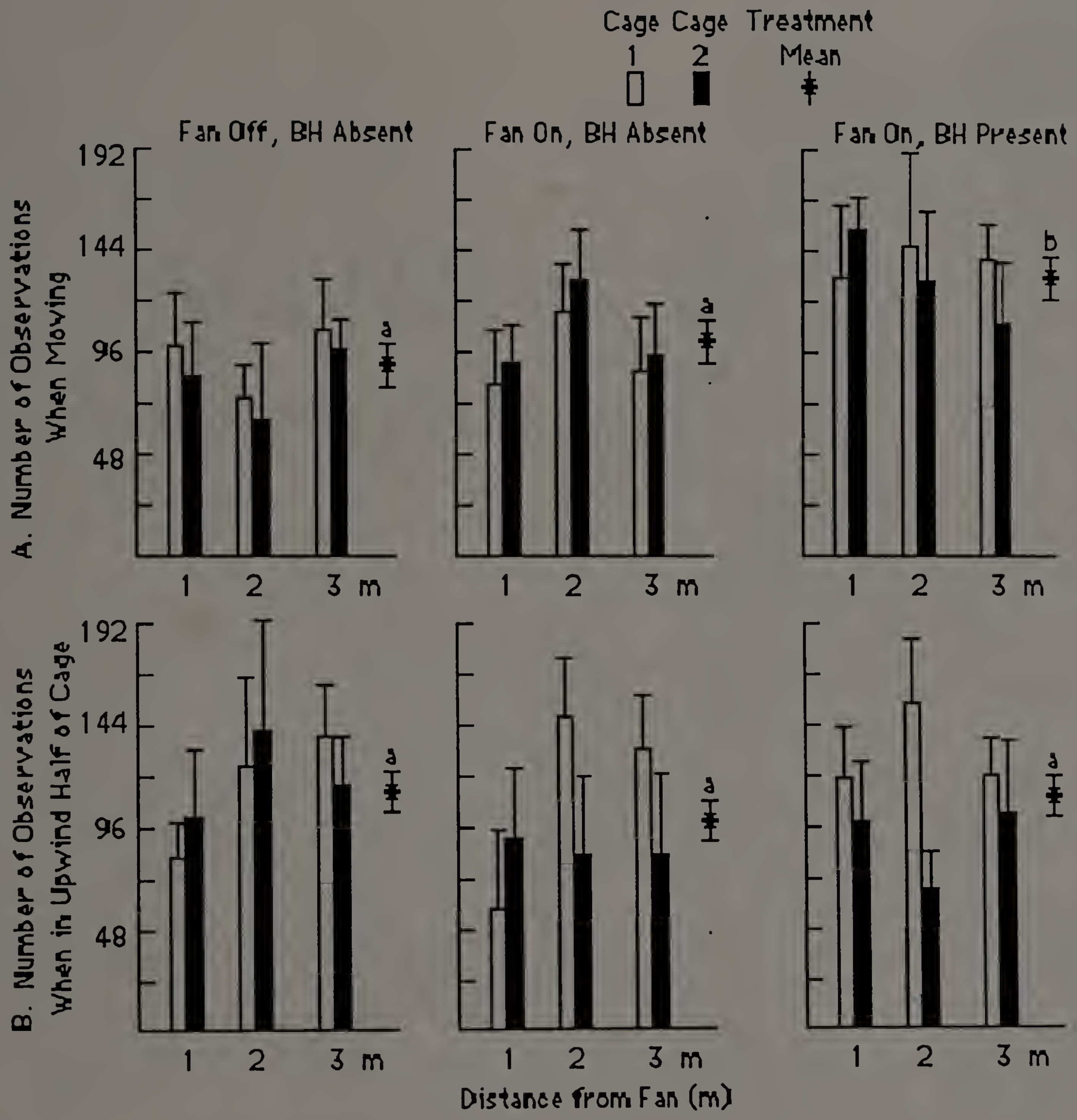
Cage 1 ▯
Cage 2 ▮
Treatment Mean ⫳
Fan Off, BH Absent
Fan On, BH Absent
Fan On, BH Present
A. Number of Observations When Moving
B. Number of Observations When in Upwind Half of Cage
192
144
96
48
a
b
1
2
3 m
Distance from Fan (m)

Figure 7. Results, experiment 2. Of 180 total observations per fly (one every 5 s for 15 min), mean number (± S. E.) when individually-caged AMF were (A) moving vs. stationary, and (B) in the upwind 1/8 of the cage. For each 15 minute test, 1 or 12 empty or BH-filled polyethelene vials were maintained 1, 3.5 or 5.5 m continuously upwind of the central cage. Analysis of variance indicated for (A) effects of BH were not significant, and for (B) the presence of BH was highly significant ($P \leq 0.005$)(treatment means not followed by the same letter significantly different, single degree of freedom contrasts, $P \leq 0.05$). Effects of distance and levels of BH (1 vs. 12 vials) were not significant. N = 16 flies per treatment at each distance.

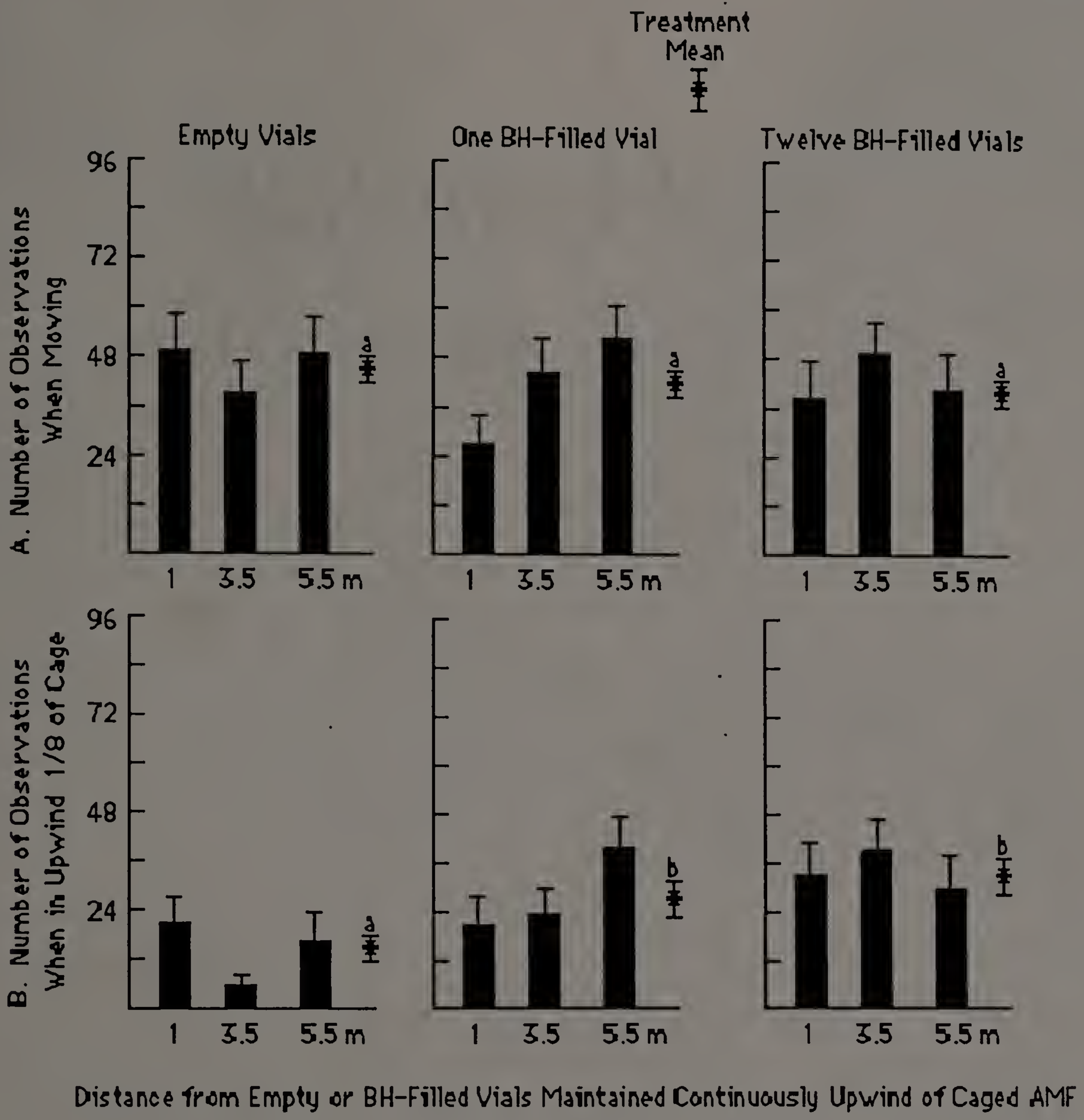
Treatment Mean
Empty Vials
One BH-Filled Vial
Twelve BH-Filled Vials
A. Number of Observations When Moving
B. Number of Observations When in Upwind 1/8 of Cage
96
72
48
24
1
3.5
5.5 m
a
a
a
a
b
b
Distance from Empty or BH-Filled Vials Maintained Continuously Upwind of Caged AMF

Figure 8. Results, experiment 3. Of 180 total observations per fly (one every 5 s for 15 min), mean number (± S. E.) when individually-caged AMF were (A) moving vs. stationary, and (B) in the upwind 1/8 of the cage. For each 15 minute test, 1 or 12 empty or BH-filled polyethelene vials were positioned 6, 12, or 24 m upwind of two cages. Analysis of variance indicated for (A) differences between cages and effects of treatment (BH and distance) were significant, and for (B) effects of treatment were significant ($P \leq 0.05$). Cage means for (A) and odor + distance means for (B) marked by different letters were significantly different from no-odor control (single degree of freedom contrasts, $P \leq 0.05$). Effects of level of odor (1 vs. 12) differed significantly for number of times moving in cage 1 only ($P \leq 0.01$). N = 24 flies per treatment at each distance.

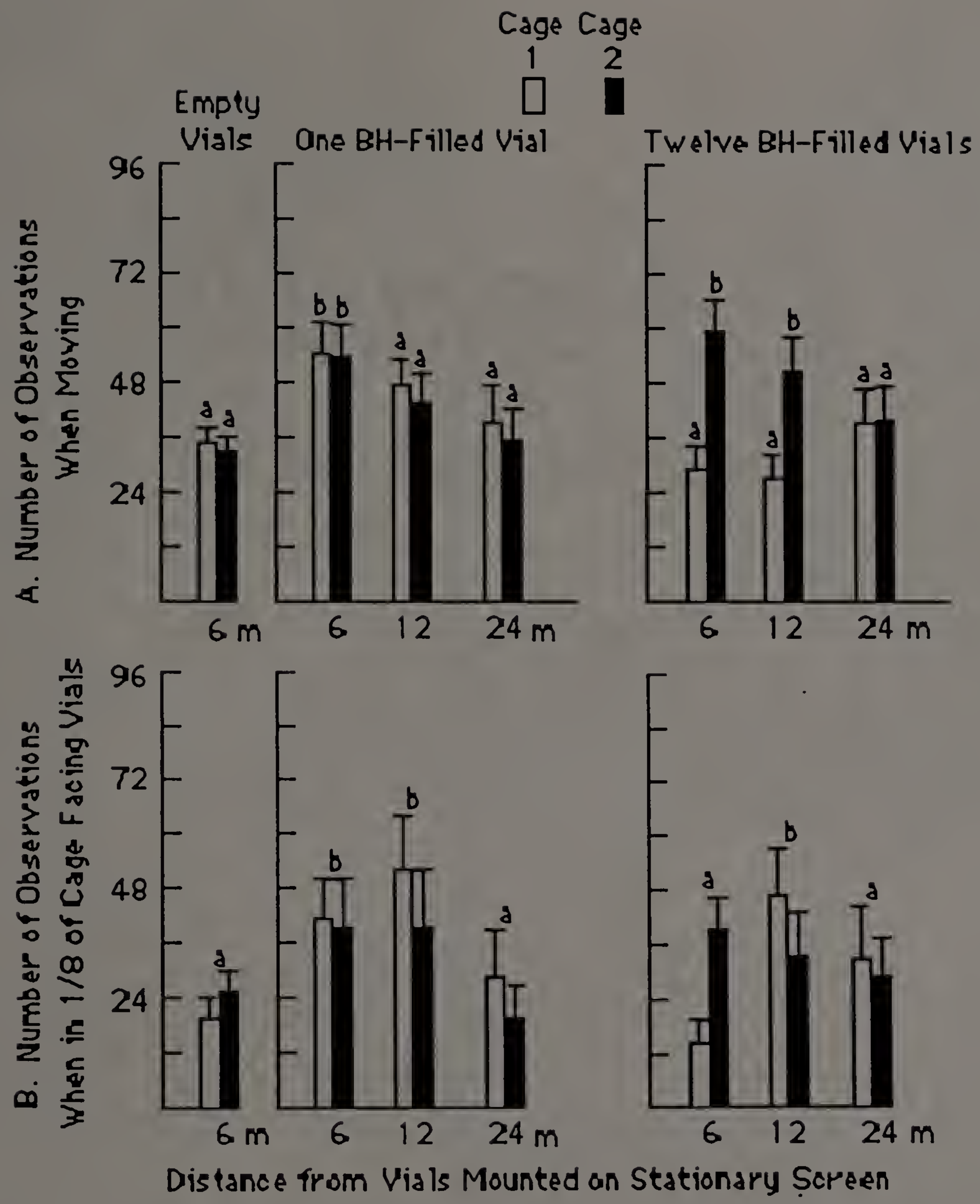
Cage 1 ☐
Cage 2 ■
Empty Vials
One BH-Filled Vial
Twelve BH-Filled Vials
A. Number of Observations When Moving
96
72
48
24
6 m
6
12
24 m
B. Number of Observations When in 1/8 of Cage Facing Vials
Distance from Vials Mounted on Stationary Screen
a
b

Figure 9. Results, experiment 4. Mean time (± S. E.) from leaving the jar until take-off, and take-off direction of flies from a platform in the center of an open field. The platform was surrounded by various numbers of BH-filled vials (or no vials, control) at several distances from the platform. Proportions taking off upwind (± 67.5°) followed by the same letter are not significantly different (logistic regression, $P > 0.05$). Mean times to take-off with solid bars are significantly different than control ($P \leq 0.03$, single degree of freedom contrasts on log transformed data adjusted for significant covariates temperature and wind speed). $N = 242$ total AMF.

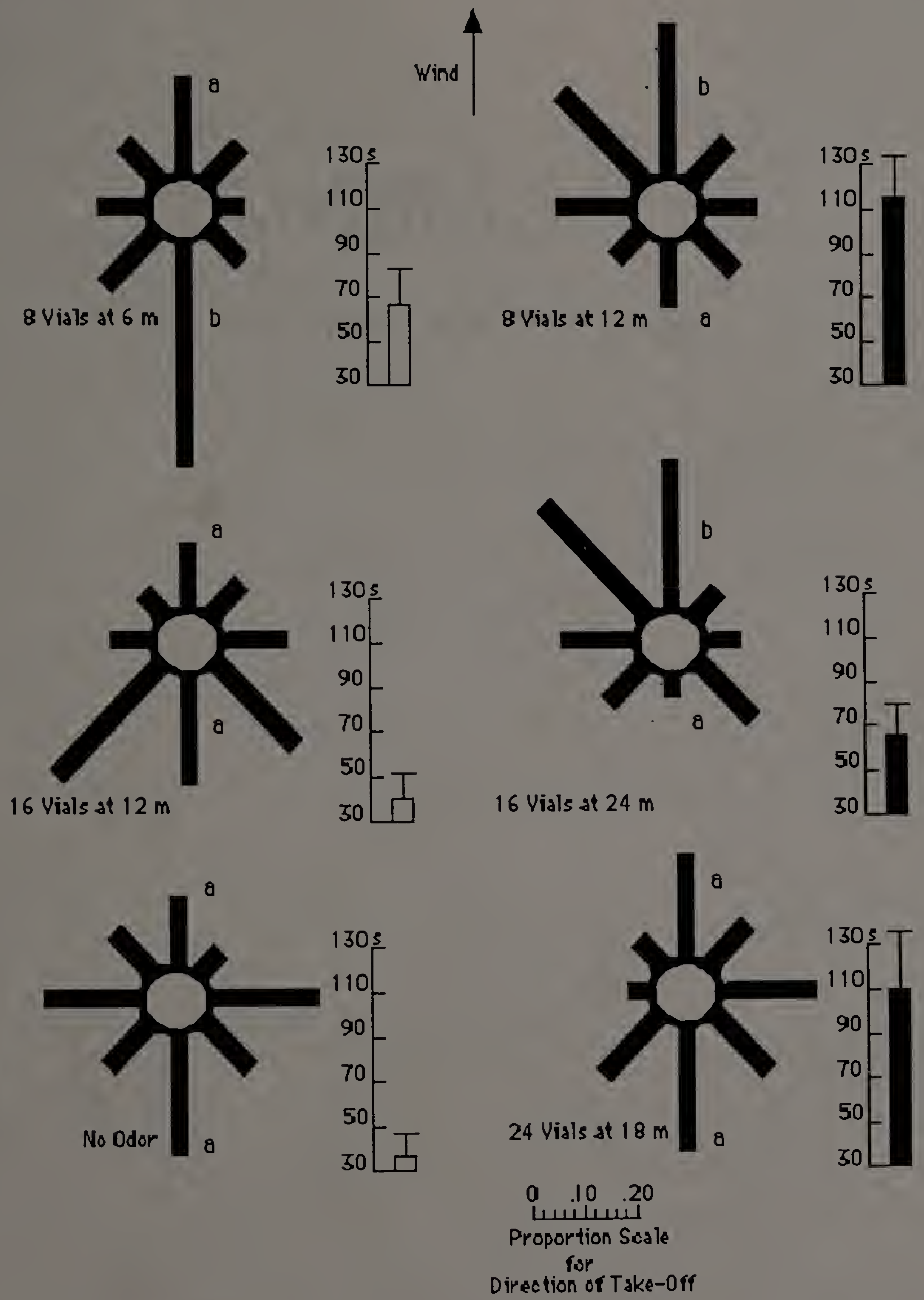
Wind
a
b
8 Vials at 6 m
130 s
110
90
70
50
30
b
a
8 Vials at 12 m
130 s
110
90
70
50
30
a
a
16 Vials at 12 m
130 s
110
90
70
50
30
b
a
16 Vials at 24 m
130 s
110
90
70
50
30
a
a
No Odor
130 s
110
90
70
50
30
a
a
24 Vials at 18 m
130 s
110
90
70
50
30
0 .10 .20
Proportion Scale
for
Direction of Take-Off

Table 1. Environmental conditions and distribution of time of day when tests were conducted. Temperature and relative humidity were recorded at the beginning and end of each test, and these values were averaged to give an individual test mean. Wind speed was measured continuously throughout each test. N= 800.

Variable[a]	Mean ± S. D.	Range
Air temperature	28.0 ± 3.44 ^{o}C	19 - 37
Relative humidity	35.8 ± 10.62 %	15 - 80
Wind speed	4.5 ± 2.16 m s^{-1}	0 - 11.2

	Time of Day[b]					
	0800-0959	1000-1159	1200-1359	1400-1559	1600-1759	1800-1959
N of Replicates	40	181	197	220	131	31
% of Total	4.9	22.6	24.6	27.5	16.3	3.8

[a] Measured at 1 m height in the center of the open field, 10 m away from the release tree.

[b] Eastern daylight savings time.

Table 2. Cox model proportional hazards regression model parameters for residence time of AMF on a fruitless hawthorne tree. With each unit change in the value of a covariate, the risk of the AMF departing from the tree changes by a factor equivalent to the exponent of the coefficient (e. g. for each 1 °C increase in temperature, the risk of an AMF departing increases 1.0333 times). Coded values for color were 0 (white models) or 1 (green models), and for odor were 0 (no odor) or 1 (odor). The effect of wind speed and relative humidity on residence time was not significant, these were dropped from the model. N = 800 total observations.

Variable	Coefficient	S.E.	P	Relative Risk	95% C. I. for Rel. Risk
Temperature	0.033	0.010	≤ 0.01	1.03	1.01 - 1.05
Odor	0.330	0.075	≤ 0.001	1.39	1.20 - 1.61
Color	0.462	0.076	≤ 0.001	1.59	1.37 - 1.84
Size	0.287	0.083	≤ 0.001	1.3	1.13 - 1.57
Distance	-0.218	0.030	≤ 0.001	0.80	0.76 - 0.85

Table 3. Logistic regression model parameters for proportions of AMF flying directly to and landing on tree models. With each unit change in the value of a covariate, the odds of an AMF flying to and landing on a model changes by a factor aproximately equivalent to the exponent of the coefficient (e. g. with each meter increase in distance between the release tree and the model, the odds of landing on the model decreases by a factor of approximately 0.44). Coded values for color were 0 (white models) or 1 (green models), and for odor were 0 (no odor) or 1 (odor). The effect of temperature, wind speed and relative humidity were not significant and so were dropped from the model. N = 800 total observations.

Variable	Coefficient	S.E.	P	Odds Ratio	95% C. I. for Odds Ratio
Odor	0.411	0.210	≤ 0.05	1.51	0.99 - 2.28
Color	0.849	0.212	≤ 0.001	2.34	1.54 - 3.55
Size	0.861	0.238	≤ 0.001	2.37	1.48 - 3.78
Distance	-0.828	0.099	≤ 0.001	0.44	0.36 - 0.53
Constant	-0.508	0.273	≤ 0.08	0.60	0.35 - 1.03

Table 4. Statistics for parameters of multiple linear regression model predicting direction of AMF leaving the release tree. [a]

Variable	Coefficient	S.E.	P
Wind direction at time of departure	0.16	0.035	≤ 0.001
Distance	-0.21	0.057	≤ 0.001
Time of day (pre- or post-noon)	0.54	0.235	≤ 0.02
Color	0.46	0.216	≤ 0.04
Constant	3.72		

[a] Overall F = 11.65 ($P \leq 0.001$), d. f. = 550, $r^2 = 0.071$.

Table 5. Statistics for parameters of multiple linear regression model predicting number of leaves visited by AMF foraging on the release tree[a]

Variable	Coefficient	S. E.	P (F)
Total time on tree	0.01	0.001	$P \le 0.001$
Wind speed	-2.11	0.535	$P \le 0.001$
Relative humidity	-0.23	0.108	$P \le 0.04$
Model size	-3.63	1.684	$P \le 0.03$
Constant	37.44		

[a] Overall F = 29.72 ($P \le 0.001$), d. f. = 550, r^2 = 0.18.

Table 6. Environmental conditions when tests were conducted. Temperature and relative humidity were recorded at the beginning and end of each test, and averaged to give an individual test mean. Wind speed was measured continuously throughout each test (experiments 2-3), or at time of take-off only (experiment 4).

	Air Temp (^{o}C)		RH (%)		Wind Speed ($m\ s^{-1}$)	
Exp.	Mean±S. E.	Range	Mean±S. E.	Range	Mean±S. E.	Range
1	30.2±0.36	23-36	41.7±1.35	20-73	----	----
2	28.8±0.38	20-38	37.7±0.89	19-66	1.2±0.11	0-6.0
3	29.2±0.38	18-35	44.0±0.64	25-68	1.0±0.03	0.2-2.8
4	29.6±0.22	23-36	46.0±0.58	30-60	1.0±0.05	0.1-4.5

Table 7. Results of analysis of variance and covariance for experiments 1-4.

	Experiment 1		Experiment 2		Experiment 3		Exp. 4
Source of Variation	Movement Prob (F)[a]	Orientation Prob (F)	Movement Prob (F)	Orientation Prob (F)	Movement Prob (F)	Orientation Prob (F)	Time to Take-off Prob (F)
Treatment:							
Odor + air movement	$P \le 0.001$	NS	- -	- -	- -	- -	- -
Odor	- -	- -	NS	$P \le 0.005$	- -	- -	- -
Distance	NS	NS	NS	NS	- -	- -	- -
Odor + distance	- -	- -	- -	- -	$P \le 0.03$	$P \le 0.03$	$P \le 0.001$
Temperature	NS	NS	$P \le 0.003$	NS	$P \le 0.006$	NS	$P \le 0.001$
Relative humidity	NS	NS	$P \le 0.003$	NS	NS	$P \le 0.001$	NS
Wind speed	- -	- -	$P \le 0.001$	NS	$P \le 0.001$	NS	$P \le 0.01$
Cage	NS	$P \le 0.04$	- -	- -	$P \le 0.05$	NS	- -
Cage x treatment	- -	NS	- -	- -	$P \le 0.03$	NS	- -

[a] Probability of F-value from analysis of variance and covariance. NS signifies F-value not significant ($P > 0.05$), -- indicates test not applicable.

Table 8. Experiment 4, logistic regression model parameters for proportions of AMF taking off upwind or downwind (± 67.5^o) from a platform in the center of an open field. The platform was surrounded by a circular array of BH-filled vials, or no vials (control). Vials were 4.7 m apart (8 vials at 6 m, 16 vials at 12 m, or 24 at 18 m) or 9.4 m apart (8 vials at 12 m, 16 at 24 m) along the circumference of the circle. The odds of upwind take-off increases approximately 1.14 times for each additional BH-filled vial used, over no odor controls. Coefficients for wind speed, temperature and RH were not significant.

Variable	Coef-ficient	S.E.	P	Odds Ratio	95% C. I. for Odds Ratio
<u>UPWIND</u>					
Odor	0.12	0.051	≤ 0.01	1.14	1.03 - 1.26
Distance	-0.18	0.059	≤ 0.01	0.83	0.74 - 0.94
Constant	-1.00	0.272	≤ 0.001	0.37	0.22 - 0.63
<u>DOWNWIND</u>					
Odor	-0.09	0.036	≤ 0.01	0.91	0.85 - 0.98
Distance	0.13	0.033	≤ 0.001	1.13	1.06 - 1.20
Constant	-0.89	0.251	≤ 0.001	0.41	0.25 - 0.67

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