FACTORS INFLUENCING HOST FINDING BEHAVIOUR OF HESSIAN FLY

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Dedicated in loving memory to Donna Louise Beresford,
Marine Biologist

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My best friend, confidente and soul-sister.
Without her inspiration and encouragement,
I would never have begun this research.

Taken from us by the ocean
in which she loved to work and play.

Abstract

The influence of environmental and plant variables on the behaviour of female Hessian flies (*Mayetiola destructor* Say) during oviposition were investigated. Female behaviour was observed with respect to different spatial and plant variables in a large arena in a greenhouse. The distance between patches of wheat (*Triticum aestivum* L.) plants and the number of plants in patches did not influence the allocation of time to flight, examining and oviposition behaviours on plants, or time spent in a patch and the numbers of eggs laid there. Females did alter their behaviour by partitioning time differently within large versus small patches. When the ratio of wheat to non-host plants, oat (*Avena sativa* L.) was altered, females spent more time and laid more eggs on wheat, despite non-selective alighting.

Influences of wind and plant stimuli on flight and egglaying decisions were studied in a wind tunnel. As wind speed increased, the time spent on wheat and oat plants before leaving increased and the number of oviposition bouts on the plant increased proportionately. Observed flights showed females losing control of flight direction and less able to reach plants in winds over 0.9 m/s. Under such conditions, females moved in a down-wind direction in the wind tunnel.

The consequences of egg clutch size for a female offspring were studied by manipulating egg clutches on individual plants. Mortality increased and offspring size decreased with increasing clutch size. As adult body size is proportional to fecundity in female Hessian fly, females maximise reproductive fitness by laying small clutches. However, if adult females do not survive to lay all their eggs, reproductive fitness may be increased by laying larger clutches. These different oviposition strategies are visible in female behaviour under differing environmental conditions.

A study of the movement of female Hessian flies in small field plots extended and verified results from lab-based studies. Females moved faster through an area of plants than was predicted by random diffusion models. The percentage of females recaptured from circular arrays of wheat or oat plants using a D-Vac insect sampler decreased as the time since release into a central patch increased. Recapture rates were lower in non-host compared to host plant arrays. Results suggest that female Hessian flies can readily move considerable distances in the field, and if eclosing in a non-host field habitat, will move extensively in search of host plants.

The degree to which spring wheat crops in New Zealand are presently under threat from Hessian fly was ascertained through a field survey. Some areas of mid and south Canterbury showed high pupal numbers. All cultivars presently sown in New Zealand appeared to be susceptible to feeding by Hessian fly larvae.

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COMMENT ON BIBLIOGRAPHIC STYLE

The bibliographic style of chapters 1 through 5 of this thesis conform to those required by the Journal of Ecological Entomology, produced by the Royal Entomological Society. In the case of chapter 6, the style conforms to the requirements of the New Zealand Plant Protection Society Proceedings in which it is published.

CHAPTER ONE

Review of the literature pertaining to Hessian fly

> "Searching behaviour is an active movement by which an animal finds or attempts to find resources. It is perhaps the most important kind of behaviour an animal engages in, because it is the means by which most motile organisms acquire refugia, and even new or different habitats. Since resources such as these are absolutely essential for the growth, development, and maintanence of an individual, and for insuring the success of future generations, efficient searching and accurate assessment of resources are crucial to an individual's survival chances and reproductive potential " (Bell, 1994).

General introduction

The need to control insect pest populations has revealed that more knowledge is needed about the behavioural mechanisms that underlie the search for host plants by insect herbivores. Movement, in respect to this search for plants, is important because insect pests are mobile creatures, capable of moving to previously uninfested areas. The Hessian fly is an ideal organism for studying searching behaviour. The Hessian fly belongs to the family Cecidomyiidae, within the order of Diptera. Interest in the Hessian fly is substantial because of its status as a major insect pest of one of the world's staple food crops, wheat. Attitude to the Hessian fly is aptly expressed in the following quote: "On account of the importance of the wheat crop to man, probably no insect pest has received more attention or has ever had more said or written about it and its depredations than the Hessian fly" (Drake *et al.*, 1924). Throughout many of the wheat-growing areas of the world, Hessian fly outbreaks sporadically result in major wheat crop losses. For example, in the 1980's, annual losses attributed to the Hessian fly in the U.S.A. were in the US $10-30 million range. The Hessian fly continues to be one of the most studied insects in the world.

One of the most effective methods for controlling this pest is the use of resistant cultivars. Wheat cultivars have been bred with resistance to larval feeding. The genetic interaction between resistant wheats and Hessian fly larvae has been studied in much detail. In the 1970's biotypes of Hessian fly virulent to resistant wheats evolved, increasing the need to understand the biological interactions of Hessian fly with its host plants. In particular, it became clear that insufficient knowledge existed on many aspects of adult biology.

The work by Harris and co-workers in the 1980's contributed substantially to the understanding of adult Hessian fly behaviour. The production of sex pheromone by females and male movement to and mating with females were examined (Foster *et al.*, 1991; Harris & Foster, 1991; Foster & Harris, 1992). The reproductive behaviour of females was examined, particularly during the transition from virgin to mated behaviour and the temporal changes in egg-laying that occur during the oviposition phase (Harris & Rose, 1989; Harris & Rose, 1991). The reproductive potential of females and males was positively correlated to body size (Bergh *et al.*, 1990; Bergh *et al.*, 1992). Females locate host plants using multiple cues. These were shown to be tactile, visual and chemical, differing in importance at different phases in the host-finding sequence (Harris & Rose, 1990). The exact nature of the visual cues used by females on approach to and acceptance of host plants was ascertained (Harris *et al.*, 1993). These studies provided the foundation on which this thesis research is based.

The primary objective of this dissertation research was to document the behavioural decisions made by ovipositing females during host plant finding. More specifically, the effects of various exogenous and endogenous stimuli on the behaviour of mated female Hessian flies were investigated at several spatial scales, ranging from behaviour while on a single plant to movement through small field plots. The importance of Hessian fly as a pest currently in New Zealand, and how wind influences field infestation patterns was also studied.

The first chapter of this thesis reviews relevant literature on the biology of the Hessian fly, including larval feeding, plant damage, adult biology and Hessian fly control. Literature relating to aspects of insect ecology and behaviour is discussed within each of the relevant chapters.

Systematics

The Hessian fly is classified in the family Cecidomyiidae (suborder Nematocera), the sixth largest family, in terms of number of species, within the order Diptera. Presumed to have evolved from an ancient branch of Diptera, cecidomyiids are a particularly interesting family in evolutionary terms due to their rapid rate of species formation (Mamaev, 1975) in comparison to other closely related primitive Dipteran families. Cecidomyiids are characterised by their associations with live plants as habitats, being most commonly gall-makers. However, within the cecidomyiid family, the adoption of saprophagy, predation, and mycophagy, in addition to phytophagy, makes this group unique among the Diptera in their diversity of feeding habits.

The Hessian fly belongs to the tribe Oligotrophini, whose members are known for their diverse forms and ability to inhabit mycophagous as well as the usual phytophagous niches. *Mayetiola* is a primitive genus, physiologically unique and efficient

at breaking down host tissues before ingestion, with well-developed salivary glands and a larval intestine with enlarged midgut (Mamaev, 1975). All *Mayetiola* species feed on plant material and typically live in the stems of grasses in the tribes Festuceae, Hordeae, Avenae and Agrostideae. Examples are *Mayetiola ammophilae* (Gagne) which lives within the stems of American beachgrass, and *Mayetiola arenaria* which lives on a closely related grass in north-eastern Europe (Gagne, 1989). Another peculiarity of the genus *Mayetiola* is the lack of feeding by the third larval instar. This instar develops within the skin of the second instar (Gagne, 1989). These characteristics associating *Mayetiola* species with phytophagous niches, immediately makes them likely to fall within the category of a "pest".

The Hessian fly shares its status as a major agricultural pest with other cecidomyiids in the subfamily Cecidomyiinae. Of economic importance are the sorghum midge (*Contarinia sorghicola* Kirby), the brassica pod midge (*Dasineura brassicae* Winn), the wheat blossum midge (*Sitodiplosis mosellana* Gehin), the pine needle gall midge (*Thecodiplosis japonensis* Uchida et Inouye) and the apple leaf curling midge (*Dasineura mali* Kieffer), (Barnes, 1956; Gagne, 1989). These species all share the characteristic of being well adapted to and closely synchronised with their host plant species. The difficulties inherent in controlling gall midges may relate to their particular phytophagous niche. Damaging feeding stages are well-protected from insecticides and natural enemies within the habitat provided by the gall or sheltered feeding sites. The window of time during which predation or chemical control can occur in gall midges is therefore narrow, perhaps being restricted to the adult (which is short-lived) and the egg stages.

Distribution

The Hessian fly is a pest of cereals and other grasses principally in the northern hemisphere cereal belt which extends eastward from the pacific coast of North America across Europe and as far east as Siberia, and into parts of Asia and North Africa. In the southern hemisphere, Hessian fly has been found in only one country, New Zealand (Barnes, 1956; Gagne, 1989). The Hessian fly, although first described in Europe in 1817, is thought to have originated in the Middle East in the area of the Euphrates River, the area where cereals such as wheat and barley are also thought to have originated (Barnes, 1956).

Host range

Hessian flies are oligophagous and can live not only on cereals such as wheat, barley and rye, but also on some pasture grasses. Genera known to include species that support larval feeding include *Elytrigia* (e.g., couch) (Noble, 1931; Stokes, 1957), *Hordeum* (e.g., barley), *Triticum* (e.g., wheat), *Secale* (e.g., rye), *Aegilops* (e.g., goat grass), *Elymus* (e.g. wheat grass), *Phleum* (e.g., timothy), and *Bromus* (e.g., prairie grass),

(Jones, 1936; Jones, 1938; Jones, 1939; Prestidge *et al.*, 1987). Susceptibility to Hessian fly is not consistent within these genera however, as Hessian fly live on some, but not all species within these genera. The host range of Hessian fly may also differ in different parts of the world. For example, *Phleum sp.* was originally reported as a likely host (Jones, 1939), but did not support a New Zealand population of Hessian fly (J. Dando, unpub. data). Recently in New Zealand the pasture grass, prairie grass *Bromus willdenowii* (Kunth) has become a major host for Hessian fly (Prestidge *et al.*, 1987). This species can suffer substantial tiller death from Hessian fly larval feeding (Prestidge & Van der Zijpp, 1988; Thom *et al.*, 1992). Hessian flies are at least as successful on this grass as on wheat, having three generations each year and showing larval and pupal infestation levels from 1-5 per tiller, a higher rate than generally recorded on wheat in New Zealand (Prestidge, 1992). The oligophagous habit of Hessian flies undoubtedly adds to their persistence as a major insect pest.

The host range of a phytophagous species is determined by two factors, first the willingness of the females to oviposit on a plant species, and second the ability of resulting offspring to survive and complete development on that plant species (Barbosa, 1988). Hence, although species in the genera *Aveneae* (e.g., oat), *Agrostus* (e.g., browntop), *Festuca* (e.g., fescue) and *Lolium* (e.g., ryegrass) are generally not suitable for Hessian fly larval feeding and development, eggs are sometimes laid on species in these genera (Stokes, 1957; Zeiss *et al.*, 1993b). Female insects often accept for oviposition a larger range of hosts than can sustain their larvae, so this apparently unsuitable oviposition behaviour is not unexpected (for a review of this subject, see Courtney & Kibota, 1990). When tests for host range are conducted, the discrepancy between host acceptance and suitability is accounted for by doing both oviposition choice tests with a range of plants available (e.g., Cartwright & LaHue, 1944), and forced oviposition tests wherein females are caged with single hosts until death (e.g., Gallun & Hatchett, 1969; Sosa & Foster, 1976), so that larvae are forced to feed on less preferred or genetically unsuitable hosts. Host acceptance by an ovipositing female must be understood in terms of female responses to stimuli (Courtney & Kibota, 1990). This has been investigated by Foster & Harris (1992). Wheat, barley, rye and oat extracts were tested for effects on oviposition. The order of preference for these extracts followed that of the whole grasses, wheat $\geq$ rye $\geq$ barley $>$ oat. It appeared that at least two chemicals in the foliar waxes of these grasses influenced oviposition behaviour of female Hessian flies. Differences in preferences were related to quantitative differences in the amounts of the active chemicals in the most polar fractions tested (Foster & Harris, 1992). In addition to plant chemistry, there are a number of factors that influence oviposition preference and host suitability of grasses to Hessian fly. These factors include foliar form, colour, leaf texture (Harris & Rose, 1990), genetics, and the character of the leaf sheath (Anonymous, 1971; Barnes, 1956; Blair & Morrison, 1949).

Hessian fly biology

- General

The adult Hessian fly has a lifespan limited to a maximum of three days (Enoch, 1891). Eggs tend to be laid on the upper surface of leaves, mortality of migrating larvae being greater when placed as eggs on the oldest leaf (Painter, 1930b; Morrill, 1982). Eggs hatch after a period related to environmental conditions, generally 3-5 days, but up to 12 days in the field (McColloch, 1923). The first instar larva after hatching from the egg, turns 180° and then migrates down to a feeding site in the crown of the plant. Sometimes females oviposit while facing toward the base of the leaf. These eggs are then laid inverted. The larva hatches, turns 180° and goes to the tip of the leaf. Upon reaching the tip, it then turns and proceeds to the base (McColloch and Yuasa, as cited in Barnes, 1956; Morrill, 1982). Like all insects, growth rates of larvae are temperature dependent (Foster & Taylor, 1975). The first instar moults after 6 to 9 days of feeding (Gagne & Hatchett, 1989). The second instar feeds for another 10 to 14 days before spinning a silken cocoon. This hardens into a puparium within which the third instar develops. Depending on the crowding of individuals within the restricted niche of a plant stem, some pupae can appear compressed and deformed.

- Seasonal emergence patterns

The length of time that Hessian flies spend in the third larval instar is variable, being influenced by a number of factors. Low relative humidity can delay emergence, and be fatal at extremes (Barnes *et al.*, 1959). Optimum conditions for emergence are considered to be high humidity and temperatures between 20 and 25° C (Barnes *et al.*, 1959). One study where insects were reared in temperatures of between 15.6° and 26.7° C reported maximum growth and adult eclosion rates occurring at 21.1° C, with developmental extremes at a minimum of 15.6° and maximum of 26.7° C (Foster & Taylor, 1975). Low temperatures are known to cause final instar larvae to enter diapause for extended periods (Barnes *et al.*, 1959). During such extended diapause Hessian flies are susceptible to dessication. In addition to diapause induction at low temperatures (McColloch, 1923), third instar larvae enter aestivation (a conditition of endocrine deficiency) on exposure to high temperatures (fluctuating 17 to 36° C) and dry conditions (Wellso, 1991). It is likely that Hessian flies, like swede midges (*Contarinia nasturtii* Kieff.), have a strong moisture requirement for the termination of aestivation. In the swede midge, emergence occurred 14 days after a moist to thorough wetting, following storage in dry soil for extended periods (Readshaw, 1966). At the opposite extreme however, there is historical evidence from the field that excessively high rainfall can delay the emergence of diapausing Hessian fly (Cartwright, 1923). There are many examples of extreme weather patterns

having influenced the timing of population emergence (Parks, 1923; Pike *et al.*, 1983). A particularly cold and wet autumn delayed Hessian fly emergence of a fall generation (Cartwright, 1923), the progeny of which caused total loss of 24% to 38% of wheat plants sowed on the usual recommended dates. Environmental conditions also have been shown to influence adult diapause in sorghum midges (Baxendale & Teetes, 1983), swede midges (Readshaw, 1966), and orange wheat midges (Hinks & Doane, 1988). Diapause induction occurred in these cecidomyiids after exposure to low (2-5^{o} C) temperatures, and was terminated after exposure to high (>20^{o} C) temperatures. These influences of environment on Hessian fly life history dictate how long each generation takes to complete. The shortest measured time from egg to adult, has been 28 days under laboratory conditions (Barnes *et al.*, 1959). The number of generations of Hessian flies that occur per year is temperature dependent (Buntin & Chapin, 1990) and can vary between one and six (Stokes, 1957). Thus, although protected to a certain extent from environmental conditions by its puparium, a final instar larva is still sensitive to such factors as temperature, humidity and moisture.

- Diurnal emergence patterns

Within each day, emergence of adult male Hessian fly follows a bimodal pattern (Enoch, 1891; Bergh *et al.*, 1990). The majority of males emerge about 12 h before the peak of female emergence. Males remain inactive for approximately the first 10 h, and begin flying about between one and three hours before the females begin emerging (Bergh *et al.*, 1990). A smaller number of males emerge during the peak of female emergence and calling in the hours before and after dawn (0300-0700 h). Similar patterns of males emerging before females have been recorded in other cecidomyiids, e.g., *Contarinia lolii* Metcalfe (Metcalfe, 1933, cited in Bergh *et al.*, 1990), and *Dasineura alopecuri* Reuter (Barnes, 1930). This synchronisation of activity and emergence patterns between the two sexes (Bergh *et al.*, 1990; Gagne, 1989) effectively coordinates their reproductive activity patterns.

- Larval feeding

- Feeding mechanism

Investigations into the feeding mechanism of the Hessian fly larva began in the 1930's when Haseman described the physiology of larvae and concluded the mouth organs were of the correct structure for obtaining plant juices (Haseman, 1930). From this time until the late 1980's, it was believed that larval secretions softened cell walls, allowing larvae to obtain the cell contents through an intermittent sucking action (Refai *et al.*, 1955; Refai, 1956) causing a reduction in plant growth. Later it was demonstrated that plant stunting did not result purely from larvae extracting substances from the plant. In addition to

feeding on plants, Hessian fly larvae discharge a substance into the plant which inhibits plant growth (Byers & Gallun, 1972). In Hessian flies the basal region of the salivary gland takes up a proportionally greater area in first instar larvae and then degenerates during the second and third instar (Stuart & Hatchett, 1987). This physiological change varies in proportion to the periods of larval feeding that induce stunting in the plant. Based on this observation, the salivary gland was proposed as the most likely source of this plant-growth inhibiting substance (Stuart & Hatchett, 1987).

Though small in size, and virtually immobile, Hessian fly larvae are effective at obtaining sufficient food from the plant they have been placed on as an egg by their mother. It has been shown more recently, that first instar Hessian fly larvae have minute retractible mandibles which are actually inserted into plant epidermal cells (Hatchett *et al.*, 1990). Once the mandibles are inserted, salivary gland fluids are ejected through the mouth cavity. After salivary materials have been injected the mandibles are retracted and the larva brings its oral cavity over the puncture site. The pharyngeal tube is then brought in contact with the epidermal cells, and liquid is drawn from the plant through a sucking action initiated from the pharyngeal cavity. Hatchett *et al.* (1990) proposed that the first instar larva remains in a single feeding cavity on the leaf surface over the first few days where it repeatedly feeds from closely-situated sites. The loss of creeping pads in second instar larvae (Gagne & Hatchett, 1989) and the degeneration of the salivary gland adds evidence that second instar larvae may simply suck the plant fluids being exuded from the earlier feeding sites without needing to create any new sites in the leaf.

- Feeding duration

Larvae have been shown to feed on susceptible wheats for up to 14 days (Gallun & Langston, 1963), showing a maximum uptake of plant fluids on day five of feeding. Larvae feeding on resistant cultivars of wheat show a range of abilities to sustain feeding (Shukle *et al.*, 1990). Some wheat cultivars contain genes that prevent even the initiation of feeding by first instar larvae. On other cultivars larvae feed for up to 48 h, but cease feeding between 48 and 96 h and are dead after 6 days (Shukle *et al.*, 1990). Therefore, some plants do have mechanisms for preventing Hessian fly attack, but the interaction between the larva and the plant is complicated.

- Larval-plant interaction

Hessian fly feeding causes a physiological reaction in both susceptible and resistance plants. The duration of Hessian fly feeding on a susceptible plant (Asavanich & Gallun, 1979) influences the degree of growth inhibition shown by the plant: measurable growth inhibition occurred after five first-instar larvae fed on a single plant for two days, with permanent stunting occurring after six days of feeding (Asavanich & Gallun, 1979). The physiological response caused by Hessian flies feeding on susceptible plants is not an

actual gall in the plant stem (Abrahamson & Weis, 1987), like that the closely related species *Mayetiola hordei* (Mesnil) causes on barley (Gagne *et al.*, 1991). Instead the area of the plant surrounding the feeding site becomes shrivelled, and an indentation occurs where each larva feeds. Young wheat plants infested with Hessian fly show a characteristic dark-greening of their leaves attributed to an increase in the concentration of chloroplasts in the leaves of infested plants (Robinson *et al.*, 1960), and greater leaf concentrations of sucrose, glucose and fructose (Refai *et al.*, 1955). Even on some resistant wheat cultivars some stunting of the plant does still result (Shukle *et al.*, 1990) when larvae feed actively for the first 48 h, before dying.

The usefulness of resistant wheat cultivars, provided the motivation for discovering the mechanism underlying the plants' resistance. Recent research (Shukle *et al.*, 1992) proposes that the mechanism behind resistance in wheat involves "recognition" of an avirulent gene product or process from avirulent larvae and elicitation of a response which then confers resistance to the plant. The factors involved in recognition of avirulent larvae could be enzymes or toxins secreted by the larvae. Virulence in larvae is then achieved by an altered gene product that avoids eliciting this reaction by the host plant. Such a mechanism fits the gene for gene relationship shown to function in the genetic analyses of resistance conducted to date (Hatchett, 1986). The physiological mechanism does not provide complete control : feeding by a single virulent larva effectively inactivated the plants' resistance mechanism (Day, 1974), and allowed all normally avirulent larvae that subsequently infested the plant to survive (Grover *et al.*, 1989). In addition, plant resistance in some cultivars breaks down under high temperatures (Maas *et al.*, 1987; Sosa & Foster, 1976; Tyler & Hatchett, 1983). This resistance failure is clearly a plant, not insect, based phenomenon, as it is differently expressed in homozygotes compared to heterozygotes in some cultivars (Tyler & Hatchett, 1983). The interaction between susceptible plants and Hessian fly larvae, is therefore a complex one, involving many aspects of physiology, anatomy and genetics.

Reproductive behaviour

- Mate-finding and pheromone production

The sexual behaviour of cecidomyiids was not extensively studied until the 1980's. Early observations of Hessian flies (Enoch, 1891) reported that females extended their ovipositors soon after eclosion and hung in a calling position from leaves of wheat plants. This female behaviour is typical of sex pheromone release. Males were observed flying over 3-5 m upwind to unmated females caged in the field (Cartwright, 1922). Cartwright (1922) and McColloch (1923) both observed mating activity to be greatest in the early morning. It was not until 1984 that experiments (McKay & Hatchett, 1984) provided strong evidence for the production of a volatile sex pheromone by female Hessian flies.

Males were shown to be highly attracted to excised female ovipositors and extracts from ovipositors, suggesting the ovipositor to be the pheromone production and release site. The sex pheromone of the Hessian fly undoubtedly consists of a blend of chemicals (Harris & Foster, 1991), the major component of which has been identified as (2S)-(E)-10-tridecen-2-yl acetate (Foster *et al.*, 1991; Millar *et al.*, 1991). The pheromone is biosynthesised in a cyclical fashion throughout the virgin female lifecycle (Foster *et al.*, 1991), with high pheromone titre coinciding with the peaks of sexual activity shown by males and females in the early hours of the morning. Pheromone production by the female ceases after mating occurs (Foster *et al.*, 1991).

Male movement in response to sex pheromone has been studied in a wind tunnel (Harris & Foster, 1991). In the presence of sex pheromone, males flew upwind, 2 to 6 cm above ground level towards the source, exhibiting flights consisting of both zigzagging and straight upwind flight. Casting was sometimes exhibited by the males when contact with the odour plume was lost, a behaviour similar to that described in male moths (Baker, 1989). After the male located the female he landed alongside her, grasped her abdomenal tip with his claspers, and transfered sperm (McKay & Hatchett, 1984). Independent of when mating occurs, the average duration of copulation is 14 s (range of between 10-20 s) (McKay & Hatchett, 1984; Bergh *et al.*, 1992). As with most cecidomyiids, females generally mate only once (Stokes, 1957; Readshaw, 1966), although Hessian fly females have been observed mating again if a male approached within 1 min of the first mating (Bergh *et al.*, 1992). Males fertilised all or most of the eggs of between 10 and 15 females (Bergh *et al.*, 1992).Up to another 10 matings can occur, although the number of eggs fertilised in these mated females declined rapidly. A mating that resulted in insufficient sperm being transferred caused some females to resume calling within 20 minutes. These females that resumed calling behaviour were quickly mated again when exposed to other males (Bergh *et al.*, 1992). The maximum number of matings a male can perform is positively correlated to male fresh weight (Bergh *et al.*, 1990). This relationship suggests that larger males should obtain a proportionate increase in potential fecundity over smaller males. Male reproductive behaviour therefore has important consequences not only for males, but also for females, particularly on the expression of the mated state, behaviour and achievable fecundity.

- Transition from virgin to mated behaviour in females

Female insects respond to mating by changing their behaviour and physiology. The female Hessian fly retracts her ovipositor during mating and after mating continues to sit for a period that ranges between 1.5 and 3 h. The duration from mating to oviposition is shortened in higher temperatures and when the female is mated at an older age (Harris & Rose, 1991). These changes from virgin to mated behaviour are induced by a factor, originating from the male reproductive tract, that is transferred with sperm to the female

during mating (Bergh *et al.*, 1992). A period of quiescence following mating with minimal movement occurring has been reported for other cecidomyiids (Spence, 1969). After the rapid transition from quiescence to activity, females begin active foraging and egglaying (Harris & Rose, 1991). Unmated females will lay some unfertilised eggs before they die, these eggs are not viable (McColloch, 1923; Harris & Rose, 1991). Once the transition from virgin to mated behaviour has occurred, the adult phase of a female Hessian fly lifecycle becomes dominated by the search for suitable oviposition sites for egglaying.

- Foraging behaviour

Female Hessian flies are semelparous, i.e. they eclose containing their full compliment of eggs, and do not mature any further eggs or feed as an adult. This biology has important consequences on reproductive behaviour, putting a fixed upper limit on achievable fecundity. Females have been found to contain extremes of between 11 and 474 eggs (McConnell, 1921), but average in the range of 200-300 (Walken, 1945). The number of eggs a female contains is positively correlated to her body size (McConnell, 1921), which is easily assessed by measuring winglength (Bergh *et al.*, 1990). Female Hessian flies continue oviposition behaviour until all or most of their eggs have been laid. It was shown in the laboratory that females that were mated at 0700 h laid 99% of their eggs by 1500 h, with mortality following in most females by 1800 h (Harris & Rose, 1991). There is therefore a time constraint on females laying all their eggs. Efficient host location behaviour promotes the laying of a large number of eggs within these time constraints.

Phytophagous insects use a combination of their sensory modalities to locate and identify suitable host plants on which to lay their eggs: the Hessian fly is no exception. It was known that female Hessian fly showed oviposition preferences for some species of grasses over others (McColloch, 1923; Jones, 1938; Stokes, 1957; Morrill, 1982), and also that eggs were generally laid on the adaxial surface of the youngest leaves (McColloch, 1923; Morrill, 1982). It was shown (Harris & Rose, 1990) by manipulating plant models within choice bioassays that females laid more eggs when tactile (parallel vertical grooves equating to leaf venation), colour (green), and chemical (presence of wheat chemicals from leaf extracts) cues were simultaneously present. Tactile cues may be important in guiding the ovipositing female to the upper side of the leaf, where most eggs are laid (Harris & Rose, 1989). When the grass foliar chemicals stimulating oviposition behaviour in Hessian fly were studied in greater detail (Foster & Harris, 1992), females approached and landed more frequently on foliar-extract treated papers. After landing, females spent more time and laid more eggs on papers with host rather than non-host plant extracts. Two chemical fractions of wheat leaf extract were shown specifically to have a stimulatory effect on oviposition (Foster & Harris, 1992). Analyses of the visual cues emanating from host plants revealed both spectral and spatial

information to be influencing orientation to targets during flight (Harris *et al.*, 1993). Specifically, stimulatory wavelengths for approach to targets during flight were in the region of 530-560 nm, while inhibitory wavelengths lay in the region of 400-500 nm. Orientation and approach to targets during flight were increased by vertical rather than horizontal orientation of edges, and by targets with a higher density of vertical contour lengths (Harris *et al.*, 1993). Use of these cues will effectively direct the approach of female Hessian flies onto plants with the form of likely hosts (i.e. grasses). Once landed, the decision to oviposit is thought to be made after an assessment of the tactile and chemical cues via mechano- and chemoreceptors situated on the tarsi, antennae and ovipositor.

- Host plant finding in other cecidomyiids

Species in the family Cecidomyiidae have a life cycle that is characterised by limited movement during the larval stage (Mamaev, 1975). Adults are invariably shortlived and have elongated limbs and long narrow wings which are thought to be adapted for passive dispersal rather than active migration (Mamaev, 1975). "Of decisive importance in the dispersal of gall midges is their passive transfer by air flows which alternates with limited active searches for substrates for the development of the larvae in the area in which the female arrives through purely random factors" (Mamaev, 1975).

The capability of an insect pest to disperse and move into areas of previously uninfested or susceptible host plants, holds obvious importance for pest management practices. Yet only a small number of studies have been conducted on the dispersal behaviour of cecidomyiids (Schutte, 1965; Chiang, 1968). Field observations on the flight of the brassica midge, *Dasyneura brassicae*, revealed wind-aided migration for distances up to 500 m in the presence of light to moderate winds (Schutte, 1965). However what proportion of the insects recaptured, actually originated from the field or from the release was not ascertained in this study. The most comprehensive dispersal study of this insect, indeed of all cecidomyiids, was a field-based study of radioactively-labelled *D. brassicae* dispersing from an oil-turnip field (Sylven, 1970). Migration was extensive and wind-dispersed at 1.5-2.5 m above ground level. Within the plant canopy however, there appeared to be an upwind flight orientation towards areas of host plants, a behaviour that has not been observed with Hessian flies. Wind-aided dispersal would be an explanation for some historical observations of the Hessian fly (McColloch, 1917), where a limited number of mated females were caught in nets over three kilometres downwind of infested wheat fields. The knowledge of female Hessian fly field movement is limited to this single report, and the full extent to which movement within a crop habitat and wind-aided dispersal occurs is unknown.

Population ecology

- natural enemies

Parasitism by natural enemies can exert considerable control on Hessian fly populations, with summer peaks of 55% parasitism having been recorded (Hill & Smith, 1928). *Platygaster hiemalis* (Forbes) is the most common and effective summer and autumn-active egg parasitoid of the 42 parasitoid species attacking Hessian fly in the U.S.A. (Hill, 1926). Females are produced parthenogenetically from unfertilised eggs and males only from fertilised eggs, and on average, females out-number males 2:1. Females that have been mated will readily oviposit both fertilised and unfertilised eggs at a single oviposition (Hill, 1926). Parasitism of Hessian fly by *P. hiemalis* occurs predominantly in the egg stage but perhaps also during migration of the first instar larva as it moves from the leaf to the crown of the plant. The egg is located through chemical and visual cues by the female, who lays an average of 4.2 eggs per host egg (Hill, 1922). The frequent occurrence of embryonic twinning increases the number of *P. hiemalis* offspring reared to six per host pupa, with a maximum of 16 adults recorded from one puparium (Leiby & Hill, 1923). Females are longlived under suitable conditions, and Hill estimates the potential fecundity of an individual female to be around 3000 eggs (Hill, 1926). This parasitoid therefore has many attributes contribute to its success as a natural enemy of the Hessian fly.

Platygaster hiemalis is specific to Hessian fly and has been recorded parasitising both generations of Hessian fly, though more heavily in the autumn (Hill & Smith, 1928; Parks, 1923). Parasitism occurs at levels of 8-43% in the eastern States, 1-47% in the north central States (Hill *et al.*, 1939; Hill, 1953), and 40% in Georgia (Morrill, 1982). However, it must be remembered *P. hiemalis* is only one of a complex of natural enemies of the Hessian fly. Surveys of parasites over a period of nine years within the states of Pennsylvania, Maryland and Virginia in the U.S.A. recorded the relative abundances of 18 species of parasites on Hessian fly (Hill & Smith, 1928). Apart from *P. hiemalis*, there are two more serphoids in the genus *Platygaster*, the remainder being in the superfamily Chalcidoidea. Parasitoids would appear to effect a range of from slight to substantial control on Hessian fly populations in different areas over time (Hill & Smith, 1928; Macfarlane, 1990). Parasitism was found to be substantially reduced on those cultivars inducing Hessian fly larval antibiosis, therefore, genetic and biological methods of controlling Hessian fly are best viewed as mutually exclusive (Chen *et al.*, 1991).

Other natural enemies of adult Hessian flies include ants, predatory mites, spiders and coccinelid larvae (Barnes, 1956). Entomophagous fungae have been known to cause mortality in other cecidomyiids, particularly in the sedentary larval or pupal phases (Gagne, 1989). An epidemic of *Entomophthora brevinucleata* (Zygomycetes: Entomophthoraceae) killed related gall midges on grasses in Europe in 1983 (Keller &

Wilding, 1985). It is not known whether this particular fungus attacks Hessian fly, but it is likely that entomophagous fungi would cause some Hessian fly mortality from time to time.

- Hessian fly genetics

Experiments showed conclusively in the early 1900's (Painter, 1930a) that Hessian fly populations consist of a mixture of genetically distinct strains which differ in their ability to infest wheat genotypes. Hessian flies that are identical with respect to their genes for virulence to a range of wheat genotypes are assigned a biotype designation (Dent, 1991). A nomenclature system for these Hessian fly biotypes has been proposed using a system of digits (Patterson *et al.*, 1992). The biotypes of a Hessian fly population found in the north island of New Zealand have been classified according to this system (Harris, 1993). Different biotypes of Hessian fly exist (Gallun *et al.*, 1961; Hatchett & Gallun, 1968; Gallun, 1978; Stebbins *et al.*, 1980) and may continue to evolve over time (Black *et al.*, 1991). A genetic interaction exists between Hessian fly and wheat conferring a biotype-specific resistance that has been shown (Hatchett & Gallun, 1970; Hatchett *et al.*, 1981; Hatchett, 1986) to operate on a gene-for-gene basis. Historically however, this gene-for-gene resistance is not expected to be durable (Dent, 1991), with Hessian fly populations responding rapidly by evolving virulence within monocultures of resistant cultivars.

Indeed the Hessian fly and wheat interaction is a text book example of the costs of modern agriculture, and the need for sustainable methods of pest control. The planting of a single resistant cultivar in large areas of U.S.A. wheat belt has placed selection pressure on Hessian fly populations and resulted in the evolution of virulent biotypes (Hatchett & Gallun, 1968; Hatchett, 1969; Gallun & Kush, 1980). Hessian fly populations containing low variability in their genotypes would be likely to be decimated if a new resistant wheat cultivar for which they do not carry virulence genes suddenly appeared. But Hessian flies are quite mobile, meaning genetic mixing occurs between different populations increasing genetic variability in the population. Genetic variability confers a broader gene pool more likely to contain individuals carrying virulent genes. All this means that the greater the mobility and host-finding behaviour of the insect, the more rapidly the gene-for-gene system will evolve in the insects' favour (Dent, 1991). Although there is no evidence that Hessian flies can selectively oviposit on cultivars for which they contain genes for virulence (Day, 1974), the evolution of such a behaviour would also greatly reduce durability of single-gene resistance in wheats (Dent, 1991).

- Sex determination

The entire progeny of individual Hessian fly females is usually of a single sex (Painter, 1930b; Stokes, 1957), though bisexual progenies do also occur. The mechanism behind monogenous progenies is the elimination of the sex chromosomes during embryogenesis

(Gallun & Hatchett, 1969). In the Hessian fly it is the paternally-derived chromosome that is eliminated. When bisexual progenies do occur, the exceptional individuals are the result of nondisjunction of sex chromosomes during oogenesis (Stuart & Hatchett, 1991). This loss of the paternally derived chromosome holds implications for modelling population ecology of Hessian flies, as it means males breed as though homozygous, because they transmit only maternally-derived chromosomes. Females breed as heterozygotes showing normal transmission of both genomes, therefore only the phenotypes of the original maternal parent are recovered in each F_2 progeny and never both parental genotypes or the double recombinant (Day, 1974). This form of sex determination therefore means that migration of female Hessian flies carries a greater importance to increasing genetic variability of populations, than the migration of males, in comparison to a more "normal" genetic system. Predominant monogeny also has the effect of encouraging out-breeding (Stuart & Hatchett, 1991), another mechanism that increases genetic diversity within populations.

Hessian fly as a pest

- Influence of infestation on yield

Hessian fly infestations reduce crop yields in several ways. Infested young wheat and barley plants suffer the greatest damage, with extensive stunting often leading to either whole tiller or whole plant death. Hessian fly larval feeding after spike emergence weakens stems, which reduces yields (Hill & Smith, 1925), primarily through reduced grain set, reduction of heading, or closer to harvest by causing stem breakage (Blair & Morrison, 1949). The most substantial grain yield losses are attributed to a significant reduction in grain weight and number and in the number of spikelets produced per spike (Buntin & Raymer, 1992; Arias-Giralda & Bote-Velasco, 1992; Amri *et al.*, 1992). When wheat is grown for forage, losses through stunting from Hessian fly feeding can be measured as significant reductions in total forage yield (Buntin & Raymer, 1989). In these cases the quality of the wheat forage, in crude protein content, was not affected (Buntin & Raymer, 1989). In susceptible barley, grain yields declined significantly when infestation exceeded one larva per stem (Buntin & Raymer, 1992). Overall these losses of grain and forage production through Hessian fly feeding can devastate fields to the extent that it is not economically viable for the farmer even to harvest his grain. Hence the need for effective control measures.

- Cultural control methods

Cultural control measures, particularly the timing of sowing to avoid infestation, was one of the earliest measures developed to reduce Hessian fly populations. It was used for both spring-sown and winter wheat (Dean, 1917; McColloch, 1923), and typically involved

the delay of sowing until the majority of flies had emerged and oviposited their eggs. The "safe-sowing date" is effective when calculated for different geographic areas (Buntin *et al.*, 1990; Lidell & Schuster, 1990; Zelarayan *et al.*, 1991) and if it takes into account unusual weather patterns that can alter Hessian fly emergence (Headlee, 1912). Control can be even more effective if Hessian fly populations are monitored (Barnes, 1956) by estimating emergence from samples taken from fields (Foster & Taylor, 1974; Gossard, 1916).

Other cultural methods of reducing Hessian fly infestations also involve minimising the survival of overwintering pupae by burning off stubble and deep ploughing paddocks to prevent emergence through the soil (Barnes, 1956; Blair & Morrison, 1949; Dean, 1917; McColloch, 1923). Rotational cropping (Lidell & Schuster, 1990) and the destruction of alternative sites for overwintering such as volunteer wheats and grass hosts in field borders (Buntin & Chapin, 1990) are other cultural aids to control. The burning of stubble on its own is not effective (Zeiss *et al.*, 1993a), but coupled with disking or deep ploughing gives effective control (Chapin *et al.*, 1992). In some sandy soils, however, repeated ploughing of paddocks can be an ineffective control by bringing buried pupae back to the soil surface (Chapin *et al.*, 1992). In the early 1900's it was known that the effectiveness of cultural methods in controlling Hessian fly populations needed to be based on local biology, such as the number of generations per year and the effect of environmental conditions. Local knowledge needs to be integrated with co-operative effective farming practices throughout the effected regions (Blair & Morrison, 1949; Dean, 1917; Gossard, 1916). This advice still holds true today, even with the added advantages conferred by host-plant resistance.

- Host plant resistance

Cultivars of wheat containing single resistance genes (McColloch & Salmon, 1923) have been used extensively as a method of controlling Hessian fly populations (Gallun, 1977). The nature of this resistance to Hessian fly is through larval antibiosis (Shukle *et al.*, 1990) and is controlled primarily by single dominant genes (Gallun, 1977). However, as previously mentioned, the effectiveness of this strategy is limited by rapid evolution of resistant biotypes of Hessian fly (Gallun & Kush, 1980; Stebbins *et al.*, 1980). Genetic variability in wheats is large, giving a substantial genetic pool from which wheat breeders can select new lines of resistance. However, the genes that cause larval antibiosis to Hessian fly in wheat are limited to 20 (Patterson *et al.*, 1992), and two of the 13 identified resistance genes have already been effectively lost by the evolution of virulence (Sosa, 1981). Models have been developed by population geneticists to explore the effectiveness of various strategies for deploying resistance genes (Cox & Hatchett, 1986, Gould, 1986). Several strategies have been proposed to delay the evolution of virulent biotypes (Gould, 1986) including sequential release of two pure cultivars, each with a single

resistance gene, until virulence develops in the Hessian fly population. At this stage, another cultivar, containing another resistant gene is deployed, and so on. The alternative strategies involve methods to reduce genetic homogeneity present in monocultures containing a single major resistance gene by increasing genetic diversity in time and space (Cox & Hatchett, 1986). These include release of a random spatial mixture of two cultivars, and pyramiding, which is the incorporation of more than one resistant gene into a single wheat cultivar, or sowing more than one wheat cultivar at one time, each containing different genes for resistance. Models testing these strategies for durability of resistance have proposed pyramiding, with resistant plants mixed with totally susceptible plants (Gould, 1986). However, there are also proponents for sequential release of single gene cultivars (Cox & Hatchett, 1986). All these methods are designed to reduce the rate at which virulent biotypes of Hessian fly will evolve in the field.

The most important factor in deciding which strategy will be most effective is an understanding of the ecology of the insect (Kennedy *et al.*, 1987). Durability of strategies such as field mixtures will be strongly linked to the migration rate of Hessian flies (Gould, 1986), which influences the interbreeding of subpopulations in the field. Each of the suggested deployment strategies comes with its disadvantages. The sowing of mixtures of wheat genotypes with different resistance genes may effectively reduce the rate of virulent biotype evolution by enhancing genetic heterogeneity. However, for this approach to be practical both genotypes must exhibit identical characteristics such as maturation time, yield and quality (Dent, 1991). The regional deployment of different resistance genes would avoid this difficulty, with wheat genotypes being rotated between districts. The practicalities of such a solution mean it would only succeed where agriculture is heavily controlled by an outside force and is not market-driven. When market-driven, farmers would be more likely to sow the cultivar that they have experienced and which will give them the greatest short-term profit and are less likely to follow a rigidly controlled rotation of unfamiliar cultivars (Dent, 1991). The breeding of two or more resistance genes into a single variety ('pyramiding') would appear to remain the most viable option. Pyramiding also has its drawbacks, however. Breeding two resistance genes into a single cultivar is time-consuming and costly. Also if a virulent biotype should evolve against the pyramided cultivar, the two genes could both be rendered useless sooner than if they had been deployed singly in separate cultivars (Dent, 1991).

Sequential release of resistance genes is another popular strategy that can sustain the use of resistance genes (Cox & Hatchett, 1986). As virulent biotypes evolve different cultivars with new genes can then be released. The difficulty with this strategy is that careful and constant monitoring of the genetic makeup of pest populations is required so that new resistance genes can be released before the original resistance gene is overwhelmed by virulent individuals. A similar alternative involves the rerelease or

rotation of a resistance gene at a later period when the frequency of virulent biotypes is greatly reduced (Foster *et al.*, 1991). Which method proves to be the most effective for genetic control may depend on the result of further studies into the field movement and genetic mixing that occurs in Hessian fly populations.

- Chemical control methods

In situations where cultural control methods are ineffective or inconvenient and resistant cultivars are not available, the use of pesticides to control Hessian fly has been investigated as an alternative (Brown, 1960). Treating of seed with systemic insecticides was investigated but tended to cause phytotoxicity problems to the germinating seedlings (Brown, 1960). Further research into systemic insecticides such as carbofuran have since resulted in yield increases without the associated phytotoxicity problems (Morrill & Nelson, 1976; Buntin, 1990). Disulfoton in-furrow treatment gave economically viable control of Hessian fly of autumn infestation in South Carolina and coastal Georgia, U.S.A. (Chapin *et al.*, 1991; Zelarayan *et al.*, 1991), and on autumn wheat in Morocco (Lhaloui *et al.*, 1992). The same result was not reported from experiments in Florida, U.S.A. (Hartman *et al.*, 1992) and Spain (Duran *et al.*, 1992), where such treatments were deemed to be ineffective or could not be economically justified. A study in Georgia confirmed a well-known disadvantge of chemical usage: parasitoid activity was reduced by the use of broadcasting systemic insecticide against the Hessian fly (Morrill, 1982). This means chemical control methods should preferably only be used when cultural methods and biological control are not sufficient to control pest population density.

- Postharvest disinfestation

Hessian fly is not present in Japan. Therefore, before U.S.A. wheat straw could be imported into Japan, it was required to be free of Hessian fly pupae. Effective mechanisms for destroying pupae in bales have been developed in order to meet these objectives. Methods that are effective include heat treatment (Sokhansanj *et al.*, 1993), high-pressure compression (Yokohama *et al.*, 1993a) and the multiple approach of compression following fumigation with hydrogen phosphide (Yokohama *et al.*, 1993b). Development of these techniques means that U.S.A. wheat straw has now gained access to the Japanese market, with no threat to cereal industries in Japan resulting.

Hessian fly as a pest in New Zealand

- Wheat in New Zealand

Wheat was first introduced to New Zealand by colonial missionaries in the mid 1800's, but initially was only sown in low acreages. By 1873 about 157000 acres were estimated to be sown to wheat (Hilgendorf, 1939). In the early 1900's a semisolid straw variety,

'Solid Straw Tuscan' became popular, and soon accounted for 70% of the total yields from the Canterbury area. This was such a popular variety because it was less likely to fall over in strong winds than the hollow straw varieties (Hilgendorf, 1939). In the 1950's and onwards, the New Zealand wheat industry consisted of a number of wheat varieties bred for New Zealand conditions (McEwan, 1959). The characters shared by many of these wheats at that time were classified as intermediate growth period, short semi-solid straw, very high yield, and low resistance to disease (McEwan, 1959). Some cultivars were developed for their bread-making, and some for their pasta-making properties. The most popular varieties included resistance to the most common rusts as well as to Hessian fly (McEwan, 1959). At some stage, probably the 1980's, wheat breeders in New Zealand stopped incorporating resistance to Hessian fly in their wheat breeding programs and wheat was bred purely for yield and flour-making qualities (B. Griffin, wheat breeder N.Z. Crop & Food Research Inst., pers. comm.). The deregulation of the wheat industry (Dunbier, 1993) has meant cultivar development and sowing is market-driven and extensive areas of wheat are sown in the same cultivar. It remains to be seen whether under these conditions Hessian fly and other pests will become severe problems in New Zealand wheat.

- Hessian fly in New Zealand

Early in 1888 the Hessian fly was first identified as infesting New Zealand wheat crops. While the first reports of infestation were from the north island (Marton area) reports from the south island (Nelson and Blenheim areas) soon followed (Kirk, 1894). The Minister of Agriculture reported "the fly appears to have been introduced, while in the pupa stage, among straw packing of agricultural machinery imported from America". In 1893 Hessian fly outbreaks again occurred in the Rangitikei area and were reported in the Masterton district and in Otago (Kirk, 1893).

There were no published reports of Hessian fly again until the 1930's (Morrison, 1938). In a survey of wheat crops in Canterbury and north Otago during the summer seasons of 1936-37 and 1937-38, Morrison measured the percentage of broken straws in a crop due to Hessian fly larval feeding. The districts worst affected were south Canterbury and north Otago, with averages of 9.2% and 7.8%, respectively (Morrison, 1938). Within these districts the areas of Hook, Tokarahi, and Willowbridge suffered crop losses of over 15%, losses expected to well exceed the economical threshold level (Chapin *et al.*, 1989). At least two generations of Hessian fly are present each season in New Zealand (Blair & Morrison, 1949), the first generation on young wheat between October and December causes the greatest damage, with severe stunting and death of affected tillers. The second generation which attacks in January-February is more likely to cause stem breakage and shrivelled grains.

In New Zealand cultural control methods of crop rotation and burning-off stubble followed by deep ploughing were thought to be vital to the prevention of Hessian fly outbreaks (Blair & Morrison, 1949). Comments made by Kirk would suggest that in the 1890's farmers did not consistently use these methods, thereby probably contributing to the spread of Hessian fly (Kirk, 1898). A special deep plough to bury wheat stubble containing puparia was supplied by the Government to the Marton district after the 1888 outbreak. However this plough was never used, because farmers complained that it would injure their ground by bringing clay to the surface (Kirk, 1894). Another factor identified as affecting severity of Hessian fly attack on wheats was the variety sown. In Canterbury and north Otago infestation was found to be related to wheat variety, with cultivars 'Dreadnought' and 'Hunters' infested at 12% and 15% of all straws, respectively (Morrison, 1938). 'Tuscan' was the most resistant cultivar, at 3.2% of straws infested. These solid straw varieties, such as 'Tuscan' showed a lower percentage of plants and stalks infested and the average number of pupae per stalk were lower than in the more susceptible varieties (Blair & Morrison, 1949; McEwan, 1959).

There are no records of Hessian fly outbreaks from the 1950's through to the 1980's. A 1971 New Zealand Department of Agriculture report on the Hessian fly stated that "though formerly important, with resistant wheat varieties it is no longer of major concern" (Anonymous, 1971). It is likely that these resistant varieties and more widespread adoption of cultural control methods will have kept the incidence of Hessian fly to well below economic levels up to the 1980's. However, in the late 1980's farmers began to again report losses of wheat to Hessian fly in south Canterbury (D. Penno, crop farmer south Canterbury, pers. comm.), and Hessian fly was discovered in high numbers in a wheat field in the Manawatu (T. Withers, 1992) where excessive rain had been blamed for poor yields. The Hessian fly therefore, remains active in New Zealand, though not always at noticeable levels.

- Parasitoids of the Hessian fly in New Zealand

One of the factors contributing to the low incidence of Hessian fly outbreaks from the early 1900's through to the present may have been natural enemies. Parasitoids were reared from pupae collected from the first outbreak of Hessian fly in Marton in 1888 (Kirk, 1898). These specimens were identified as being Proctotrupidae, most certainly *Platygaster hiemalis* . In 1894 a consignment of *Pediobius epigonis* (Walker) and *Platygaster hiemalis* were shipped from England in the steamship "Gothic", and released in infected districts (Kirk, 1894). It is thought the shipment probably contained more than a thousand parasitoids (Macfarlane, 1990). These two parasitoids established well and are now present throughout the country in wheat growing areas.

Platygaster hiemalis is reported to be the most widespread and effective parasitoid specific to Hessian fly in the world. *P. hiemalis* has been recorded on Hessian

fly in all areas of New Zealand from pupae collected from wheat, barley and prairie grass host plants (Macfarlane, 1990; Prestidge, 1992; Thomson, 1922). Levels of parasitism in the 1890's from wheat from various sites ranged from 0-25% of pupae (Kirk, 1898). In 1987, 38% of Hessian fly on barley (Macfarlane, 1990) were parasitised by *P. hiemalis*. Over two seasons in the Waikato between 26-42% and 3-34% of pupae from prairie grass (Prestidge, 1992) were parasitised, with a mean of 3.2 *P. hiemalis* emerging per pupa. These levels of parasitism are comparable to those reported in the U.S.A. (Morrill, 1982).

Other parasitoids attacking Hessian fly in New Zealand include *Pediobius acantha* (Walker) and *Aprostocetus zosimus* (Walker) (north and south islands), *Macroneura vesicularis* (south island, Macfarlane, 1990) and two previously unrecorded *Trichomalopsis* species from the Manawatu (T. Withers, unpub. data). A survey of the distribution and levels of parasitism of Hessian fly over the season and on different host plants would reveal to what extent these other parasitoid species are parasitising Hessian fly in New Zealand.

- The Hessian fly and prairie grass

In 1987 the Hessian fly resurfaced as a pest of a newly released pasture grass, called prairie grass, *Bromus willdenowii* (Kunth) cv. 'Grasslands Matua' (Prestidge *et al.*, 1987). At that time prairie grass was not providing the feed levels expected of it, due to poor persistence in the field (Sellars, 1988). A survey of pests revealed Hessian fly as the cause of this poor persistence with up to 88% tiller infestation and death (Prestidge & Van der Zijpp, 1988; Thom *et al.*, 1992). An in depth study on Hessian fly infesting prairie grass in the north island revealed that the pest has three generations in a year and overwinters for four months in the pupal stage (Prestidge, 1992). Larval and pupal infestation levels were from 1-5 per tiller over the two seasons studied, a higher rate than generally recorded on wheat. The maximum infestation recorded was 50 larvae or pupae on one plant (Prestidge, 1992). Prairie grass, when present in field borders and oversown pasture mixes, undoubtedly provides a suitable overwintering site for Hessian fly. Flies emerging from prairie grass in the spring, are then in position to infest any wheat or barley fields in the vicinity.

Aims

The aims of the following experimental chapters are to examine several aspects of Hessian fly behaviour that are important in the management of this pest. Infestation of susceptible wheat crops begins when the mated female Hessian fly has passed through the post-mating pre-oviposition phase and actively begins responding to host-plant cues. The following two chapters address this phase, specifically, what aspects of the environment influence female behaviour. From observations of foraging females in arrays of host and

non-host plants, I examined how the female Hessian fly partitions her time and resources between egglaying and foraging behaviours. By altering aspects of the host plant arrays, I identified aspects of foraging behaviour that are random or flexible, and what aspects are non-random or fixed by the female. Chapter three addresses how these foraging behaviours may be altered by a commonly encountered environmental factor in the field, wind. The effect that exposure to wind has on the survival and flight ability of the female fly and how wind alters oviposition, are also investigated.

During the above experiments, I observed a plasticity in the number of eggs that were oviposited in clutches by a female Hessian fly on single host plants. A logical step was to investigate the benefits, to the female and to larvae hatching from those eggs, of being deposited in small versus large clutches, assuming the plant has a limited carrying capacity. Chapter four, covers an experiment which examined this variation in clutch size on Hessian fly survival and potential fecundity. The experimental work in these chapters has contributed to a greater understanding of the factors and complex of processes influencing the oviposition and foraging behaviour of female Hessian flies.

The review of the literature revealed a lack of understanding of the ability of the Hessian fly female to move during the foraging phase. The previous experiments, were on a small spatial scale and did not allow me to measure the rate or distances females can move over time. In addition, no field studies have ever been reported on the Hessian fly, despite its importance as a major pest, and the nature of its spread throught the cereal growing regions of the world. Chapter five uses a combination of methods to examine the ability of females to locate patches of wheat in the field, and compares the rate of movement of females in host compared to non-host plant habitats. Movement rates as well as distances over which plants can be located are both factors presently missing from models used to predict the rate of gene flow between neighbouring populations of Hessian flies. In addition the distances females can move during foraging is important to the effectiveness of cultural control methods. This chapter provides information that may be useful for the design of these methodologies.

Finally, chapter six of this thesis reports on a survey of wheat fields conducted in the spring of 1994 in the major wheat growing regions of New Zealand. Fields of wheat were sampled and examined for the presence of Hessian fly in order to ascertain its status as a pest of wheat in New Zealand. In addition, pupae were collected to ascertain parasitism levels. This survey addresses the uncertainty over the presence and distribution of Hessian fly in New Zealand, and whether or not it is the major pest affecting wheat crops. This chapter also reports on an examination of the rate of spread of Hessian fly infestation in a wheat field in the Manawatu district in relation to wind direction, thereby complementing the predictions made in chapter three.

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CHAPTER TWO

Foraging for oviposition sites in the Hessian fly: random and non-random aspects of movement

Abstract

Movements of ovipositing Hessian flies, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), were quantified in plant arrays which varied in one of three ways: (1) in distances between patches of host plants, (2) in the size of host plant patches, and (3) in the density of host plants within arrays of non-host plants. Durations and frequencies of a range of behaviours were quantified, with the expectation that females would adjust some, but not necessarily all behaviours when distributions of host and non-host plants were altered. Foraging behaviours that were adjusted when plant distribution was altered were seen as evidence for nonrandom movement (sensu Morris & Kareiva, 1991). Nonrandom components of movement consisted of nonrandom settlement on host plants and area-restricted search after visiting host plants. Ovipositing females also exhibited directed responses to plants; however, directed responses appeared to be based on generalised visual stimuli from grasses rather than species-specific plant stimuli (e.g., odours). Several behavioural parameters did not change when plant arrays were altered. Females stayed in wheat patches for relatively constant periods of time and laid similar numbers of eggs before leaving wheat patches regardless of the number of plants in the patch or the time taken to find the patch. Nonrandom movements resulted in the placement of eggs on hosts rather than non-hosts, while random movement contributed to egglaying over larger areas.

Key words. Cecidomyiidae, flight behaviour, insect-plant interactions, *Mayetiola destructor*, plant stimuli.

Introduction

Many researchers studying insect-plant relationships have focused on how ovipositing females find suitable host plants. Of particular interest has been the nature of the sensory information females use when finding hosts. This sensory information has been studied by presenting females with chemical, visual or tactile stimuli associated with host and non-host plants and scoring either numbers of eggs laid or simple behavioural responses such as landing (Bierbaum & Bush, 1990; Kostál, 1991; Rivet & Albert, 1990). As a result of these studies, many plant-based sensory inputs to oviposition behaviours have been documented.

In many insect herbivores, progress in understanding sensory aspects of insect-plant relationships has not been paralleled by progress in understanding how ovipositing females actually adjust their movement in response to plant stimuli. Morris & Kareiva (1991) in a recent review of the movement of herbivorous insects, characterised movement as being either random or nonrandom relative to host plants. Random movement occurs when the "frequency, rate, and orientation of movement are unrelated to the suitability of plants within the perceptual range of the insect". Movement that shows some relationship to the location of host plants, is then considered to be non-random and can take one of several forms. In its simplest form, the rate and direction of movement are random (relative to plants) but the insect, upon contacting a plant, adjusts its movement so that it either settles on the plant (non-random settlement) or moves away. A slightly more complex form of nonrandom movement occurs when an insect contacts a plant and then, based on the information gained, adjusts its movement so that after it leaves the plant it stays longer in the area surrounding that plant (area-restricted search). The most sophisticated adjustment of movement in relation to plants consists of an oriented response to plant stimuli spatially separated from the responding insect (Morris & Kareiva, 1991).

The Hessian fly is a pest of wheat, *Triticum aestivum* L., but can also feed on a limited number of other grasses in the tribe Hordeae, such as barley and rye (McColloch, 1923; Jones, 1938; Stokes, 1957). By contrast, oat, *Avena sativa* L. (tribe Aveneae) does not support growth of Hessian fly larvae (Morrill, 1982). In the Hessian fly, the larva moves only once, creeping from the leaves, where it hatches from the egg, to the crown of the plant, where it feeds until pupating. The adult stage of the Hessian fly is more mobile. Males start flying several hours after eclosion (Bergh *et al.*, 1990) and fly upwind to virgin females emitting sex pheromone (Harris & Foster, 1991). Female Hessian flies do not fly until several hours after mating (Harris & Rose, 1990; Harris & Foster, 1991). However, once flight and oviposition begin, the female does little else (i.e., she does not feed or remate) until she dies 6 to 24 hours later (Bergh *et al.*, 1990).

How Hessian fly females adjust their movement to enhance their encounter rate with host plants is poorly understood. Simple laboratory assays (Harris *et al.*, 1993) in which the movements of females were followed for short periods of time (less than 60 s) indicate that the responses of Hessian fly females to host plant stimuli include directed movement and nonrandom settlement. Directed movement towards host plant stimuli was suggested by the greater number of females that flew into 1 cm zones surrounding plant models that had vertical edges, reflected 520-570 nm light, and emitted wheat odours (Harris *et al.*, 1993). Nonrandom settlement was evident when plant models were treated with either chloroform extracts of wheat foliage or chloroform alone: females stayed six times longer and laid ten times more eggs on models with wheat extracts (Foster & Harris, 1992). Whether female Hessian flies also exhibit random movement or area-restricted search in addition to non-random settlement and directed movement during foraging behaviour is not known.

In this paper I examine the contributions of random and nonrandom movement to the foraging behaviour of female Hessian flies. We recorded for periods up to 25 minutes the movements of individual females released into plant arrays which varied in one of three ways: (1) in distances between patches (i.e., groups) of host plants; (2) in the size of host plant patches; and (3) in the density of host plants (wheat) within arrays of non-host (oat) plants. Durations and frequencies of a range of behaviours were quantified, with the expectation that females would adjust some, but not necessarily all behavioural variables when distributions of host and non-host plants were altered.

Materials and methods

Insect rearing and plant material

Hessian flies that originated from a wheat field in Palmerston North, New Zealand, were reared for 1-8 generations in the laboratory on a susceptible wheat cultivar, 'Karamu', before being used in experiments. In this laboratory culture, females oviposited on plants in the 2-3 leaf stage. After being held for ca. 30 days in the greenhouse (20 ± 5° C), infested wheat plants were moved to an environmental chamber (24°C, 70% r.h., 12:12 L:D, with lights on at 0700 h). Adult Hessian flies started emerging from plants ca. 7-10 days later.

Virgin females were collected daily during the hour of peak eclosion (0700 - 0730 h) and were placed at 0730 h in glass containers with an excess of males. Females that mated within 10 minutes (as indicated by the cessation of the "calling" posture, Bergh *et al.*, 1992) were transferred to a 50 x 50 x 50 cm cotton mesh and aluminum frame cage which had moist soil covering the floor. After passing through the stationary phase that

follows mating and precedes oviposition (Harris & Rose, 1991), females began flying at ca. 1100 h.

Wheat (cultivar 'Karamu') and oat (cultivar 'Awapuni') seeds were planted in plastic pots in a peat pumice sand mix with a slow-release fertiliser. Plants were grown in a glasshouse and used in experiments when in the single leaf stage.

Experimental arena and general procedures

Females were introduced into plant arrays situated within an observational arena. The arena consisted of a square wooden base (2 x 2 m across and 0.1 m deep) and a cover made of white netting (2 x 2 m and 1 m high) suspended over the wooden base by wires from the glasshouse ceiling. The arena was filled with a moistened sand and peat mix. Pots containing plants used in arrays were sunk into the mix so the media within pots was level with the mix in the arena. The observer stood to one side of the arena, inside the netting. Plots of flight directions taken by flies (as in Root & Kareiva, 1984) showed the position of the observer did not influence the movement of flies.

Observations of females foraging within plant arrays were made between 1100 to 1400 h (3-6 females tested each day). At the time of their introduction into the arena, females had not oviposited or contacted plants (except see Experiment 3); however, females were pre-exposed to grass volatiles from within the glasshouse. For each observation, a female that had been actively flying in the holding cage was moved by aspirator to the soil in the centre of a patch designated for each experiment as the release patch (arrows in Fig. 1). The female then walked or flew a short distance to one of the plants in that patch. Behavioural recording then commenced for the next 25 min.

Locations and behaviours of Hessian flies were recorded to the nearest second with a Psion Organiser microcomputer (Model LZ50, Psion PLC, London, UK) programmed using the behavioural software 'The Observer' (Noldus, 1990, Wageningen, The Netherlands). Locations of flies were categorised as mutually exclusive events: in the air, on the soil, against the netting, lost from sight, or on a plant (each plant within the array was numbered).

At the end of each observation, the female was transferred to a glass vial and held in a freezer at 0° C. Several hours later the female was removed and winglength measured (being the distance between the axillary sclerite and end of radial sector vein, Bergh *et al.*, 1990). Plants were removed from the arena and the numbers of eggs/plant recorded separately for each plant in each patch. Thus, the spatial arrangement of eggs laid within each plant array was recorded for each individual female.

Female Hessian flies are small (4-6 mm long and 1-2 mm diam), fly rapidly and thus easily can be lost from sight during observations. In 43% of the total observations, the fly was lost once during the observation (in 65% of these cases, the fly was lost for

less than 60 s). If a fly was lost for more than 200 s the observation was abandoned; however, if the fly was successfully relocated within 200 s, the observation continued for the full period. In the latter case, the time that the fly was lost was subtracted from the total observation time for data analyses. Observations were terminated prematurely if a female landed on the netting and remained there for over five min. If a female did not oviposit on more than two plants during the 25 min or never moved to a second patch after release, that female was excluded from analysis.

During observations, weather conditions varied from heavy cloud to bright sun. Flies appeared less active in duller light conditions. The effects of sunlight and perhaps also temperature (range of 24-36° C) on the behaviour of females undoubtedly added variability to the data; however, I assumed that these effects were evenly distributed across all treatments because presentation order was randomised over time.

Experiment 1: Interpatch distance

In these three plant arrays (Fig. 1A), the distance between the four wheat patches was varied from 20 to 40 to 80 cm. Patch size was held at four plants/patch, one plant in each of the four corners of a 5 x 5 cm pot. The first set of observations was performed over a three-week period in October 1992 (41 flies), with another week of observations completed under similar weather conditions in June 1993 (23 flies). The order of testing females in the three plant arrays was randomised within each day of testing. Of the 64 flies observed, nine were excluded from analyses because of one of the criteria described previously.

Experiment 2: Patch size

In these three plant arrays (Fig. 1B), patch size was varied from one plant (in the middle of the pot), to four plants (2 x 2 formation in each corner of a 5 x 5 cm pot), to nine plants (3 x 3 formation, spaced in a 12 cm diam pot). The number of wheat patches was held at six, with a central patch surrounded by five others, each at an interpatch distance of 30 cm. Again, this experiment was conducted during two periods, with 36 and 18 flies observed during November 1992 and June 1993, respectively. The order of testing females in the three plant arrays was randomised within each day of testing. Of the 54 flies observed, six were excluded from analysis because they never moved to a second patch during the observation.

Experiment 3: Host among non-host patches

In these three plant arrays (Fig. 1C), the ratio of wheat patches (at four plants per patch) to oats patches (also four plants per patch) was varied from 2:14 to 4:12 to 8:8. Interpatch distance was held constant at 20 cm. In this experiment, females were given a wheat plant to oviposit on for 5 to 10 min before being introduced into the flight arena into an oat patch (see Results for explanation). In this experiment, the order of testing females in the three arrays was rotated within each day rather than randomised, with a different array being the first to be tested on consecutive days of testing. This experiment was conducted during two separate periods, with 34 and 23 flies observed in December 1992 and July 1993, respectively. Of the 57 flies observed, 12 flies were excluded from analysis because they either never landed on plants or did not lay any eggs.

Data analysis

Flies were included in analyses except where noted above or (in the case of four flies) when identified as an extreme outlier on a Mahalanobis distance plot (JMP, SAS, 1989). Entering a patch was defined as the time when a fly landed on any plant within that patch. Exiting a patch was defined as either (1) the time at which the female initiated a flight that resulted in movement between patches, or (2) as the time at which a flight of more than five sec duration was initiated. This later category was necessary to distinguish the short circling flights that took females back to the same patch from the longer flights that took females away from the original patch but eventually brought the female back to the same patch. Five sec was chosen as the cutoff point because a five sec flight would normally take a female 30 to 50 cm away from the original patch, a distance at which the female no longer appeared capable of sensing the patch she had left. Females that left the immediate boundaries and reentered the same patch after a short (<5 s) circling flight were not considered to have exited the patch.

Deprivation time was estimated as time from mating (07.30 h) until introduction to the arena. Mean eggs laid per patch was calculated only for those patches which were not revisited during the observation. Intrapatch flights were defined as flights taken between plants in the same patch, including return flights to the same plant of less than five sec duration. Since the duration of these flights could not be measured accurately, only their frequency was analysed. Interpatch flights were defined as those flights taken between plants in different patches, or back to the same patch of five sec or more duration. Flights between plants and the soil or netting were excluded from this category. Both the duration and frequency of interpatch flights were analysed.

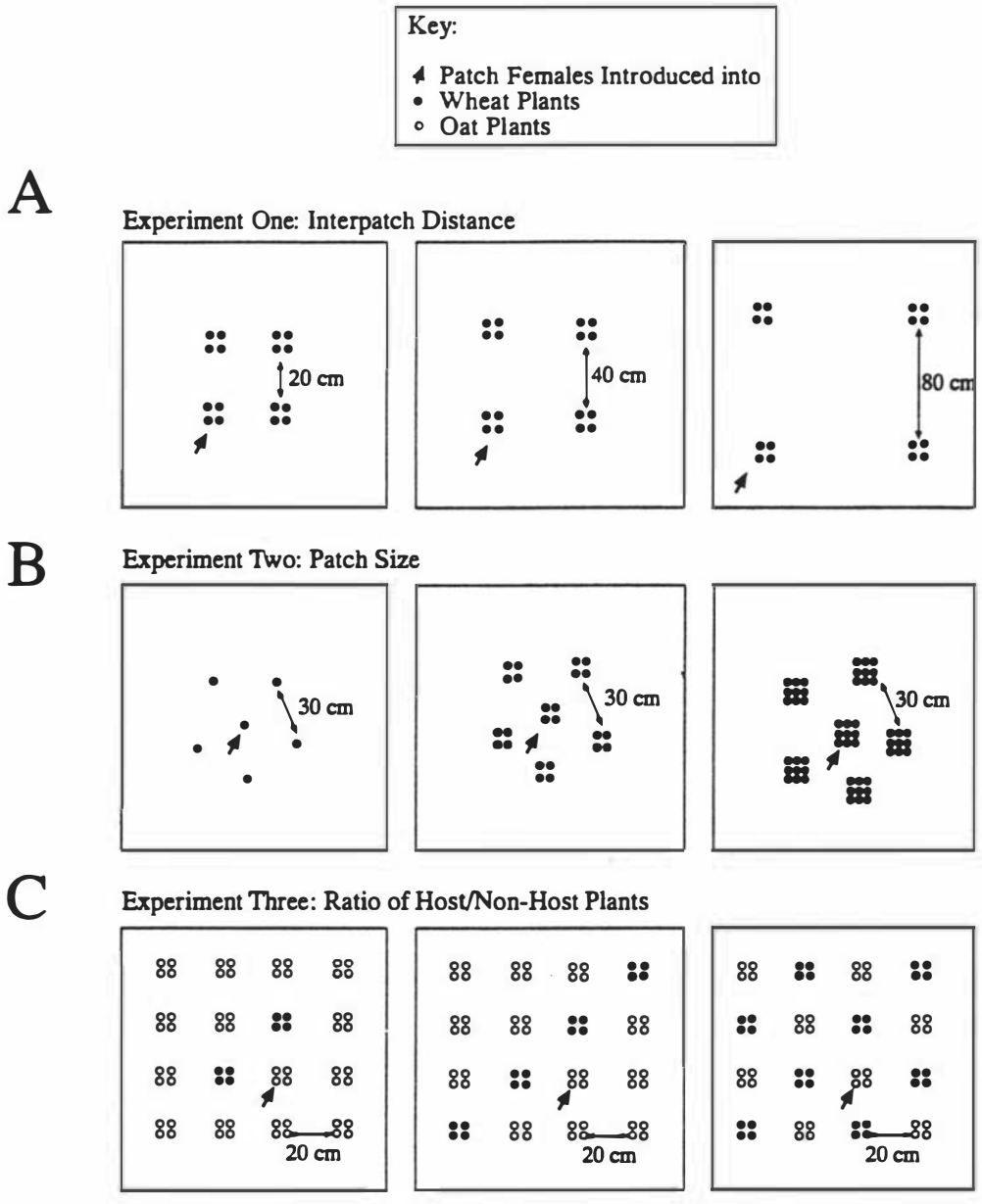

Fig. 1. Spatial arrangement of plants in (A) Experiment 1 on interpatch distance, wheat patches 20, 40, or 80 cm apart with patch size of four plants, (B) Experiment 2 on patch size, wheat patches composed of one, four, or nine plants with interpatch distance of 30 cm, and (C) Experiment 3 on hosts among non-hosts, ratios of wheat:oat patches 2:14, 4:12, or 8:8 with patch size of four plants and interpatch distance of 20 cm. The patch the female was released into by aspirator is indicated by an arrow.

Data were initally separated into two blocks, based on the two sets of observation dates; however, as there were no block differences, both data sets were subsequently pooled for analyses. Since the variances of almost all behavioural parameters were not homogeneous according to Bartlett's test (JMP, SAS, 1989) and could not be made homogeneous by transformation, non-parametric tests were used (Wilcoxon and Kruskal-Wallis, JMP, SAS, 1989). Distributions of eggs were compared using G-tests of independence, adjusted with the Williams' correction factor (Sokal & Rohlf, 1981).

Results

General observations

In almost every introduction of a female into the release patch, the female flew or walked directly to the nearest plant, and commenced examining behaviours (see Harris & Rose, 1989 for detailed descriptions). Flights were of several types. The most frequently seen were the short (1- 4 cm), rapid flights between plants within a patch (intrapatch flights). After a series of intrapatch flights, exiting flights out of the patch then occurred. Sometimes these flights took females directly back to the patch they had just exited (circling flights). Other interpatch flights occurred directly between two patches. Interpatch flights with more meandering flight paths also occurred. Some of these brought females near other patches, which were sometimes entered or other times ignored. Other meandering flights took females to the netting of the arena, where they flew parallel to the netting for various periods of time (seconds to minutes) before returning into the main arena and reentering plant patches. Overall, females spent most of their time within plant patches, with interpatch flight times comprising only a small percentage of foraging time.

Experiment 1: Interpatch distance

Decreasing the distance between wheat patches from 80 to 40 to 20 cm apparently made patches easier to find. This was reflected in shorter durations of interpatch flights (Table 1), a greater number of patches being located during the observation period (Table 1), and in more eggs being laid in patches other than the patch where the female was initially released (Fig. 2, distributions of eggs significantly different, G test of independence, G_{adj}=168.7, df=6, P<0.05).

Other behavioural parameters were not influenced by interpatch distance. In terms of flight parameters, the number of interpatch flights taken (Table 1) and the percentage of time spent flying (Table 1) were not significantly different for females

foraging at different interpatch distances. Mean patch durations (Fig. 3A), mean numbers of eggs laid within patches (Fig. 3B), on-plant egglaying rates (Table 1, eggs laid/seconds on plants), and overall egglaying rates (Table 1, eggs laid/seconds observation time) also did not vary with interpatch distance.

Changes in the frequency or duration of behaviours occurred within the 25 minutes females foraged, regardless of the distribution of plants. For example, females spent more time (Kruskal-Wallis, Chi^2=68.8, df=6, P<0.001) and laid more eggs (Kruskal-Wallis, Chi^2=41.2, df=6, P<0.001) in the release patch than in the second and subsequent patches encountered, regardless of interpatch distance (see Fig. 4 for examples). We also examined relationships between deprivation time (time from mating to introduction to the arena) and various behavioural parameters. No significant relationships were found between (1) deprivation time and eggs laid in the first patch (ANOVA, $F_{1,46}$=0.69, P<0.5; deviation from zero, t= -0.83, P< 0.5), (2) deprivation time and overall egglaying rate (ANOVA, $F_{1,52}$=0.0012, P<0.99; deviation from zero, t=0.03, P<0.99) or (3) deprivation time and on-plant egglaying rate (ANOVA, $F_{1,52}$=0.061, P<0.9; deviation from zero, t=0.25, P<0.9). However, on-plant egglaying rates showed a positive relationship with wing length (ANOVA, $F_{1,44}$=13.1, P<0.001; deviation from zero, t=3.6, P<0.001) and wing length was positively correlated (Fig. 5) with numbers of mature eggs found in the ovaries (ANOVA, $F_{1,31}$=149.4, P<0.001; deviation from zero, t=12.2, P<0.001).

Experiment 2: Patch size

Increasing the size of wheat patches from 1 to 4 to 9 plants (with a constant interpatch distance of 30 cm) also made patches easier to find. When females foraged among larger patches (Table 2), interpatch flight durations were significantly shorter, a significantly smaller proportion of time was spent flying, and a significantly larger proportion of time was spent on plants. The ease of finding plants was not, however, reflected in numbers of patches visited, which were similar for all three arrays (Table 2). Numbers of interpatch flights performed did not differ for females foraging in the three different arrays (Table 2).

Patch size also influenced within patch time allocations. Females in patches containing nine plants spent less time visiting the first plant they encountered within the patch than females visiting patches with one or four plants (Fig. 6A). Patch size also influenced within-patch flight activity (Fig. 6B), with more short flights between plants occurring in patches containing nine plants. However, in spite of these differences, females did not spend more time in larger patches (Fig. 7A) and did not lay more eggs

Table 1. Results of Experiment 1 on the influence of interpatch distance on various foraging flight and ovipositional parameters.

Interpatch Distance	n	Duration of interpatch flights[1] (s) x+SE	Number interpatch flights[2] x+SE	Percent time flying x+SE	Number patches visited[3] x+SE	Percent time on plants x+SE	Rate of on-plant egglaying (eggs/s) x+SE	Overall rate of egglaying (eggs/s) x+SE	Duration of observation (s) x+ SE
20 cm	19	7.0 ± 1.6	2.7 ± 0.4	6.6 ± 0.9	2.9 ± 0.21	71 ± 4.7	0.056 ± .005	0.036 ± .003	1401 ± 46
40 cm	20	11.0 ± 1.6	1.9 ± 1.6	4.9 ± 0.85	2.1 ± 0.20	68 ± 4.5	0.056 ± .005	0.037 ± .003	1371 ± 45
80 cm	16	17.4 ± 2.0	2.5 ± 0.5	6.8 ± 1.0	1.9 ± 0.23	61 ± 5.0	0.053 ± .005	0.029 ± .003	1308 ± 50
Kruskal-Wallis test, Chi^2 :		11.2	3.1	1.8	9.8	2.5	0.04	2.3	0.52
$P<$		0.004	0.21	0.41	0.007	0.28	0.83	0.32	0.77

[1] Mean duration of interpatch flights was first obtained for each individual, so value is a mean of a mean.
[2] Only those flights directly between patches are included.
[3] Number of patches visited is out of a total of four patches, that were visited during the observation period, corrected up to the value for full 1500 seconds.

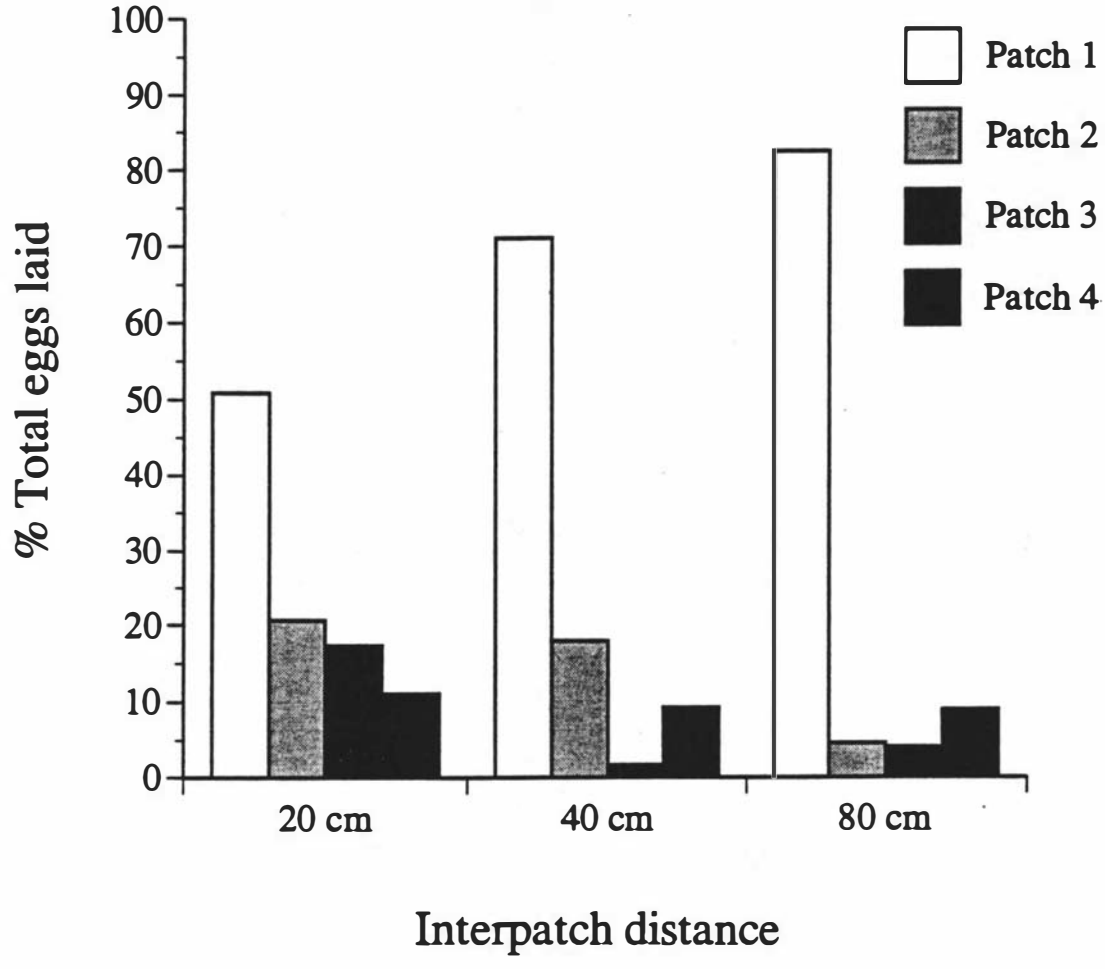

Fig. 2. The distribution of eggs laid among wheat patches in Experiment 1 at the different interpatch distances. Females were always introduced into patch one. Total number eggs for interpatch distance of 20 cm= 1037; for 40 cm= 1039 eggs; for 80 cm= 668 eggs.

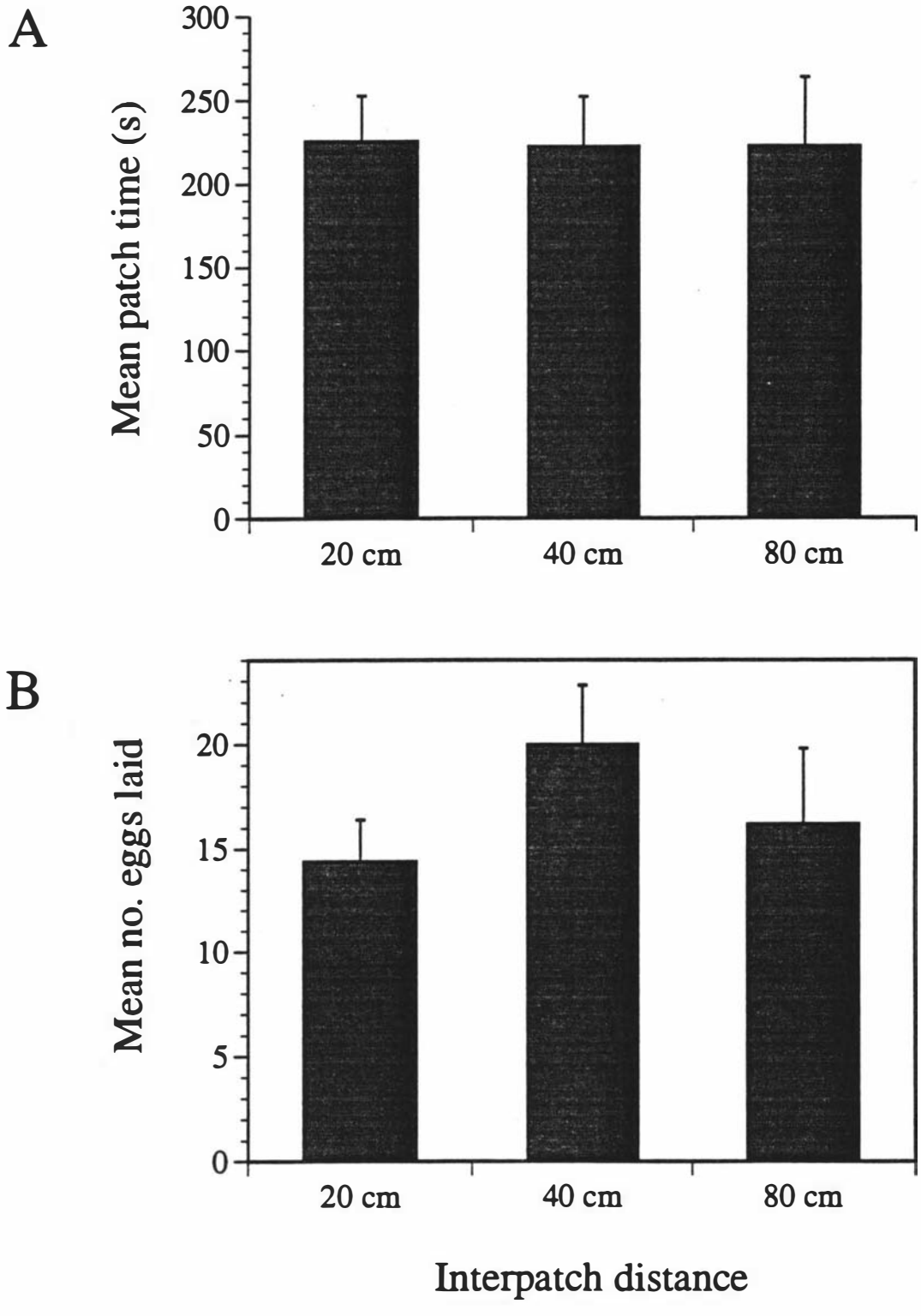

Fig. 3. The relationship between interpatch distance in Experiment 1 and (A) the mean time spent in each patch (s) and (B) the mean number of eggs laid per patch visit in plant arrays. Within each graph, means are not significantly different ($P<0.05$, Kruskal-Wallis). Bars indicate standard errors of the means.

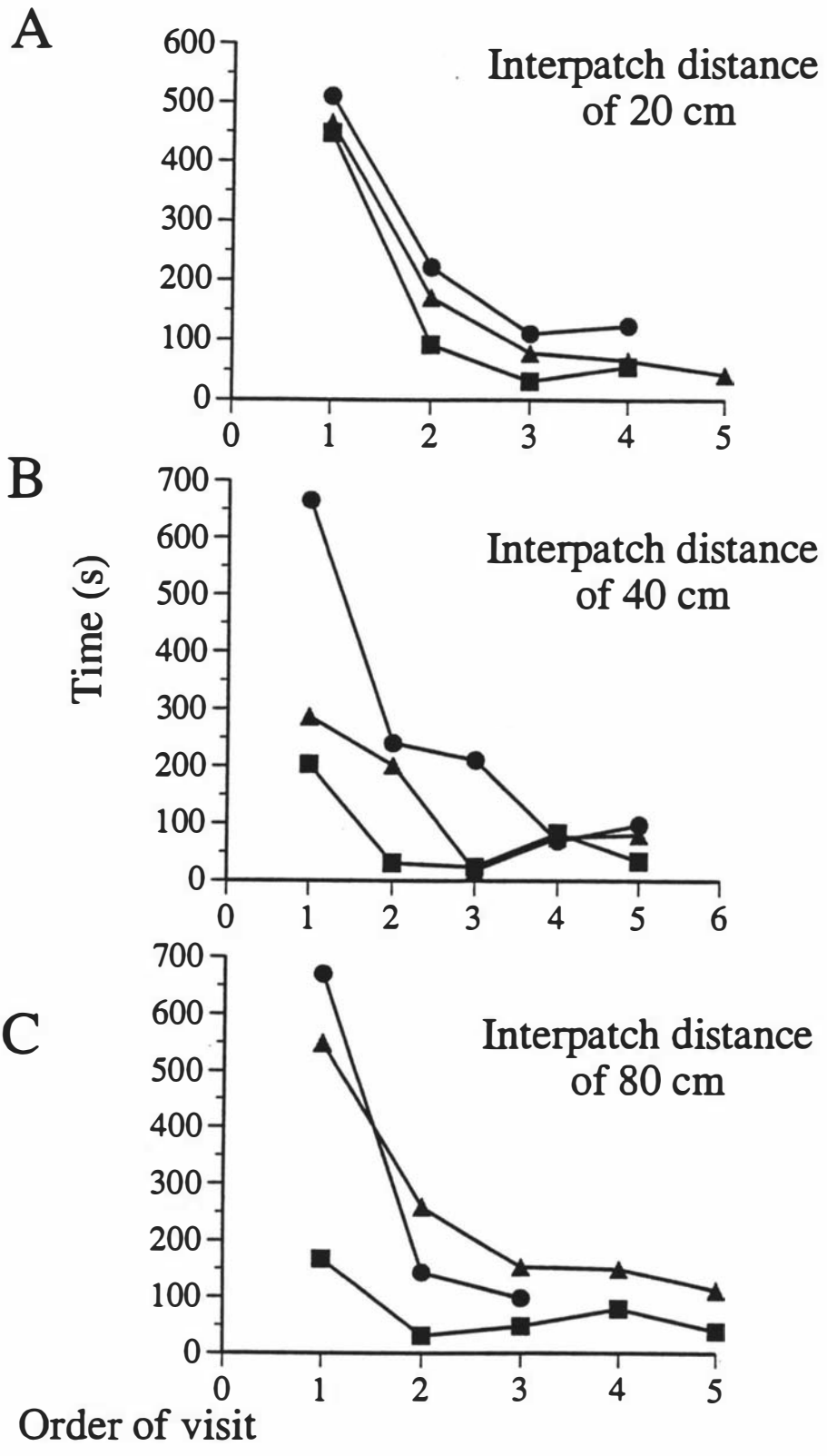

Fig. 4. The relationship between interpatch distance in Experiment 1, and the time allocated to a sequence of patch visits. Examples of three females from each treatment array (interpatch distances of (A) 20 cm, (B) 40 cm, and (C) 80 cm) were randomly chosen to illustrate the change that occurs after the first patch visit. Overall, time allocated to the first patch visit was significantly greater than times allocated to subsequent patch visits (see text).

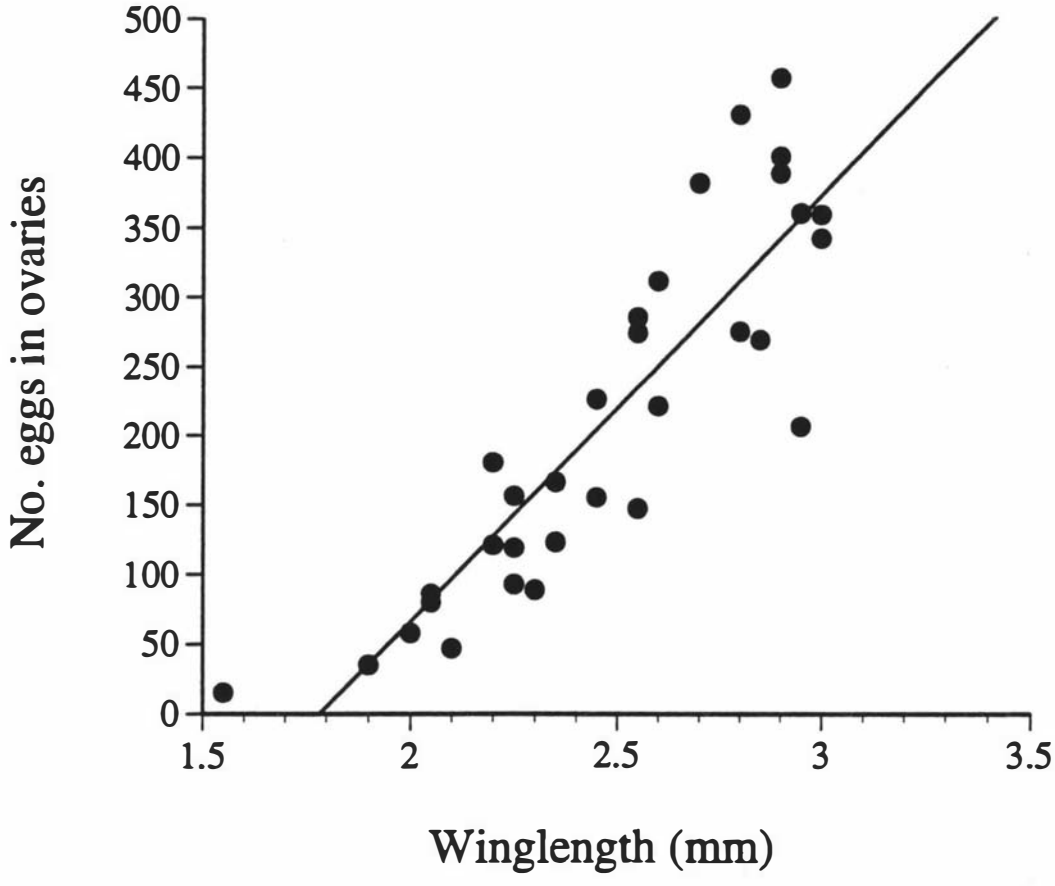

Fig. 5. The relationship between female Hessian fly wing length and numbers of mature eggs present in the ovaries (n=33, r^2=+0.83).

before leaving large patches (Fig. 7B). On-plant and overall egglaying rates (Table 2) also did not differ with patch size, but again showed a positive relationship with body size (r^2=+0.11, ANOVA, $F_{1,40}$=4.9, P<0.03; deviation from zero, t=2.21, P<0.03).

As in experiment one, changes in the frequency and duration of behaviours occurred during the 25 minutes females foraged regardless of patch size. Females stayed longer (Kruskal-Wallis, Chi^2=129.9, df=15, P<0.001) and laid more eggs (Chi^2=66.4, df=15, P<0.001) in the release patch than in the second and subsequent patches encountered (Fig. 8). Relationships between deprivation time and various behavioural parameters were also examined. No significant relationships were found between (1) deprivation time and number of eggs laid in first patch (ANOVA, $F_{1,33}$=1.84, P<0.2; deviation from zero, t=-1.36, P<0.1), (2) deprivation time and overall egglaying rate (ANOVA, $F_{1,44}$=0.45, P<0.6; deviation from zero, t=0.67, P<0.6), or (3) deprivation time and on-plant egglaying rate (ANOVA, $F_{1,45}$=2.5, P<0.2; deviation from zero, t=-1.57, P<0.2).

The effect of deprivation of egglaying within the 25 minute observation period was also explored. Because patch size influences interpatch flight durations (Table 2), relationships between the duration of individual interpatch flights occurring between two patches (range of flight times = 2 to 61 s) and the time spent on the plant reached by that flight were examined separately within each of the three patch size arrays. Females did not stay longer in patches after flying for longer periods of time (patch size of one plant, ANOVA, $F_{1,34}$=0.2, P<0.7; patch size of four plants, ANOVA, $F_{1,23}$=0.51, P<0.5; patch size of nine plants, ANOVA, $F_{1,52}$=0.16, P<0.7).

Experiment 3: Host among non-host patches

Increasing the proportion of wheat (host) patches within an array of oat (non-host) patches, from two to four to eight patches out of a total of 16 patches (Fig. 1C), significantly increased the number of wheat patches (Fig. 9) visited by females (Kruskal-Wallis, Chi^2=8.2, df=2, P<0.017). However, when rates of visitation to wheat and oat patches were expressed as the proportion of available wheat and oat patches visited, they were similar for wheat (43%) and oats (46%) for all three arrays (Wilcoxon test, Chi^2=0.03, P<0.6). Thus, visitation rates to wheat and oat patches were dependent on their relative abundance within a plant array.

Durations of visits to wheat and oat patches were not adjusted when the abundance of wheat and oats patches within the plant array was altered (Table 3). Moreover, durations and numbers of interpatch flights (Table 3), overall time spent flying (Table 3), and overall rates of egglaying (Table 3) were all similar. On-plant egglaying rates on wheat also did not differ among the three arrays (Table 3), but were related to

Table 2. Results of Experiment 2 on the influence of patch size on various foraging flight and ovipositional parameters.

Patch Size	n	Duration of interpatch flights[1] (s) x+SE	Number interpatch flights[2] x+SE	Percent time flying x+SE	Number patches visited[3] x+SE	Percent time on plants x+SE	Rate on-plant egglaying (eggs/s) x+SE	Overall rate of egglaying (eggs/s) x+SE	Duration of observation (s) x+ SE
1 plant	18	11.7 ± 0.95	8.0 ± 0.93	11 ± 0.94	3.8 ± 0.4	69 ± 3.5	0.068 ± .004	0.051 ± .004	1366 ± 44
4 plants	14	8.7 ± 1.1	6.1 ± 1.1	7.5 ± 1.1	3.7 ± 0.4	76 ± 3.9	0.062 ± .005	0.052 ± .005	1420 ± 50
9 plants	16	6.8 ± 0.98	6.9 ± 1.0	6.3 ± 1.0	4.0 ± 0.4	84 ± 3.8	0.064 ± .005	0.062 ± .005	1430 ± 46
Kruskal-Wallis test, Chi^2 :		9.8	2.0	10.3	0.52	7.3	0.90	3.2	1.3
$P<$		0.008	0.38	0.006	0.77	0.03	0.64	0.2	0.5

[1] Mean duration of interpatch flights was first obtained for each individual, so value is a mean of a mean.
[2] Only those flights directly between patches are included.
[3] Number of patches visited is number reached in observation time, corrected up to the value for full 1500 seconds.

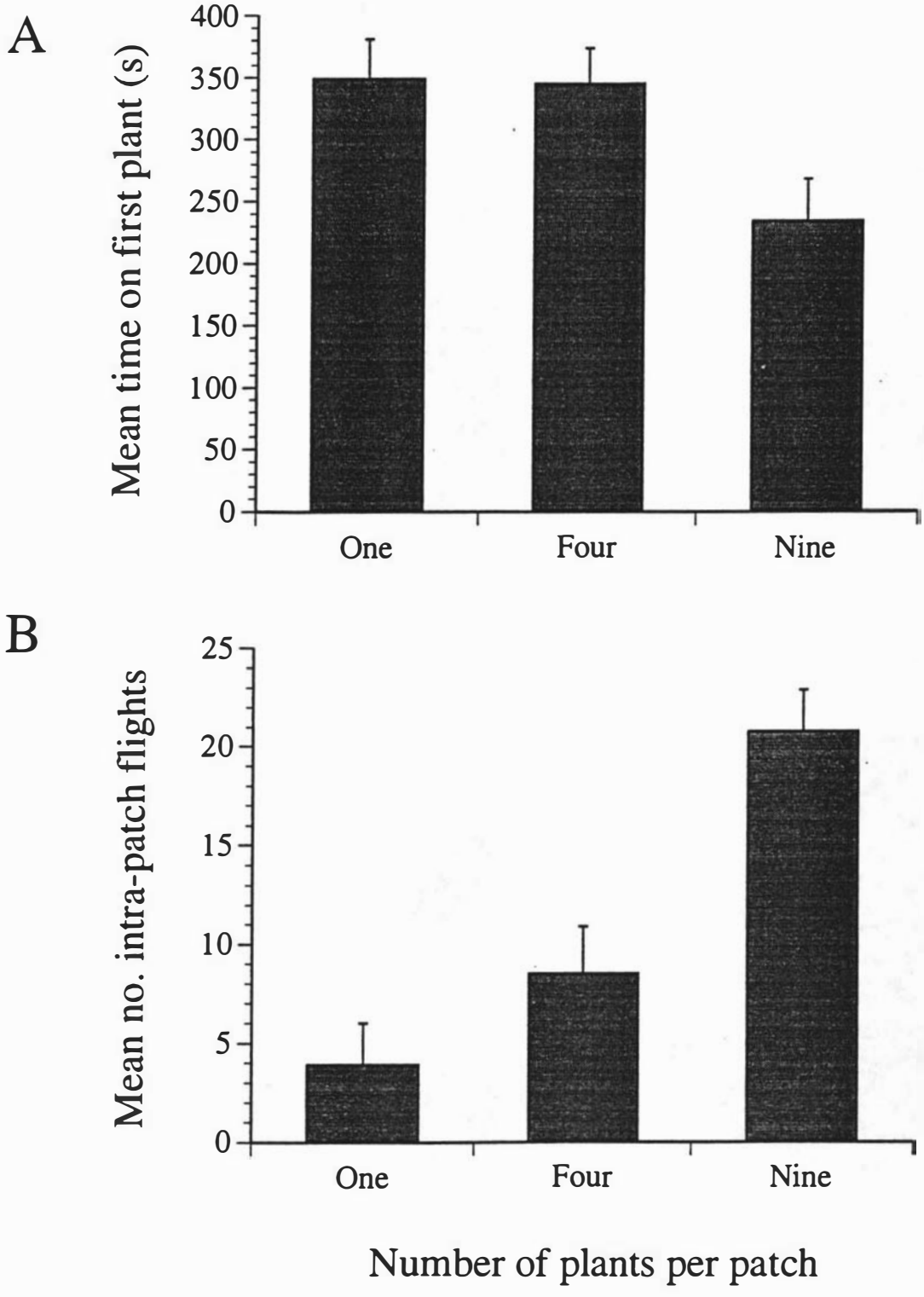

Fig. 6. The relationship between patch size in Experiment 2, and (A) time spent on the first plant visited within a patch and (B) the number of flights between plants within a patch. Within both graphs, means were significantly different at $P<0.05$ (Kruskal-Wallis). Bars indicate standard errors of the means.

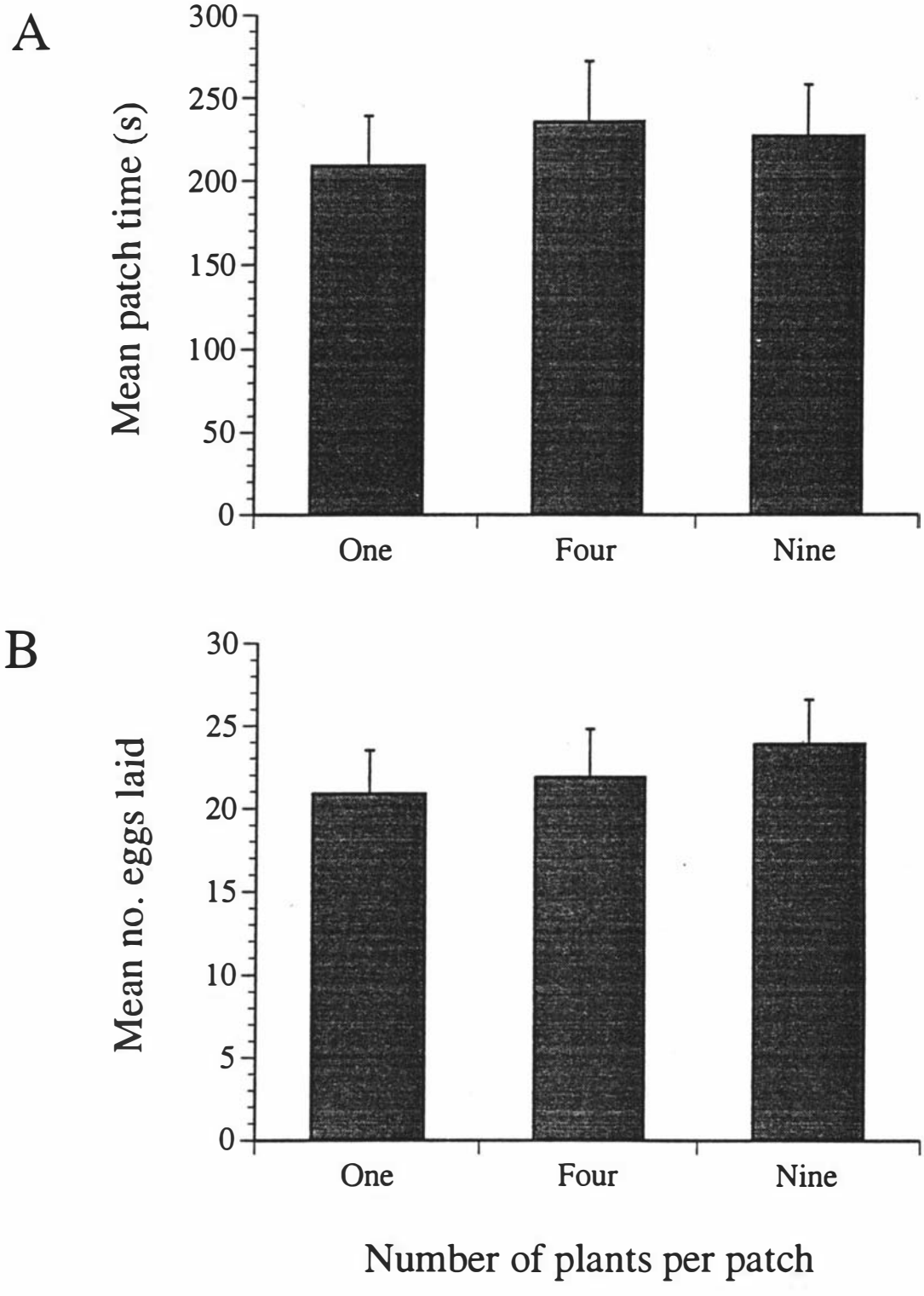

Fig. 7. The relationship between the number of plants per patch in Experiment 2 and (A) mean time spent per patch, and (B) mean number of eggs oviposited per patch. In both graphs, means are not significantly different at $P<0.05$ (Kruskal-Wallis). Bars indicate standard errors of the means.

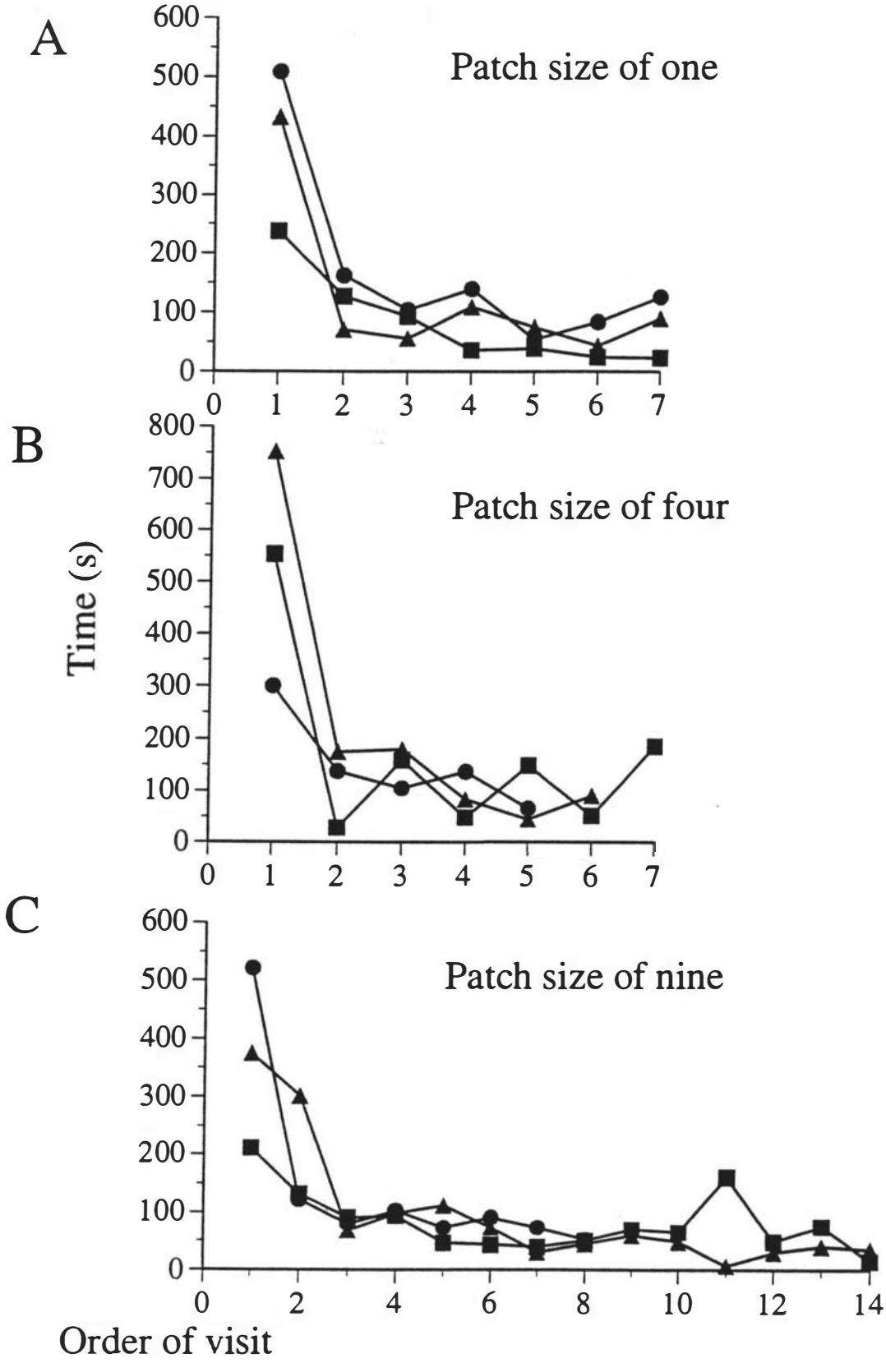

Fig. 8. The relationship between patch sizes in Experiment 2, and the time allocated to a sequence of patch visits. Three females from each treatment array (patches with (A) one, (B) four, or (C) nine plants) were randomly chosen to illustrate the change that occurs after the first patch visit. Overall, time allocated to the first patch visit was significantly greater than times allocated to subsequent patch visits (see text).

body size (ANOVA, r^2=+0.22; $F_{1,39}$=11.3, P<0.002; deviation from zero, t=3.36, P<0.002).

Plant species had much greater effects on foraging behaviour than did the relative abundance of the plants. On entering a patch, females in wheat spent, on average, 199 s before leaving, while females in oats stayed only 31 s (Wilcoxon test, Chi^2=51.4, P<0.001). During patch visits, females in wheat and oat patches made, on average, 1.9 and 1.1 intrapatch flights, respectively (Wilcoxon test, Chi^2=9.03, P<0.002), and laid a mean of 11.3 (±0.8) and 0.94 (±0.8) eggs (Wilcoxon test, Chi^2=65.1, P<0.001), respectively, before leaving. On-plant egglaying rates (eggs laid/ seconds on plants) were significantly greater (mean±SE) on wheat (0.063±0.004, n=44), than on oats (0.038±0.005, n=17; Wilcoxon test, Chi^2=13.0, P<0.001).

In this experiment, the procedure for introducing females into arrays differed from that used in the first two experiments. Instead of depriving females of wheat plants until their introduction into the experimental array, I allowed females to oviposit on wheat for 5-10 min before their introduction. This procedural change was made because experience with wheat plants before introduction to an oat patch greatly reduced the inactive periods and vertically oriented flights which occurred when naive females were first introduced to oats patches. Perhaps because of this procedural change, females did not spend more time in the first wheat patch encountered (Kruskal-Wallis test, Chi^2=1.3, P<0.6) and did not lay more eggs in these patches (Kruskal-Wallis test, Chi^2=3.9, P<0.5).

Durations from the females' introduction to the oat release patch to landing on the first wheat plant (hereafter referred to as foraging time) ranged from 45 to 895 s while the number of oat patches encountered before finding wheat ranged from zero to 20. However, time in the first wheat patch encountered (ANOVA, $F_{1,43}$=2.1, P<0.2), numbers of egg laid in that wheat patch (ANOVA, $F_{1,32}$=0.49, P<0.5) and time on the first wheat plant in that patch (ANOVA, $F_{1,43}$=1.2, P<0.3) did not increase with foraging time. These same behaviours were also not related to the number of oat patches visited before finding wheat (patch time and number of oat patches visited, ANOVA, $F_{1,43}$=0.014, P<0.99; numbers of eggs laid in the first wheat patch encountered and number of oat patches visited, ANOVA, $F_{1,32}$=0.006, P<0.99; time on the first wheat plant and number of oat patches visited, ANOVA, $F_{1,43}$=0.68, P<0.5).

Discussion

It has been reported previously (Harris & Rose, 1989; Harris & Rose, 1990; Foster & Harris, 1992; Harris *et al.*, 1993) that, in Hessian flies, oviposition is strongly influenced by stimuli emanating from host plants. In these studies, directed movement and nonrandom settlement (sensu Morris & Kareiva, 1991) were identified as important

behavioural responses to host plant stimuli. Research on the Hessian fly reported here confirms most of these previous reports and, additionally, reveals other important aspects of foraging for oviposition sites, including: distances over which directed responses occur, how area-restricted search contributes to host location, and components of movement which appear to be unrelated to the distribution of host plants. Each of these subjects will be discussed in separate sections of the Discussion.

Directed responses to plants

Perhaps the most sophisticated form of nonrandom movement involves directed responses, which occur when the insect is at some distance from the plant and orients its movements relative to stimuli emanating from the plant (Morris & Kareiva, 1991). In past work on the Hessian fly, directed responses have been measured by counting the number of females flying into a 1 cm radial zone surrounding plant models (Harris *et al.*, 1993). By changing the characteristics of these models, it was shown that both visual characteristics of the model and plant odours emanating from the model influenced the number of females flying into this 1 cm zone. While visual characteristics eliciting the response were not particularly host-specific (e.g., vertical edges, larger overall area, and reflectance of 530-560 nm wavelengths in the absence of 400-500 nm wavelengths), odours stimulating movement were probably host-specific (e.g., only chloroform extracts of wheat leaves stimulated the response, Foster & Harris, 1992).

Given these previous results, it might have been expected that, in the third experiment reported here, in which both wheat and oat plants were present (Fig. 1), directed responses towards wheat would result in females visiting more wheat than oat patches. However, in this experiment, rates of visitation to wheat and oat patches depended on the relative abundance of each species within the plant array rather than on host-specific characteristics. The difference between this result and that reported previously may be related to differences in the sensory complexity of the experimental arrays used in the two experiments. Females in earlier experiments foraged in a small arena containing only two models, while females in experiments reported here foraged in plant arrays which contained 64 plants. Whatever the explanation, these apparently contradictory results illustrate the dangers of overestimating the directed components of

Table 3. Results of Experiment 3 on the influence of host within non-host patches on various foraging flight and ovipositional parameters.

Ratio wheat/oat patches	n	Duration interpatch flights[1] (s) x+SE	Number interpatch flights[2] x+ SE	Percent time flying x+ SE	Duration visit to wheat patch (s) x+ SE	Duration visit to oats patch (s) x+ SE	Rate on-plant egglaying[3] (eggs/s) x+ SE	Overall rate of egglaying (eggs/s) x+ SE	Duration observation (s) x+ SE
2:14	8	10.8 ± 2.7	15.9 ± 2.1	10.3 ± 2.3	206.6 ± 52	16.4 ±14.9	0.07 ± .008	0.032 ± .004	1178 + 108
4:12	17	11.1 ± 1.9	16.1 ± 1.4	10.8 ± 1.6	189.5 ± 36	32.4 ± 10.2	0.063 ± .006	0.028 ± .003	1122 + 73
8: 8	20	14.7 ± 1.8	13.0 ± 1.3	10.3 ± 1.4	204.2 ± 33	36.5 ±9.5	0.059 ± .005	0.025 ± .003	1315 + 74
Kruskal-Wallis test, Chi^2 :		0.35	2.8	0.012	0.66	1.1	3.2	1.3	3.6
$P<$		0.84	0.24	0.99	0.72	0.57	0.2	0.52	0.16

[1] Mean duration of interpatch flights was first obtained for each individual, so value is a mean of a mean.
[2] Only those flights directly between patches are included.
[3] Rates of on-plant egglaying are based only on visits to wheat.

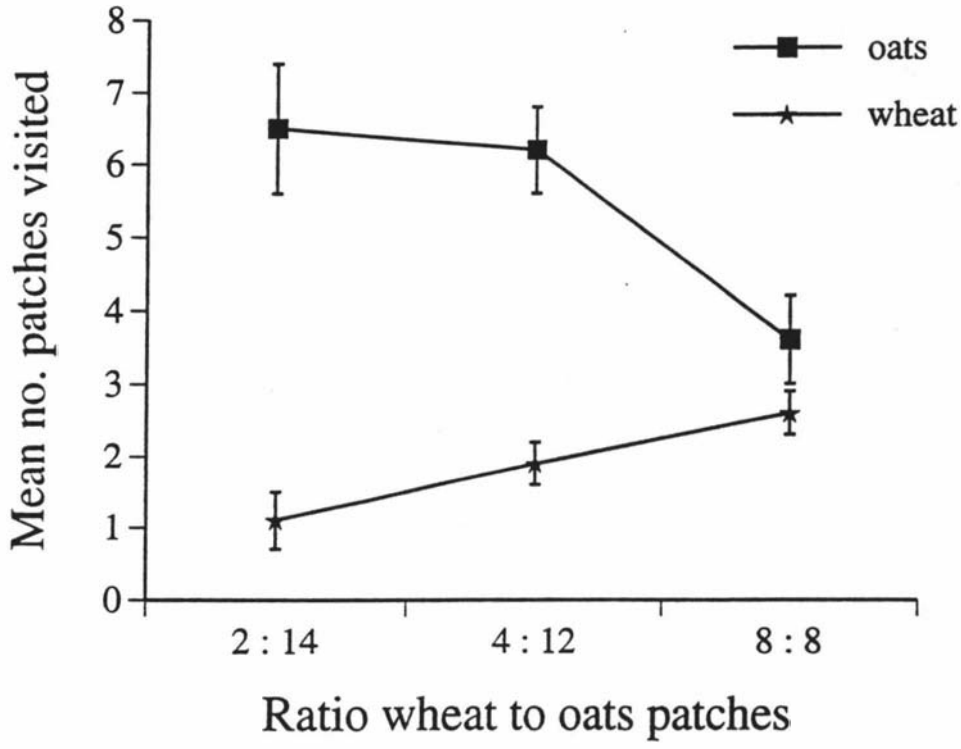

Fig. 9. The influence of host abundance on the mean number of wheat and oat patches visited by female Hessian flies during the observation period in Experiment 3, on host among nonhost patches. Bars indicate the standard errors of the means.

insect movement if behavioural responses are measured using highly simplified arrays of resources.

While the above result indicates that Hessian fly females foraging in more complex plant arrays do not exhibit directed responses to host-specific stimuli (e.g., plant odours), females do exhibit directed responses to non-specific visual stimuli from plants (Harris *et al.*, 1993). The experiments described here provide some insights into the nature of these directed responses. For example, the observation that females foraging in arrays of wheat plants had shorter interpatch flight durations and found more available patches when interpatch distances were reduced (from 80 to 40 to 20 cm; Table 1) suggests that reactive distances to plant visual stimuli from wheat seedlings may be rather small, perhaps only 20 cm for a patch of four wheat plants in the one-leaf stage. Increasing the number of plants in a patch apparently increased the distance over which females responded visually. For example, interpatch flights were of shorter duration (Table 2) when patch size was increased from one to four to nine wheat plants per patch. Precise determination of reactive distances and the relationship between reactive distance and the size of visual targets will require tracking of Hessian fly flights by video and quantitative analyses of flight tracks relative to visual targets.

Nonrandom settlement

Once flight brings female Hessian flies to the immediate vicinity of a plant (1 cm away or less) the decision to land or leave depends to a large extent on host-specific chemical cues (but also plant colour, Harris *et al.*, 1993). Females first contact the plant with the antennae and tarsi (and perhaps also the ovipositor) while hovering in flight near the leaf surface, and after this contact either proceed to land or leave by flight. Because the decision to land or move away from the plant is made after contacting the plant, this change in movement can be described as nonrandom settlement. Having landed on the plant (i.e., folded the wings), females again exhibit nonrandom settlement. Here the decision to settle or leave is based on information gathered by chemoreceptors, which sense host specific chemicals present in the epicuticular waxes of wheat leaves (Foster & Harris, 1992), and by mechanoreceptors, which in some way sense the parallel and vertically oriented grooves associated with leaf venation in many grasses (Harris & Rose, 1990). At this stage plant colour no longer appears to have any influence on behaviour.

Experiments reported here reveal that as well as plant species, the number of wheat plants within a patch influences how much time a female spends on a plant. A comparison of times spent visiting the first plant encountered in a wheat patch (Fig. 6A) revealed that females flying into a patch containing one or four plants stayed longer during this first visit than females that flew into a patch containing nine plants. Thus, it appears that, if the female senses a large number of plants nearby, she then allots less

time to the plant she has just landed on. How the size of a patch is sensed (whether by visual or odour cues) and when it is sensed (before or after landing on the plant) were not apparent from these experiments.

Area-restricted search

In a third form of nonrandom movement (Morris & Kareiva, 1991), the insect contacts the plant, and then based on information gained from that contact, adjusts its movement upon leaving the plant, either by remaining in the area near the plant (area-restricted search) or by moving out of that area. The spatial scale over which movement is adjusted will influence whether this form of nonrandom movement is easily identifiable. Over the spatial scale used in these experiments (2 x 2 m) only one variable indicated that female Hessian flies may adjust their small-scale movement after contacting a plant: females entering a patch of four wheat plants spaced 4 cm apart, typically flew to two other plants before leaving the patch, while females entering a patch of four oat plants flew to only one other plant before leaving. Based on this observation, I suggest that, relative to females that have just visited a wheat plant, females that have visited an oat plant have a more rapid decline in responsiveness to plant visual stimuli, and therefore are more likely to initiate a flight that takes them out of the patch

Random movement

Morris & Kareiva (1991) define random movement as occurring when the "frequency, rate, and orientation of movement are unrelated to the suitability of plants within the perceptual range of the insect". Because the perceptual range of a flying female Hessian fly has not been documented, I found this definition problematical. Indeed, most researchers working on insect herbivores that scan for host plants when in flight, would not be able to define the perceptual range of their test animals. When the visual perception of insect herbivores has been measured, it was with species that scan for hosts from a stationary position, such as caterpillars (Saxena & Khattar, 1977) or *Rhagoletis pomonella* (Roitberg, 1985). The visual abilities of insects in flight are considered to be quite different (Wehner, 1979) and are more difficult to quantify.

In spite of not being able to use Morris and Kareiva's definition of random movement in its fullest sense, I did find components of movement that seemed to occur independently of plant stimuli. For example, rather than entering a wheat patch and allotting time spent in the patch according to the size of the patch (as in *R. pomonella*, Roitberg, 1985), female Hessian flies stayed 3-4 minutes in both small and large patches and laid ca. 15-25 eggs before exiting the wheat patch. Time allotted to wheat patches was also unrelated to the time the female had flown before she entered the patch.

Furthermore, within each experiment, flights that took females away from patches (interpatch flights) occurred at a fairly constant rate (Tables 1, 2, and 3). Based on these data, it appears that interpatch flights may be triggered by internal stimuli, e.g., a decrease in responsiveness to plant stimuli which occurs after the female has laid 15-25 eggs. The alternative explanation, i.e., that the female no longer responds to plants because they have changed in some way during the time the female visits the patch, is less likely: female Hessian flies do not have marking pheromones (M. O. Harris, unpublished data) and appear to respond to fresh patches and previously-visited patches in a similar manner.

Another behavioural response that was probably unrelated to plant stimuli was the enhanced egglaying that occurred when female Hessian flies were deprived of egglaying sites before being introduced into the plant array (Experiments 1 and 2). Relative to the first wheat patch that females visited within the plant array, subsequent patches were visited for shorter periods of time and received fewer eggs. When allowed to oviposit on wheat plants before being introduced into plant arrays (Experiment 3), females did not lay more eggs in the first wheat patch, even if that patch took 15 minutes to find. The response of a female Hessian fly to the first wheat patch she encounters, therefore, may be determined to a large degree by her internal level of responsiveness, a level that can be raised if the female is not given access to wheat when egglaying behaviour commences. The time frame over which this deprivation-related change in responsiveness occurred is not known; however, once it occurred, 5-10 mins of egglaying on wheat appeared to reset levels of responsivenesss to those of females who had not been deprived (Figs. 4 and 8, and Experiment 3).

Decisions during foraging behaviour

Although the experiments described here were not specifically designed to investigate decision mechanisms in the Hessian fly, experimental evidence points to two important decisions that are made during foraging. The first of these decisions regards how many eggs a female should lay on a plant after she has landed. Based on data from this and other studies (Harris & Rose, 1989; Foster *et al.*, 1991), I propose the following mechanism for this decision. After landing on a plant the female sets her initial level of responsiveness based on an assessment of her own internal state and on an assessment of the plant (for a similar model for parasitoids, see Driessen *et al.*, 1995). Relative to a female that has oviposited on wheat, a female that has been deprived of wheat will have a higher level of responsiveness and will stay longer on that plant. A female that finds herself on a plant without close neighbouring plants (Fig. 6) may also have a higher level of responsiveness. Relative to a female on a wheat plant, a female on an oat plant will have a lower level of responsiveness and will leave the plant after a shorter duration. Once this level of responsiveness and leaving time are set, an endogenous programme then

generates alternating periods of sitting and egglaying which occur at a rate which is related to body size (see Results). Each period of egglaying produces 2-3 eggs and lowers responsiveness until it reaches a critical level. Now, instead of being followed by oviposition, sitting will be followed by flight away from the plant. This mechanism differs in two ways from that proposed by Driessen *et al.* (1995). First, in the Hessian fly I propose that initial levels of responsiveness are related not only to the quality of host resources (as in Driessen *et al.*, 1995) but also to the internal state of the female. Second, where levels of responsiveness of parasitoids decrease during search even in the absence of ovipositions (as in Driessen *et al.*, 1995), responsiveness in Hessian flies probably only decreases as a function of ovipositions.

The second important decision made by a female Hessian fly concerns the distance she will fly after leaving a plant. In our experiments, I distinguished two types of flight, intrapatch flights that took the females short distances to plants in the same patch, and interpatch flights that took the female away from patches. Intrapatch flights were common and tended to occur in groups of 3-5 flights, which were then followed by a single interpatch flight. Two possible mechanisms can be proposed for these flight decisions. First, when a female enters a patch of wheat plants her level of responsiveness is set as described above. After leaving this first plant she is still responsive to nearby plants and therefore flies to another in the same patch. After landing, her level of responsiveness is reset but at a lower level than occurred on the first plant she visited within the patch. The process of sitting and egglaying then proceeds. Each time the female lands on another plant, initial levels of responsiveness are reset at lower levels until the female no longer responds to nearby plants when in flight and therefore exits the patch vicinity. Females foraging in oat patches would show a similar but more rapid decrease in responsiveness. An alternative mechanism for flight decisions is that interpatch flights are initiated after a certain number of eggs have been laid, a number which may be related to body size of the female (Fig. 5). Here one would expect a more flexible time allocation to the plants within a patch and would not expect decreases in responsiveness (i.e., less time and fewer eggs) over a series of visits to plants within a patch. Experiments need to be designed to specifically test these mechanisms and further clarify how flight decisions are made.

Functional aspects of movement

The movements that comprise the foraging behaviour of female Hessian flies work together to concentrate eggs on host plants, but also prevent too many eggs from being laid on a single plant or within a small area of plants. This first outcome relies primarily on nonrandom movements, including directed responses to nonspecific plant visual stimuli, followed by nonrandom settlement and area-restricted search. The second outcome relies on regular interpatch flights which ensure that females maximise the area covered during foraging.

One disadvantage of regular interpatch flights appears to be an inability to fully exploit patches of host plants (see Roitberg, 1985). However, if an insect has no marking pheromone (as in the Hessian fly) and cannot reliably avoid revisiting the same plants, the costs of not fully exploiting a patch may have to be balanced against the benefits of spreading eggs over a larger area. In short-lived insects such as Hessian flies, another cost of fully assessing patch resources may be the time that such an assessment takes. Indeed, leaving the patch after a fixed period of time is predicted as the optimal strategy for parasitoids lacking recognition of previously parasitised hosts (Rosenheim & Mangel, 1994).

For Hessian fly females, the benefits of distributing eggs over more plants may include larger numbers of more fecund offspring. The maximum number of Hessian fly larvae that can develop and survive on a wheat plant in the 1-2 leaf stage is about 25 (Withers, chapter four); however, the more larvae that develop on a single plant, the smaller are the resulting adults. Small adults have reduced fecundity as females and reduced fertility as males (Bergh *et al.*, 1990).

Finally, the spatial distribution of hosts may have a major impact on adaptive strategies of foraging insects (e.g., Cain *et al.*, 1985; Stanton, 1982). When hosts are fairly homogeneous in their distributions, foraging decisions may be based on the expectation that once one host is found, others will be found nearby. The grass hosts of Hessian flies are less patchily distributed and perhaps more abundant than the hosts of other insect herbivores whose foraging decisions have been investigated.

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CHAPTER THREE

The influence of wind on Hessian fly flight and egglaying behaviour

Abstract

The influence of wind on the behaviour of female Hessian flies (*Mayetiola destructor* Say) was examined in a windtunnel. Females ovipositing on host plants (wheat) in strong winds stayed longer, exhibited more oviposition bouts, and laid more eggs than females ovipositing in lesser winds. At winds at or above 0.9 m/s, flight away from hostplants was suppressed for periods of up to 30 minutes. Flight direction upon leaving a host plant was also influenced by wind. As winds increased above 0.9 m/s, females no longer exhibited flights to upwind wheat patches and were more likely to land in downwind patches or to be blown out the end of the windtunnel. When groups of females were introduced into hostplant patches in high windspeed conditions, they laid most of their eggs in downwind patches and the patches they were released into. Females foraging in minimal winds laid eggs in upwind as well as downwind patches, and the total number of eggs laid in the test period was greater. When the effects of wind were examined in conjunction with effects of plant species, wind appeared to have a greater effect on flight initiation, the number of oviposition bouts performed, and egglaying rate, while plant stimuli had a greater effect on the duration of oviposition bouts and number of eggs laid. A model which predicts foraging decisions with respect to wind and plant stimuli made by female Hessian flies is proposed.

Key words. *Mayetiola destructor*, wind, movement, insect-plant interactions, Diptera, oviposition.

Introduction

When foraging for oviposition sites, insect herbivores must cope not only with the limitations of their sensory systems but also with environmental conditions that hinder movement. Wind is one such environmental factor and can suppress flight initiation (Kennedy, 1990) or reduce the efficiency with which flying herbivores follow plumes of host plant odours (Elkington & Carde, 1984). Wind can also alter the foraging behaviour of insects by the direct physical effects of windspeed and turbulence on flight manoeuvres (Vanwoerkom *et al.*, 1983).

Wind may pose special difficulties for insect herbivores like the Hessian fly, *Mayetiola destructor* Say (Diptera:Cecidomyiidae), a pest which is both shortlived (1-3 days) and small in the adult stage (5-8 mm in length, weighing 0.2-2.0 mg, Bergh *et al.*, 1990). Adult males typically emerge in the late afternoon while females emerge in the 2-3 h following dawn (Bergh *et al.*, 1990). Males fly upwind towards sources of female-produced sex pheromone, and thereby locate and mate virgin females (Harris & Foster, 1991). After a 1-3 h period of inactivity, mated females undergo a transition to active foraging for oviposition sites (Harris & Rose, 1991; Harris *et al.*, 1993). Wheat (*Triticum aestivum* L.) and a limited number of other grasses serve as hosts for Hessian fly larvae (Jones, 1936).

Information on how wind influences flight behaviour and egg-laying in Hessian flies is limited to an observation by McColloch (1917) who captured a small number of mated females 3.2 km downwind of what he believed to be the nearest infested wheat field. Whether the females he collected moved these distances by trivial flights (Blackmer & Byrne, 1993; Johnson, 1969; Kennedy & Ludlow, 1974) or by longer dispersal flights is not known. Harris & Rose (1989) observed an increased phototactic response in Hessian fly females held with non-host (oats, *Avena sativa* L.) versus host (wheat) plants. Such phototactic responses could result in vertical flights that take females out of the plant canopy and bring them into contact with stronger wind currents. If such vertical flights are exhibited by female Hessian flies, their destination would be determined by windspeed and direction (Johnson, 1969).

In this study I investigated how wind influences flight initiation, flight manoeuvres, and oviposition behaviour of mated female Hessian flies by observing individual females ovipositing on wheat plants under different windspeeds. After establishing that wind does have a significant effect on the behaviour of ovipositing females, I investigated the relative effects of wind and plant species on these behaviours by introducing females ovipositing on wheat or oats into low and high winds. The influence of wind on spatial distribution of egglaying was determined by releasing groups of females into wheat patches and counting eggs laid in patches upwind and downwind of

release sites. Finally, I investigated whether the suppression of flight caused by prolonged exposure to high winds effected lifetime fecundity of females.

Materials and methods

Insects and Plants

Hessian flies were collected from wheat fields in Palmerston North, New Zealand, and reared for 15-20 generations in the laboratory on a susceptible wheat (*Triticum aestivum* L., cv. 'Karamu'). In this laboratory culture, female Hessian flies oviposited on wheat in the two leaf stage. After about 28 d in the greenhouse (20± 5° C), infested wheat plants were placed in a controlled environment room (24° C and photoperiod of 12:12 L:D), with lights on at 0700 h. Adult Hessian flies began emerging about seven days later.

Seeds of the wheat cultivar 'Karamu' and the oats (*Avena sativa* L.) cultivar 'Awapuni' were planted as single plants for the trials in 5 cm diameter pots (single plants), or 10 cm diameter pots (plant patches) in a sterilised bark growth medium, and used in experiments when in the one or two-leaf stage.

Apparatus

The windtunnel used in the experiments (plexiglass walls and aluminium frame) was based on the design of Miller & Roelofs (1978), measured 0.95 high x 0.95 wide x 2 m long and contained a 10 cm deep layer of moist sand. The 0.7 m diameter fan (Woods Air Movement, G.E.C., Wellington) was connected to a variable motor speed controller. Fourteen full-spectrum composition fluorescent tubes (36 W, 2300 lm, 1.2 m long, Biolux, Hamburg) with high-frequency control circuits (Quicktronic Deluxe, Biolux, Hamburg) provided the required light source above the windtunnel. The sides of the wind tunnel were covered by a white cotton mesh and the observer wore white.

General procedures

One hour before observations commenced, females that had mated (indicated by the cessation of the calling posture, Bergh *et al.*, 1992) between the hours of 0700 and 0800 were collected and transferred to a mesh cage (50 x 50 x 50 cm) containing one pot with approximately 20 wheat plants. After passing through a postmating preovipositional transition phase (Harris & Rose, 1991), females became active at about 1100 h. Observations commenced at this time.

Active female flies were obtained for behavioural recordings by introducing an individual potted plant into the cage described above. When a single female landed on the plant and began ovipositional behaviour, the plant was quickly moved (approx. 4 s) into the windtunnel and sunk flush into a hole in the centre of the sand substrate lining the tunnel. The pot was always positioned so that the ovipositing female was on the

downwind side of the leaf. Windspeeds were adjusted prior to introducing the female, and were constant throughout each observation. Only one female was present in the tunnel at any one time.

Female behaviour was recorded to the nearest second either manually using a stopwatch and data sheet or on a hand-held microcomputer (Psion Organiser Model LZ50, Psion, London) with the behavioural software 'The Observer' (Noldus, 1990). Oviposition was distinguished by downwards curvature of the abdomen (Harris & Rose, 1989); holding the abdomen parallel to the leaf surface was recorded as sitting. When the female left this plant, the duration from introduction to the tunnel to leaving was recorded as latency to flight; the direction of flight taken, and the location of landing were also recorded. At the completion of each observation, numbers of eggs laid on each plant were enumerated using a 10X magnifying glass.

During experiments the laboratory holding the cages and windtunnel was maintained between 24 and 26° C. After each observation the temperature in the windtunnel at sand level was recorded using a digital thermometer.

Each of the windspeeds used in the experiments were measured at plant height (12 cm above sand) twice over a 60 s interval, using a hot-wire anemometer (model 9054N, Dantec, Denmark).

Responses to wheat in different windspeeds

After introduction of an individual female into the wind tunnel, the behaviour of each individual female was recorded for 12 min (to put a time-limit on inactive individuals) or until the next point of alightment after having left the wheat plant was observed. In addition to the single plant (carrying the female) that was introduced into the tunnel, four wheat patches were situated 38 cm from the single plant upwind, downwind, and crosswind. Each of these four wheat patches consisted of a total of 20-30 plants grown in 5 cm diameter pots, to make a patch size covering 20 x 5 cm with foliage trimmed to a height of 10-12 cm. Females which left the central plant were recorded as having flown to (1) one of the four wheat patches in the tunnel (identified separately), (2) the sand, or (3) out of the end of the tunnel. A small number of flies were lost from sight after leaving plants, and were recorded as such. The following seven windspeeds (mean ± 0.5 range in m/s) were presented in a randomised complete block design with the order of presentation rerandomised daily: zero, 0.64 ±0.02, 0.7 ± 0.03, 0.9 ±0.03, 1.2 ±0.07, 1.6 ±0.08, 2.0 ±0.09. Observations of 180 flies were conducted over ten days.

Whenever possible (126 out of the 180), the female was recaptured at the end of the observation (e.g., from one of the wheat patches or from the sand), transferred to a glass vial and frozen at 0° C. Winglength was then measured (distance between the axillary sclerite and the end of radial sector vein, Bergh *et al.*, 1990), using an eye-piece micrometer at 40X magnification. The relationship between female body size and latency

to flight initiation was examined using linear regression analysis, and goodness of fit tested with ANOVA.

Periods of oviposition that were followed by flight or periods of sitting for 4 s or more were termed oviposition bouts. The numbers and durations of oviposition bouts performed, numbers of eggs laid and latency to flight initiation, were tested with analysis of variance (ANOVA) using the JMP package (SAS, 1989). Log transformations were performed where necessary (latency to flight initiation and the number of oviposition bouts) to remove heterogeneity of variances (O'Briens test at $P < 0.05$). Means comparisons were conducted with the Tukey-Kramer Least Significant Difference test at $P < 0.05$.

To test whether windspeed influenced (1) the response of females during the observation period, (2) the proportions of females that stayed on the plant, and (3) the destinations of females who initiated flights (n = 154), data were subjected to contingency table analysis, and tested for significance of G at $P < 0.05$. In the flight destination analysis, flies that were lost from view or remained on the sand were combined into an "other" destination class.

Influence of windspeed on egg distribution

The windtunnel was modified by placing a 0.95 m high and 1.8 m long sheet of perspex longitudinally down the middle of the tunnel. In addition a 0.5 wide x 0.95 m high section placed in front of the fan blocked off one half of the tunnel from most of the wind movement. This created conditions of gently circulating air (ca. 0.1 m/s) and faster moving laminar air flow simultaneously within the tunnel. Ten patches each containing six wheat plants were arranged in two columns and five rows (Fig. 4A) down each section of the modified windtunnel, with pots spaced 25 cm apart. At 1200 h, 25 actively ovipositing females were introduced into the middle row of both sections. After 120 min any remaining females were removed and the eggs laid in each patch counted. Two trials were run with females tested at winds of 0.1 m/s in one section versus 0.7 m/s down the other, with two other trials run at winds of 0.1 m/s in one section versus 1.2 m/s down the other. New groups of females were used for each trial.

To compare differences in egg distributions for low and high windspeed conditions, egg counts from adjacent pots (comprising each row) were totalled for analysis. Egg distributions for each of the two windspeeds were then compared using a 2 x 5 G-test of Independence at $P < 0.01$ (Sokal & Rohlf, 1981).

Response to host versus non-host plant in different windspeeds

Procedures in this experiment were similar to experiment one (with females ovipositing on wheat at different windspeeds) with the following exceptions: (1) females were held on a mixture of wheat and oat plants, (2) females were introduced into the windtunnel on either a single host (wheat) or non-host (oat) plant, (3) no other plants were present in the tunnel, (4) only two windspeeds, low (0.65 m/s) or high (1.6 m/s), were used, (5) all individuals were observed until they left the plant (no time limit), and (6) movements after leaving the plant were not recorded. Treatments were presented in a two-level factorial design (wheat with low wind, wheat with high wind, oat with low wind, oat with high wind) with order of presentation alternated within each treatment block. A total of eighty females were observed over five days of observations.

Two-way ANOVA's with interaction were used to investigate the influence of plant species and windspeed on the following parameters: latency to flight initiation, number of eggs laid, egglaying rate, number of oviposition bouts performed, and mean oviposition bout duration.

Influence of wind on lifetime fecundity

To investigate whether prolonged exposure to wind would reduce or increase longevity by having suppressed flight activity, the following assay was carried out. Mesh cages (50 x 50 x 50 cm) were placed, one on either side of the divided windtunnel, over moist sand. Airflows within the cages on the two sides of the tunnel were 0.1 m/s and 1.2 m/s, respectively. Twenty mated females were placed in each cage at 1130 h. No plants or other oviposition substrates were available within the cages. This would ensure suppression of oviposition for the entire period of exposure to wind. After two hours, females were removed from the cages and placed into individual mesh cages covering a 10 cm diameter pot with 15 wheat plants. Females were checked hourly until death occurred, after which winglength and the total number of eggs laid was recorded.

The number of eggs laid before death was compared to female wing lengthusing linear regression analysis, and goodness of fit tested with ANOVA. Data for the two wind treatments were tested with ANOVA and means compared as in experiment one.

Results

Responses to wheat in different windspeeds

A greater proportion of females (Fig. 1A) stayed on the plant for the entire 12 min observation period at higher windspeeds ($G = 29.5$; df = 6, 179; $P < 0.01$). Of the females that did fly away from plants during the 12 min period, females introduced to the tunnel at windspeeds greater than or equal to 1.6 m/s stayed on plants longer (Fig. 1B) than females introduced into the tunnel with windspeeds of 0-0.9 m/s ($F = 7.6$; df = 6,

152; $P < 0.001$). Latency to flight from the wheat plant was not related to female body size ($F = 0.14$; df = 1, 126; $P > 0.7$).

The number of eggs laid on the wheat plant before flying away was positively correlated with time spent arching ($r^2 = 0.59$; ANOVA: $F = 250.1$; df = 1, 175; $P < 0.001$; slope different from zero: $t = 15.8$, $P < 0.001$). Arching and oviposition occurred in bouts (Martin & Bateson, 1986) which were separated by periods of non-oviposition. Windspeed did not affect the duration of oviposition bouts ($F = 2.6$; df = 6, 177; $P < 0.02$) which had an overall mean duration of 96.5 s (SE = 5 s). However, by increasing the latency to flight, windspeed had a highly significant effect on the number of oviposition bouts performed, with flies that experienced windspeeds of between 1.2 and 2 m/s performing over twice as many bouts (Fig. 2A) as flies at zero windspeed ($F = 10.2$; df = 6, 179; $P < 0.001$). Because the number of eggs laid on the plant has a positive relationship with the number of oviposition bouts performed by a female ($r^2 = 0.31$; $F = 79.6$; df = 1, 180; $P < 0.001$; slope significantly different from zero: $t = 8.9$; $P < 0.001$), the number of eggs laid on the plant not surprisingly increased at the higher windspeeds (Fig. 2B), with double the number of eggs laid at 1.6 and 2 m/s, to those at zero wind ($F = 4.2$; df = 6, 178; $P < 0.001$).

Flight responses of females during the observation period (Fig. 3A) were strongly influenced by windspeed ($G = 93.5$; df = 18, 177; $P < 0.001$). While the percentage of females that stayed on the plant or were blown out of the windtunnel increased with increasing windspeed, the percentage of females that reached one of the adjacent host patches situated upwind, downwind, and crosswind on either side, decreased. For females that flew away from the central wheat plant (see Fig. 1B), flight destination (Fig. 3B) was also not independent of windspeed ($r^2 = 0.12$; $G = 38.9$; df = 18, 151; $P < 0.01$). As windspeed increased the percentage of females reaching the left or right patch decreased (22 flies flew to each of the left and right patches over the total experiment, so there was no directional bias). The percentage of females reaching the upwind patch also decreased with increasing windspeed, with no successful upwind flights occurring at windspeeds greater than 0.9 m/s. In contrast, the percentage of flying females reaching the downwind patch or being blown out of the tunnel increased.

Influence of windspeed on egg distribution

At higher windspeeds more eggs were laid in patches downwind of the release patch than in patches upwind, in contrast to the more equitable distribution of eggs in low windspeed ($G = 106\text{-}660$, df = 4, $P < 0.01$). However overall, greater numbers of eggs were laid in the presence of minimal vs stronger winds; 3928 eggs were laid at 0.1 versus 1528 at 0.7 m/s (Fig. 4B), and 3906 eggs were laid at 0.1 versus 768 at 1.2 m/s (Fig. 4C).

Because egg numbers were so much lower in the first trial of the second experiment when females were exposed to 1.2 m/s wind, I observed the females foraging

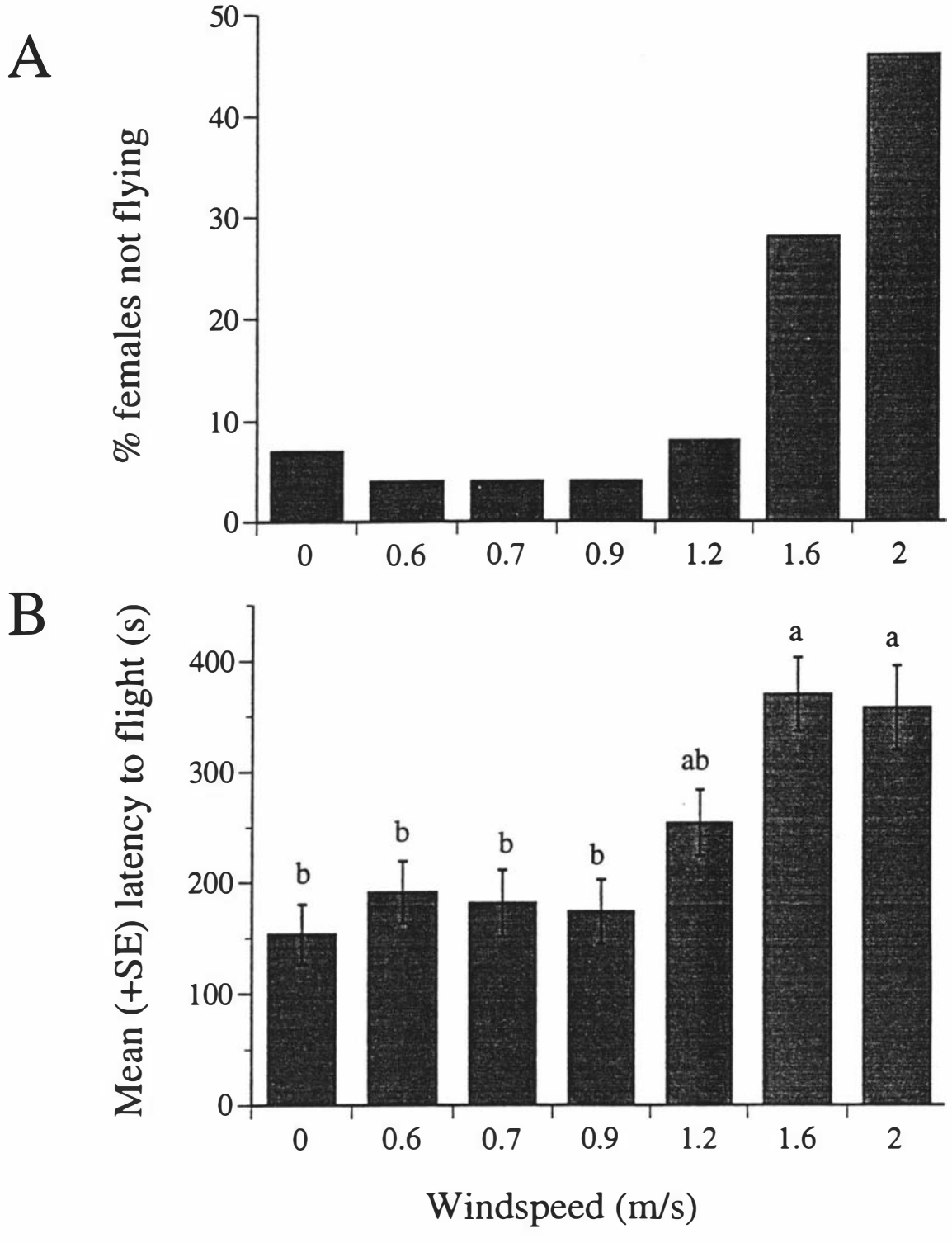


Fig. 1. (A) Relationship between windspeed and the percentage of Hessian flies not initiating flight from a wheat plant within the 12 min observation period. (B) Relationship between windspeed and mean (± SE) latency to flight initiation (data only includes those individuals that initiated flight within 12 min). Means accompanied by same letter are not significantly different at $P < 0.05$, Tukey-Kramer LSD test.

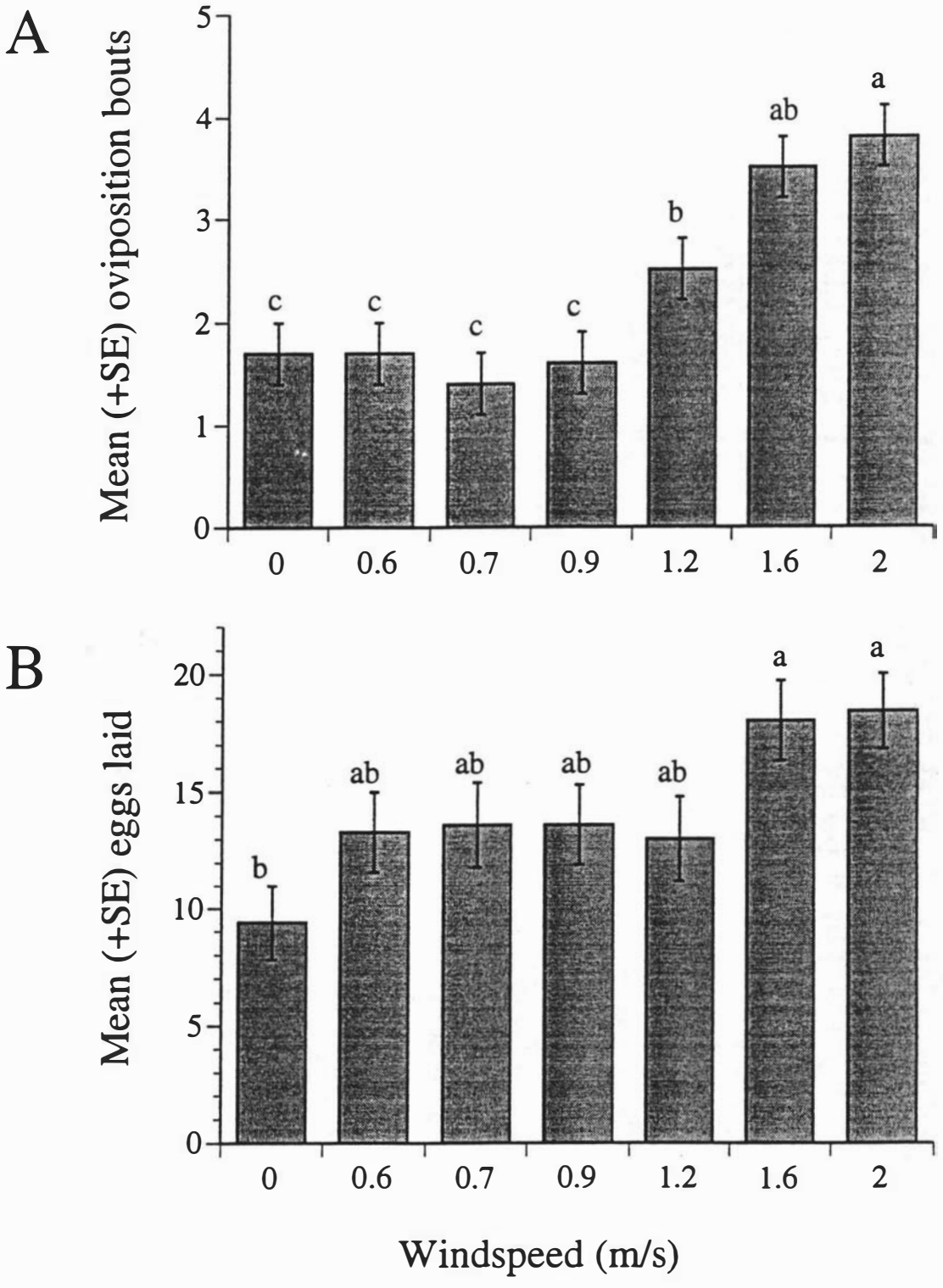


Fig. 2. Relationship between windspeed and oviposition of female Hessian flies: (A) the mean (± SE) number of oviposition bouts performed on the central wheat plant, and (B) the mean (± SE) number of eggs laid on the central wheat plant before leaving (or before termination of observation period). Means accompanied by same letter are not significantly different at $P < 0.05$ ($n = 180$).

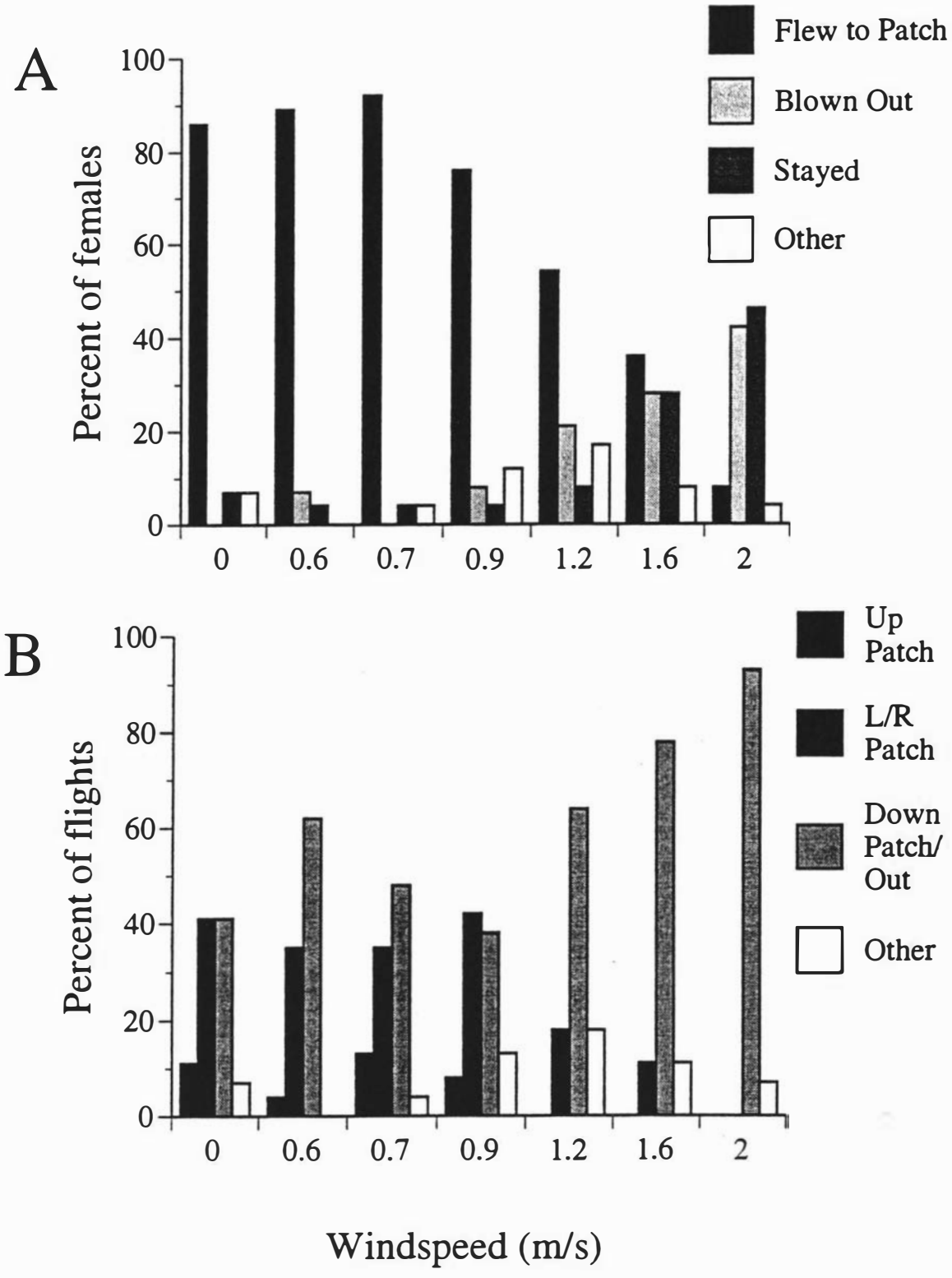


Fig. 3. Relationship between windspeed and (A) the flight behaviour of females during the observation period, and (B) the destination of females that initiated flight from the plant. The category "others" includes individuals that were lost from sight or that flew to the soil.

in 0.1 and 1.2 m/s winds in the second trial. Females observed flying away from plants (approx. n=15) in higher winds were carried 30 and 60 cm downwind onto the sand. These females then made short flights to the perspex side of the tunnel, and were blown out the end of the tunnel. During the same experiment, females foraging in winds of 0.1 m/s generally took short flights from plant to plant and were never observed losing control of their flight direction.

Response to host versus non-host plant in different windspeeds

Windspeed significantly influenced latency to flight initiation (Fig. 5A), with females on both wheat and oats staying longer on plants at higher windspeeds ($F = 16.5$; $P < 0.0001$). Plant species also had a significant effect on latency to flight ($F = 5.5$; $P < 0.02$), with females on wheat staying longer than females on oats. Although windspeed appeared to have a stronger effect on latency to flight than host plant, there was no interaction between windspeed and plant species ($F = 1.8$; $P < 0.19$). The number of eggs laid (Fig. 5B) before leaving was also significantly influenced by plant species ($F = 23.6$; $P < 0.0001$) and windspeed ($F = 4.5$; $P < 0.036$). Again there was no interaction between windspeed and plant species ($F = 1.6$; $P < 0.21$). Plant species did not significantly influence egglaying rate ($F = 2.4$; $P < 0.12$) however, windspeed did ($F = 8.9$; $P < 0.004$). There was no interaction between windspeed and plant species ($F = 1.1$; $P < 0.3$) on egglaying rate. On wheat eggs were laid at 0.082 and 0.047 eggs per second at 0.65 and 1.6 m/s wind, respectively. On oats, eggs were laid at 0.059 and 0.042 eggs per second at 0.65 m/s and 1.6 m/s winds, respectively.

Plant species significantly influenced the mean duration of oviposition bouts (Fig. 5C), with longer bouts on wheat than oats ($F = 4.5$; $P < 0.04$) but this was not influenced by windspeed ($F = 1.3$; $P < 0.3$). No interaction occurred between the effects of windspeed and plant species on bout duration ($F = 1.3$; $P < 0.27$). The number of bouts was also significantly influenced by plant species (Fig. 5D). The number of bouts on wheat was greater than the number of bouts on oats ($F = 13.9$; $P < 0.001$). Windspeed also influenced this ($F = 18.4$, $P < 0.0001$), with more bouts being performed at 1.6 m/s than at 0.65 m/s wind. There was a significant interaction between the effects of host plant and windspeed on the number of oviposition bouts performed ($F = 6.2$; $P < 0.01$).

Influence of windspeed on lifetime fecundity

The same number of eggs were laid by females which had previously been held in cages in still air and high wind conditions (mean ± SE :173.3 ± 17 versus 128.3 ± 16, respectively). For those females whose bodies were recovered at the end of the experiment (16 out of 40), numbers of eggs laid by females were positively related to winglength ($r^2 = 0.55$; ANOVA $F = 17.1$; df = 1, 14; $P = 0.001$; slope significantly different from zero $t = 4.1$; $P = 0.001$). Although no accurate measures of lifespans were

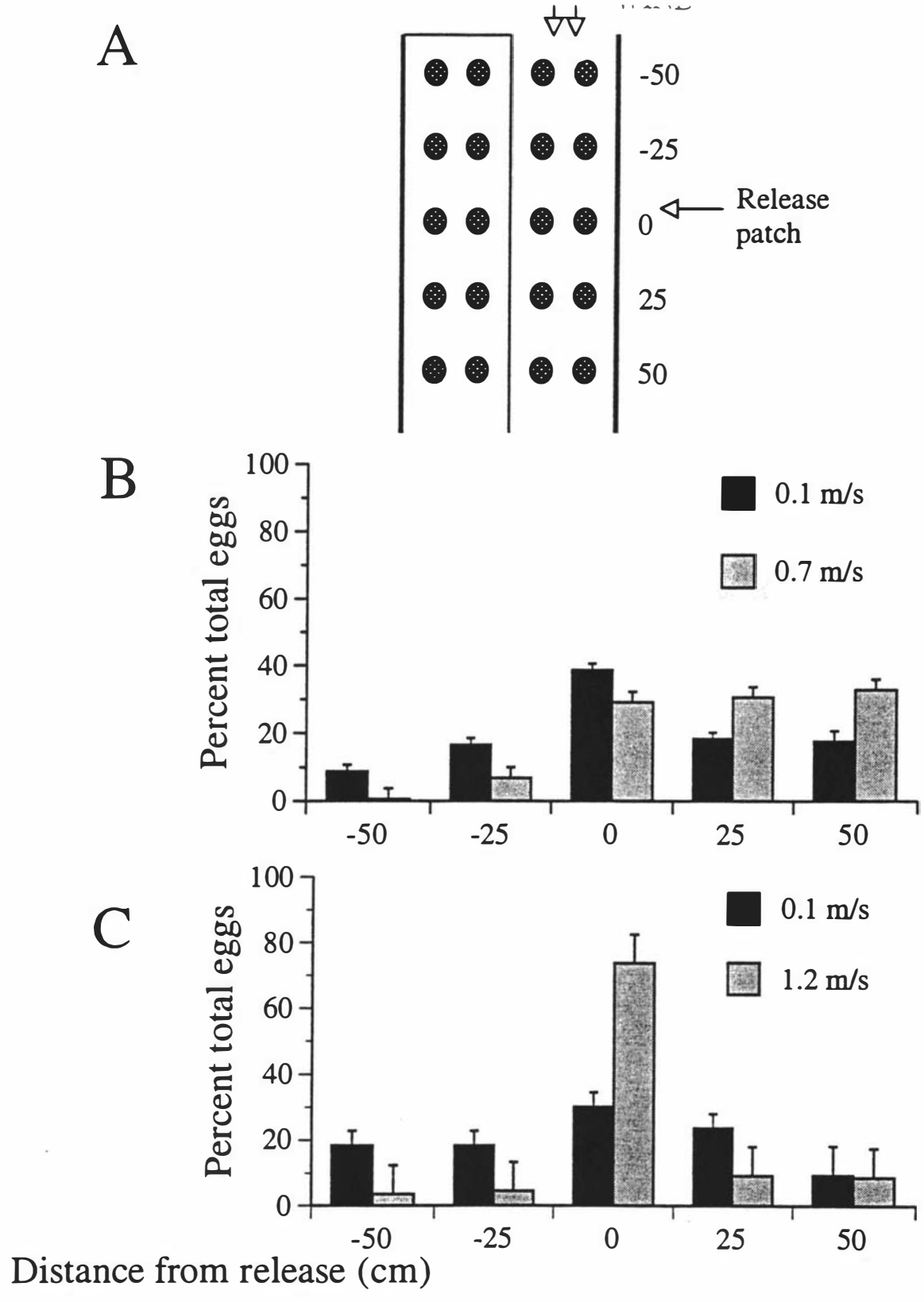
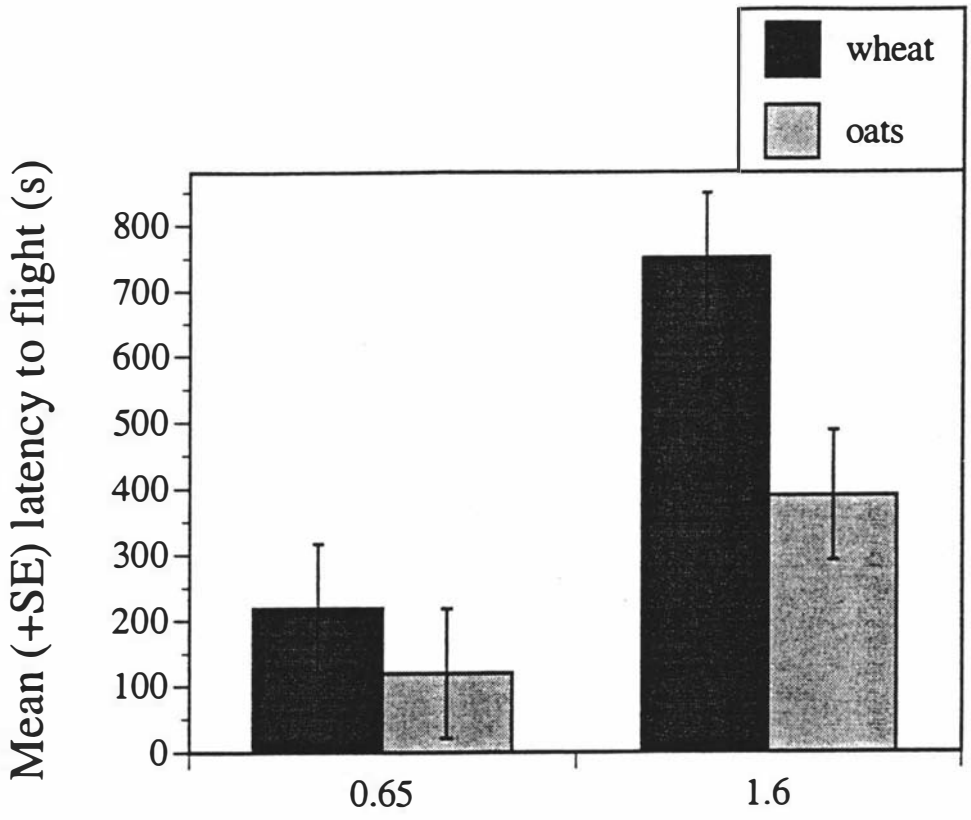
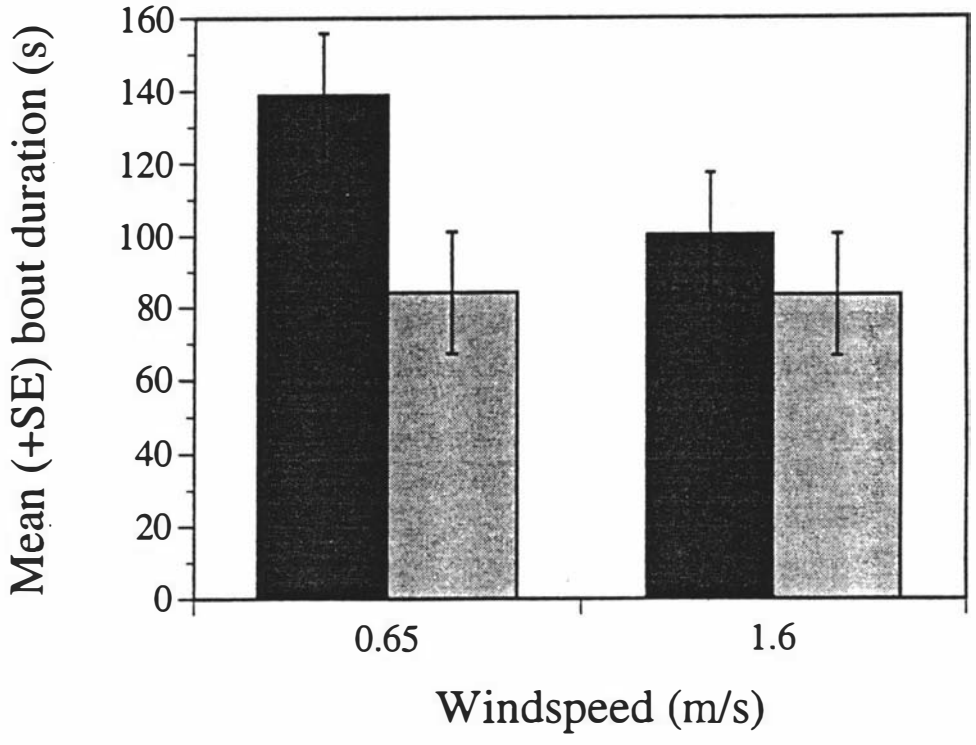


Fig. 4. (A) The experimental array used to determine the distribution of eggs laid by female Hessian flies (n = 25 released at distance = 0) to patches of wheat (circles) arranged in the divided windtunnel, with each side having different windspeed conditions. (B) The mean (±SE) distribution of eggs in 0.1 versus 0.7 m/s wind, from two trials. (C) The mean (±SE) distribution of eggs in 0.1 versus 1.2 m/s wind, from two trials. All distributions are significantly different at $P < 0.01$.

A


wheat
oats
Mean (+SE) latency to flight (s)
800
700
600
500
400
300
200
100
0
0.65
1.6

C


Mean (+SE) bout duration (s)
160
140
120
100
80
60
40
20
0
0.65
1.6
Windspeed (m/s)

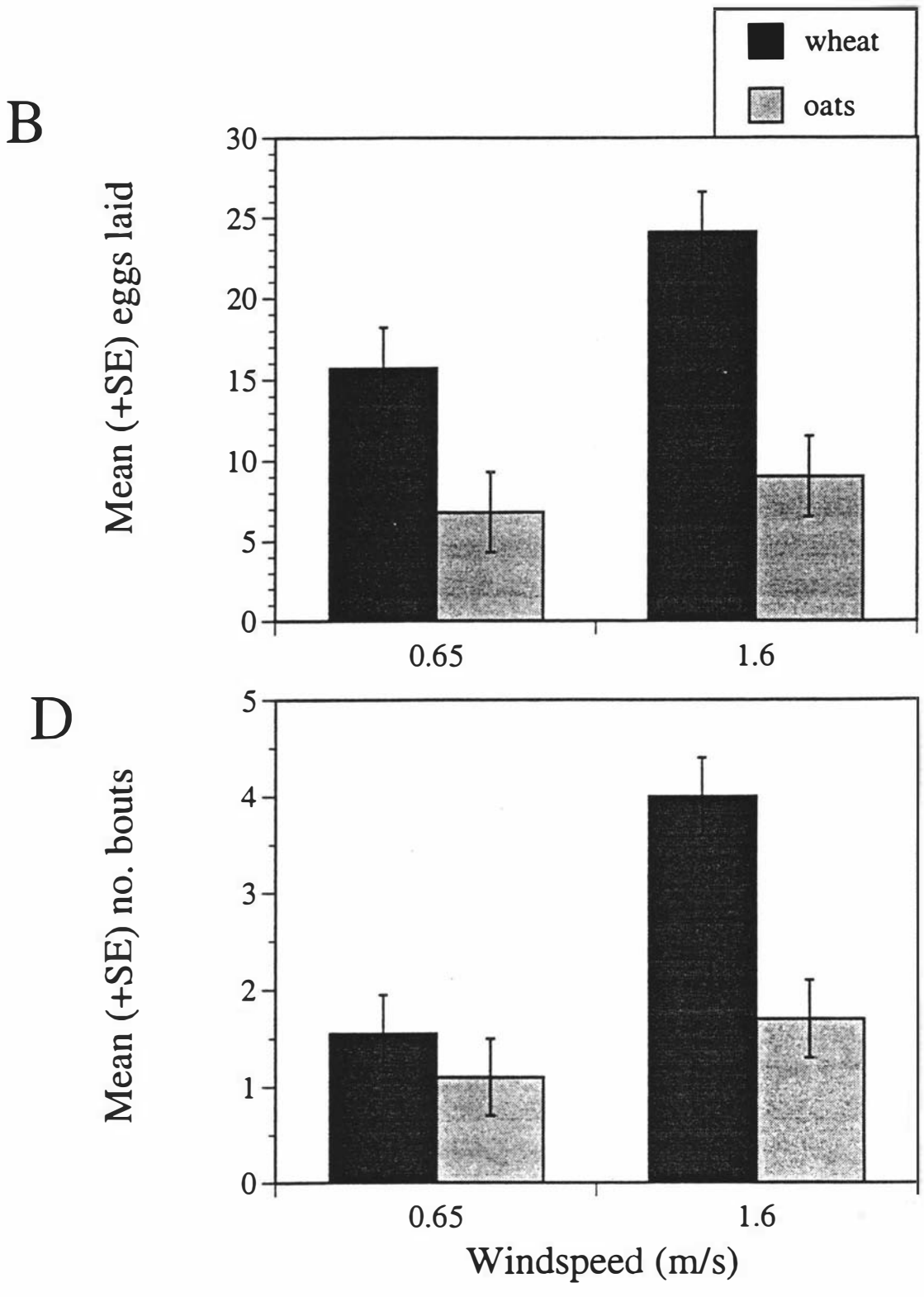


Fig. 5. The separate and combined influences of plant species (wheat versus oats) and windspeed (0.65 m/s versus 1.6 m/s) on female Hessian fly behaviour: (A) mean (± SE) latency to flight from the plant, (B) mean (± SE) number of eggs laid, (C) mean (± SE) duration of oviposition bout, and (D) mean (± SE) number of oviposition bouts performed.

obtained in this experiment, this relationship can be explained by the observation (Withers & Harris, in prep.) that larger females carry more eggs and lay eggs at faster rates.

Discussion

Once the egglaying phase begins, female Hessian flies partition their time between four behaviours: flight, examination of plant surfaces, oviposition and sitting (Harris & Rose, 1989). We have shown that wind conditions suppressed flight behaviour and thereby increased time allotted to on-plant behaviour. In light winds of up to 0.9 m/s, females typically remained on a wheat plant until they had completed one or two bouts of egglaying. As windspeed increased, females remained on the plant for longer periods and exhibited more bouts of egglaying. Latency to flight initiation increased from just over two minutes in minimal winds to over 11 minutes in winds of 1.6 m/s.

Reduced flight activity during windy conditions appears to be common in many insect species. While foraging for hosts, the herbivore *Rhagoletis pomonella* (Aluja *et al.*, 1993), and the parasitoid, *Cotesia rubecula* (Keller, 1990), flew more frequently and exhibited shorter latencies to flight initiation, respectively, in still air than in stronger winds. In the absence of hosts, black bean aphid, *Aphis fabae* (Haine, 1955), adults were more likely to initiate vertical flights in calm rather than windy conditions. These vertical flights launch aphids into faster moving wind streams which occur above the plant canopy and generally result in long distance dispersal. In the black bean aphid, the inhibition of vertical flights by strong winds results in "post-inhibitory rebound" (Kennedy, 1990) once winds subside. After strong winds, the number of aphids that initiated vertical flights exceeded the number that would have flown without strong winds having been present. The functional explanation provided for this behaviour (Kennedy, 1990) is that post-inhibitory rebound allows aphids to maximise the opportunity for vertical flights provided by periods of calm which may occasionally punctuate windy conditions.

In experiments examining the effects of wind on the distribution of Hessian fly eggs on wheat patches, strong winds were shown to reduce the number of eggs laid and change the distribution of eggs in upwind and downwind patches. This was probably a result of winds influencing the destination of females after flight. It was only in very light winds that Hessian flies were observed to fly with full control over their flight direction. In stronger winds, upwind flights decreased while flights downwind and those out of the windtunnel increased. Observations of individuals flying in stronger winds indicated that females maintained their heading into the wind but instead of making upwind progress, were blown backwards and down to the soil. Once on the soil females were generally unable to fly up again and were eventually blown out of the windtunnel at the level of the soil. This suggests that dispersal patterns in strong winds probably differs from those in light winds. McColloch (1917) observed female Hessian flies in light winds flying at heights of 6.5-7.0 m above the ground, and captured mated females in vertically-

positioned screens placed 3.2 km downwind of infested wheat fields. Whether strong winds inhibit vertical flights of Hessian flies as well as the foraging flights is not clear.

While stronger winds suppressed flight behaviour, wind did not appear to influence on-plant behaviour. Regardless of windspeed, females on plants continued to divide their time between bouts of examining/ovipositing behaviour and periods of sitting. Therefore, the number of bouts performed by females before leaving the plant did change with windspeed, simply because at higher windspeeds females stayed on the wheat plant longer and continued to exhibit oviposition bouts. The one to two bouts which were performed in minimal wind speeds increased to about four bouts at 2.0 m/s. Increases in the number of bouts performed by a female led to proportionate increases in the numbers of eggs laid on the plant.

By examining the effects of wind in conjunction with changes in plant stimuli (host versus non-host plants) I was able to gain a better sense of the relative and combined effects of each on ovipositing Hessian fly females. In a factorial analysis wind appeared to have greater effects on flight initiation, number of oviposition bouts, and egglaying rate, while plant stimuli appeared to have a greater effect on the duration of oviposition bouts and numbers of eggs laid. To the best of our knowledge the relative effects of wind and host have not been examined together in other insects. Of these five behavioural parameters (time to flight initiation, number of oviposition bouts, egglaying rate, duration of oviposition bouts and number of eggs laid), only the number of oviposition bouts showed interactive effects of wind and plant stimuli. The behavioural meaning of statistical interactions is often difficult to determine (Harris & Foster, 1995) but may indicate an integration of inputs in a particular decision-making process.

The results of the factorial experiment have contributed to a tentative model of the flight and oviposition decisions made by female Hessian flies. After ovipositing on a host plant, females show a reduced response to plant stimuli and in still air or light winds, initiate flight movements which take the female away from the plant. If, however, the female senses strong winds prior to taking flight, flight is suppressed. When flight is suppressed the female continues to sit on the plant but soon after becomes responsive to plant stimuli once again and begins examining behaviour. An assessment of plant stimuli triggers oviposition on wheat and shorter bouts of oviposition on oat plants (Fig. 5C). This bout is followed by an assessment of the wind, and another decision about whether to stay on the plant or leave. If strong winds continue, the female stays on the plant successively assessing plant and wind stimuli. However, as time on the plant increases, changes in the internal state of the female increasingly counterbalance the stimulatory effects of host plant cues on oviposition and the suppressive effects of strong winds on flight initiation. These internal changes increase the probability that the female will fly away from the plant and shorten bouts of egglaying on wheat (this contributes to the shorter bout duration on wheat at higher windspeeds, Fig. 5C). If such internal changes

did not occur in the female over time, it would be expected that in the presence of strong winds, the female would simply stay on the plant and oviposit until she dies, rather than eventually flying away.

For Hessian fly females, the suppression of flight for short periods of time in winds that do not permit controlled flight manoeuvres has obvious advantages, such as avoidance of being swept out of fields of host plants. However, because egglaying behaviours while on the plant are not similarly suppressed by strong winds, females in strong winds may lay more eggs on a plant than is optimal. In 1.2 m/s winds, a mean of 24 eggs were laid on a single wheat plant versus 16 eggs in lighter winds. If all 24 eggs were to hatch and all neonate larvae successfully migrate down to feeding sites at the crown of the plant, the number of Hessian fly larvae feeding may exceed the carrying capacity of a single plant. Suppression of flight by strong winds also does not appear to give females more time or energy to lay their eggs once winds subside. When finally given wheat plants in still air conditions, host-deprived females whose flight had been suppressed for two hours by being held in cages in strong winds did not lay more of their eggs before dying than host-deprived females whose flight had not been suppressed during the same two hour period.

In conclusion, wind has a major impact on the foraging behaviour of mated female Hessian flies, influencing flight manoeuvres as well as interactions with plants. Although I did not examine the effects of wind on male Hessian flies, strong winds probably have similar detrimental effects on their reproductive behaviour. Male Hessian flies locate virgin females by flying upwind in the presence of sex pheromone (Harris & Foster, 1991) but probably have difficulty performing such flights in strong winds: males weigh less than females and only have slightly longer wings (Bergh *et al.*, 1990). Unless adults have some way of avoiding eclosion in adverse conditions, wind could have a major effect on the dynamics and spread of Hessian fly populations.

Acknowledgments

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CHAPTER FOUR

The influence of clutch size on survival and reproductive potential of Hessian fly

Abstract

The clutch size of female Hessian flies (*Mayetiola destructor*) (Diptera: Cecidomyiidae) was manipulated over a range of 1 to 30 eggs on single wheat plants (*Triticum aestivum*, L.). Pupae developing from egg clutches were counted and reared through to adult eclosion. Winglengths of adult males and females were recorded and used as an indicator of body size. Survival to pupal and adult stages as well as the mean winglength of males and females decreased as clutch size increased. Winglength of females from clutches showed a strong positive linear relationship with mean fecundity. Male winglength has been shown in Bergh *et al.* (1990) to be related to fecundity through the number of females that can be inseminated. The benefits of small clutches for a female Hessian fly's offspring are discussed in the context of the foraging behaviour of the ovipositing female.

Key words. Hessian fly, larval density, competition, fecundity, fitness

Introduction

For phytophagous insects that have relatively immobile larval stages, the reproductive success of an ovipositing female is influenced by the the number of offspring (i.e., clutch size) she deposits on individual plants. From the females' perspective, the optimal size of egg clutches will depend on several ecological factors, including the intensity of offspring competition at each feeding site, the occurrence of density dependent mortality due to natural enemies, and the number of suitable oviposition sites the female can expect to find over her adult life span (Weis *et al.*, 1983). If competition at individual feeding sites or mortality due to natural enemies increases with offspring density, then the reproductive success of the female should be optimised by depositing very small numbers of offspring at each site. However, if the female incurs an increased mortality risk by extending the time over which she must forage to find large numbers of sites (i.e., she dies before she lays her full complement of eggs), some compromise must be made between these direct losses to her reproductive potential and those she will incur indirectly if her offspring suffer losses through competition or natural enemies.

Although the proximate mechanisms underlying clutch size in the Hessian fly (*Mayetiola destructor*, Say) (Diptera: Cecidomyiidae) have been studied in some detail (Harris & Rose, 1990; Foster & Harris, 1992; Withers and Harris, in prep.; Withers, chapter three), ecological factors that may act as selective factors upon clutch size have not been investigated. Hessian flies are semelparous, and therefore have a single complement of eggs that are matured during pupal development (Fritz *et al.*, 1982). Field as well as laboratory observations have established that the way that these eggs are allocated to individual feeding sites is somewhat flexible. A mere 3-5 eggs are laid per site when plants are abundant and environmental conditions are conducive to foraging flights. Up to 45 eggs per site are laid when females have been deprived of host plants or are exposed to windy conditions. Because Hessian fly larvae cannot move from tiller to tiller within a plant or move away from the plant they have been placed on by their mother, this flexibility in clutch size can result in widely varying numbers of larvae feeding at a single site. The consequences of such crowding at feeding sites for the reproductive fitness of the ovipositing female or her offspring have not been investigated.

We explored the relationship between the clutch size laid by individual female Hessian flies and the survivorship and reproductive potential of offspring. To do this, individual females (n=27) were used to generate small to large egg clutches on single wheat plants. Pupae resulting from these clutches were counted and held individually until adults emerged. The reproductive potential of adults was estimated by measuring winglength, a size parameter which has been shown to be related to the potential fecundity of Hessian

fly females (Bergh *et al.*, 1990), as well as the ability of Hessian fly males to inseminate large numbers of females (Bergh *et al.*, 1992). The maximum reproductive fitness of Hessian fly females is then discussed within the context of other ecological factors that may act as selection forces upon clutch size.

Materials and methods

Single wheat (*Triticum aestivum* L.) plants (cv. 'Karamu') were grown in a greenhouse (24±4° C) in 5x5 cm pots containing a sterilised bark media with 0.75 kg/m^3 fertiliser (N:P:K 14:7:15). Hessian flies were from a lab-reared colony (see Withers and Harris, in prep.). Females emerged daily (0500-0700 h), mated with males before 0800 h and were introduced singly into mesh cages (50x50x50 cm) at 1000 h. Starting at 1130 h, individual mated females were serially exposed to three to six wheat plants (two-leaf stage). Individual plants were held with the female until they each received either a small (1-3), medium (8-12) or large (20-30) number of eggs. The order that the female laid small, medium, or large egg clutches was randomised to ensure that effects of clutch size were not confounded with potential effects of oocyte position within the ovaries. If necessary, some eggs laid on the plants were punctured with a minuten pin to achieve appropriate clutch sizes. The exact number of viable eggs per plant was then recorded. Plants (n=119) were infested over a two-week period in October 1994 using 27 females. Infested wheat plants were labelled (with date and female number) and returned to the greenhouse where they were bed-watered and misted daily. Four weeks later pupae were removed from each plant by carefully pulling back each leaf comprising the tiller to expose the pupae. Starting from the top-most pupa, each pupa was placed into a labelled glass vial containing moistened cotton wool, and its feeding position, from top to crown in the stem, recorded. Vials were held under natural light, and checked daily for adult emergence. Cotton wool was remoistened with distilled water when dry.

Within 1-8 h of eclosion, adults were placed in 70% ethanol. Winglengths of preserved adults were measured (distance between the axillary sclerite and radial sector vein, see Bergh *et al.*, 1990) using an eye-piece micrometer under 20X magnification. The ovarioles of the majority of female offspring were dissected under 40X magnification and the number of oocytes within the ovaries counted. Pupae that did not produce adults within two months were dissected to ascertain whether individuals had died or been parasitised. Whenever possible the cause of death was recorded. The presence of fungal hyphae from the puparium suggested fungal infection, while a hard or shrivelled pupal mass suggested dessication.

The influence of egg clutch size on survivorship between the egg, pupal, and eclosing adult stages on each plant were explored using linear regressions. The significance of various factors (clutch size, order clutch was laid, and possible variation

between females who laid the eggs) on pupal to adult survivorship were tested with four-way analyses of variance (ANOVA) at $P<0.05$ (JMP, SAS, 1989). To investigate the influence of clutch size on adult reproductive success, all offspring eclosing from a single plant were grouped together to obtain mean winglengths of males and females and mean number of oocytes from female offspring. The significance of clutch size, order the batch was laid and variation between original females on these correlates of offspring reproductive success were tested with ANOVA as above.

The effect of feeding position on adult size was investigated by comparing winglengths of individual female and male offspring which either eclosed from the bottom-most pupa in a plant (crown) or the top-most pupa in a plant. Only those clutches that produced unisexual progeny with >50% pupal to adult survival in a large (20-30) egg clutch were analysed. This criterion produced 10 all-female progenies and 8 all-male progenies for comparison. Within single-sex progenies winglengths were compared between crown and top positions using a non-parametric Kruskal-Wallis rank test at $P<0.05$.

Results

There was evidence for density-dependent mortality according to different clutch sizes. The percentage of Hessian flies surviving from the egg to the pupal stage showed a negative linear relationship to clutch size (F=19.1; df=1,112; $P<0.001$; slope different from zero t=-4.4, $P<0.001$). The percentage of Hessian flies surviving from the pupal stage to eclosion as an adult was similarly influenced by clutch size (F=20.2; df=1,101; $P<0.001$; slope different from zero t=-4.5; $P<0.001$). Hence there was a significant influence of clutch size on Hessian fly survival from egg to adult eclosion (Fig. 1) (F=33.5; df=1, 112; $P<0.001$; slope different from zero t=-5.8; $P<0.001$).

There was low pupal survivorship (45% of all pupae died). This was attributed to entomophagous fungal infection (7% of pupae), dessication (35% of pupae), or unknown death (3% of pupae). Clutch size laid per plant had significant effects on pupal to adult survival (r^2=0.46: F=7.8; df=1; $P<0.01$), while individual variation between females laying the eggs (F=1.1; df=26; $P<0.3$) and order in which the clutch was laid (first through to sixth, F=1.9; df=5; $P<0.1$) did not.

Mean adult male body size per clutch (n=48) showed a negative linear relationship with clutch size (Fig. 2) (F=8.98; df=47; $P>0.001$; slope different from zero t=-3.0; $P<0.001$). Mean male offspring size was not only related to clutch size per plant (r^2=0.82; F=9.8, $P<0.01$) but varied significantly among females laying the eggs (F=4.6; $P<0.001$), and marginally to the number of pupae per plant (F=4.1; $P<0.06$). The size of males was not influenced by the order the clutch was laid (F=1.5; $P<0.5$).

Mean female body size per clutch (n=56) showed a negative linear relationship with clutch size (Fig. 2) (F=21.1; df=55; P<0.001; slope different from zero t=-4.6, P<0.001). Mean female offspring size was not only related to clutch size per plant (r^2=0.76; F=5.8; P<0.001) but varied significantly among females laying the eggs (F=2.6; P<0.01). The size of females was not influenced by the order the clutch was laid (F=0.9; P<0.5) or the number of pupae per plant (F=2.2; P<0.2). For the females whose eggload was quantified (165/190), mean offspring potential fecundity from each clutch was positively related to mean winglength (r^2=0.76; F=188; df=1,55; P<0.001). A two-way ANOVA indicated that mean fecundity was significantly related to clutch size per plant (F=27.5; df=1; P<0.001) as well as an effect of the female laying the eggs (F=2.34; df=18; P<0.02). The mean fecundity when expressed relative to clutch size per plant (Fig. 3) showed a negative linear relationship (r^2=0.34; F=27.6; df=1,55; P<0.001). Due to the correlation between clutch size and number of pupae per plant, mean fecundity was also negatively related (Fig. 4) to the number of pupae per plant (r^2=0.28; F=20.4; df=1,55; P<0.001).

When large numbers of Hessian fly larvae feed on a single plant, not all can feed at the crown of the plant. Thus as numbers increase, more larvae are found at greater distances from the crown. The comparison (Table 1) of winglengths of male and female adults which eclosed from positions at the crown versus the top of the plant, reveals that in some cases those from the crown of the plant did not suffer the same effects of a large clutch size as those at the top of the plant. This effect was only evident in the male offspring within large sized clutches (Kruskal-Wallis non-parametric rank test at P<0.05).

Table 1. The effect of feeding position on the mean (and range) of female and male adult winglengths arising from large clutches.

Position	**Female** (n= 10 clutches)	**Male** (n= 8 clutches)
Top of tiller	2.1 (1.7-2.4 mm)	2.1 (1.6-2.5 mm)
Crown	2.2 (1.5-2.6 mm)	2.3 (1.9-2.7 mm)
Significant difference ?	No Chi^2 =1.3; P<0.3	Yes Chi^2=8.9; P<0.05

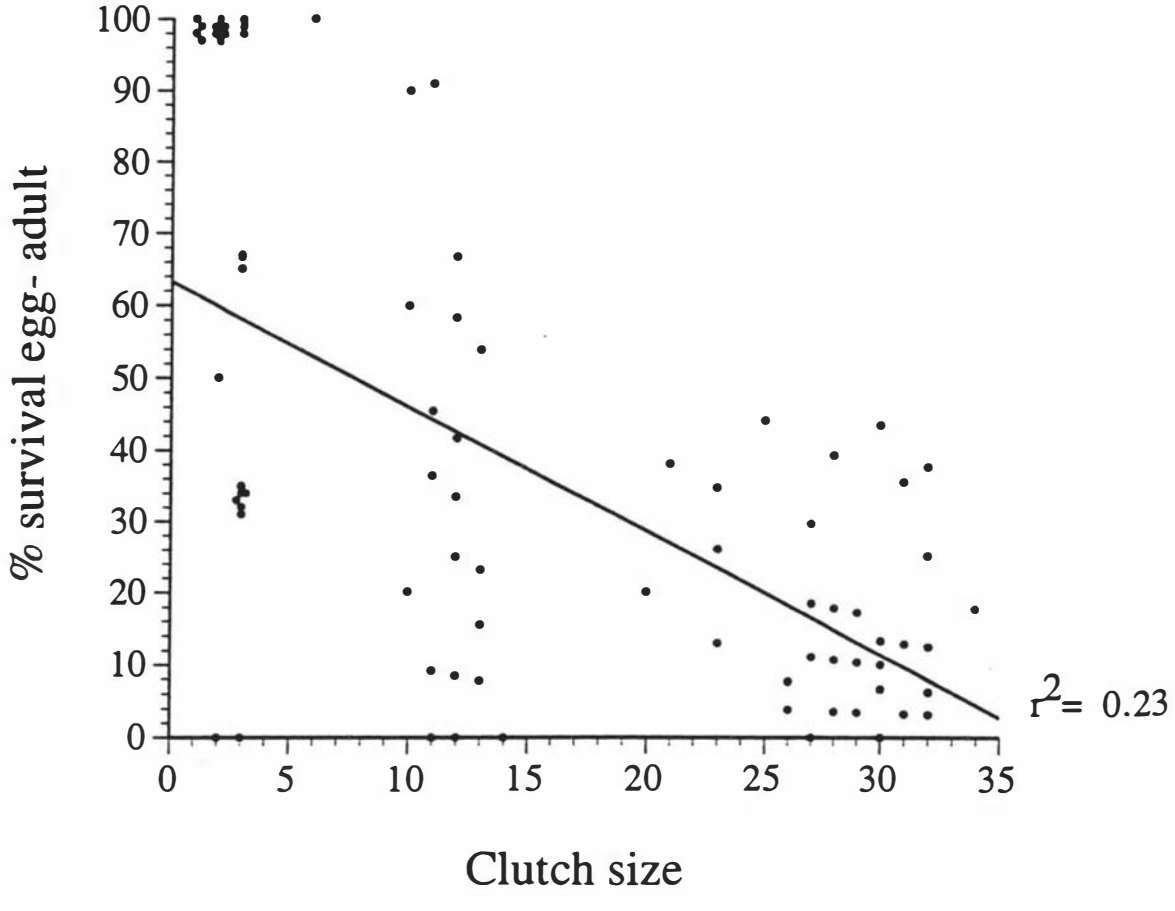

Fig. 1. Percentage survival of Hessian flies from egg to adult eclosion, as influenced by clutch size per plant.

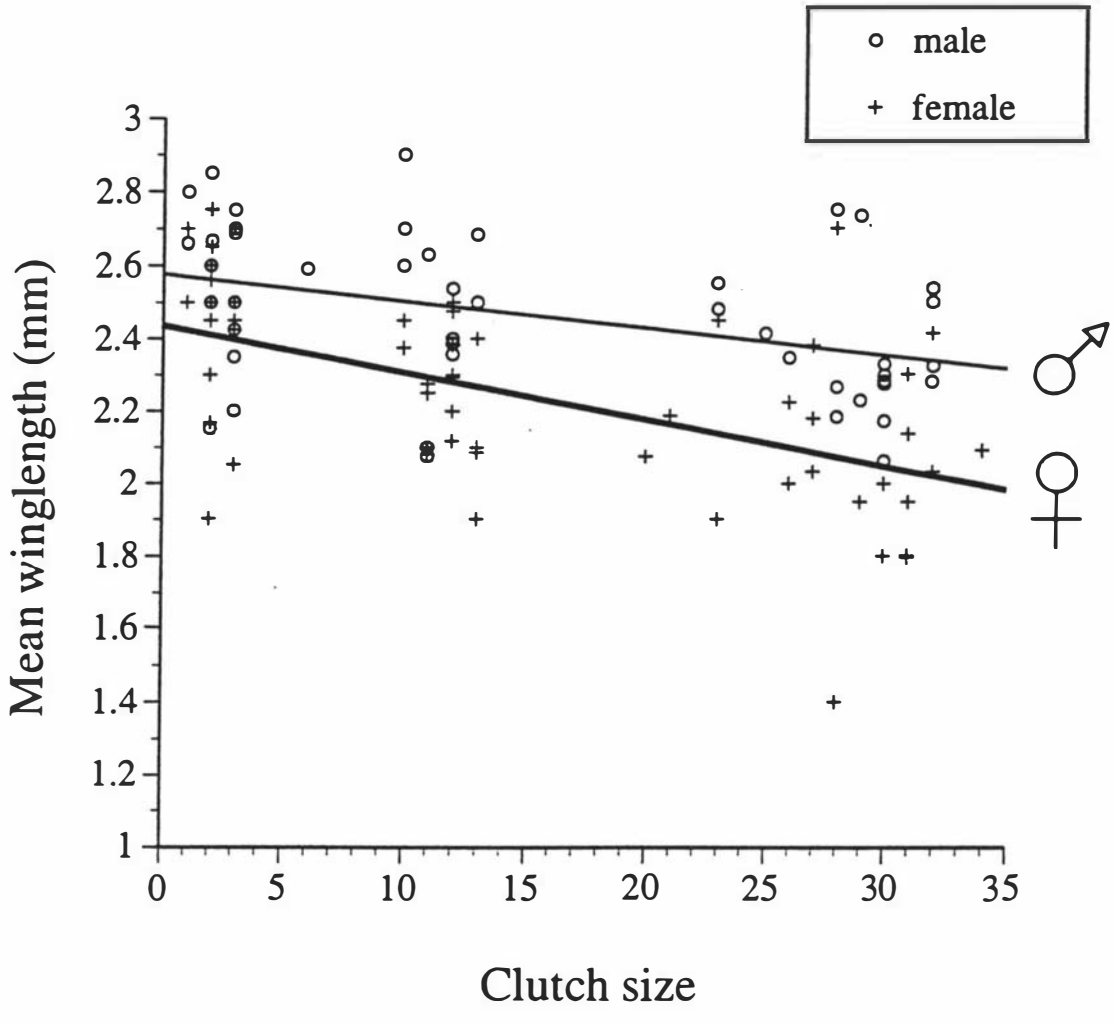

Fig. 2. The relationship between clutch size per plant and the mean winglength of eclosing adult Hessian flies per clutch. Male offspring represented by circles, females by crosses.

Because most Hessian fly females produce unisexual clutches, we explored the consequences of clutch size separately for females producing all-female versus all-male progenies. For females producing all-female progenies we assumed that each female begins with a fecundity of 200 eggs (as would be expected if she arose from a plant containing only 1-2 pupae) and survives to deposit all of her eggs (Table 2). Density-dependent mortality (see Fig. 1) as well as density dependent reproductive potential of offspring (Fig. 2 and 3) mean that a female laying 5 eggs per clutch could attain a maximum reproductive fitness three times greater than a female laying 25 eggs per clutch (Table 2).

In studies on female fecundity, the use of number of oocytes as a measure of potential reproductive fitness should be made cautiously (Leather, 1994). The use of the number of oocytes in female Hessian fly ovaries as an index for maximum reproductive fitness is, however, justified as Hessian flies are semelparous. Furthermore, under optimal conditions of high humidity and access to preferred host plants, female Hessian flies will readily lay 95-100% of their oocytes before death (Harris & Rose, 1991).

Table 2. Maximum fitness attainable for a female Hessian fly ovipositing 200 all-female eggs in fixed size clutches. Maximum potential fitness for the mother is the product of the number of clutches, the number of offspring resulting, and offspring fitness contribution.

	Clutch size			
	5	10	20	25
No. of clutches deposited	40	20	10	8
No. of offspring resulting per clutch [1]	3	5	6	6
Max. fitness contribution per offspring [2]	150	135	120	125
Maximum reproductive fitness	18000	13500	7200	6000

[1]. Mortality estimated from Fig. 1

[2]. Reproductive fitness estimated from Fig. 3

Now we can consider the alternative condition, where we assume 20% risk of mortality as females move between sites. This means that the female deposits a maximum of five clutches before dying. Under these conditions the maximal reproductive fitness of a female Hessian fly is now obtained with increasing clutch size (Table 3).

Table 3. Maximum fitness attainable for a female Hessian fly laying all-female progeny under conditions of high adult mortality during foraging. Maximum reproductive fitness for the mother is the product of the five clutches, the number of offspring resulting, and the offspring fitness contribution.

	Clutch size			
	5	10	20	25
No. of clutches deposited	*5*	*5*	*5*	*5*
No. of offspring resulting per clutch [1]	3	5	6	6
Max. fitness contribution per offspring [2]	150	135	120	125
Maximum reproductive fitness	2250	3375	3600	3750

[1]. Mortality estimated from Fig. 1

[2]. Reproductive fitness estimated from Fig. 3

The maximum reproductive fitness of female Hessian flies laying only male offspring can also be approximated. Bergh *et al.* (1992) ascertained that a male Hessian fly of 0.33-0.35 mg liveweight, fertilised approx. 2800 eggs. From the relationship between male liveweight and number of fertile matings given in Bergh *et al.* (1990), we can assume a male of this weight can mate with 17 females. This equates to fertilising 165 eggs per mating. The relationship between male winglength and liveweight (Bergh *et al.*, 1990) enables us to approximate the maximum fecundity of adult male offspring eclosing from different sized clutches in a similar way as was explored for females. This clearly shows that reproductive fitness of a female laying all-male clutches is maximised when eggs are laid in small clutches (Table 4).

Table 4. Maximum fitness attainable for a female Hessian fly laying all-male offspring clutches of fixed size. Maximum reproductive fitness for the mother is the product of the number of clutches, the number of male offspring resulting, the number of matings each male is capable of, and the number of fertilised eggs contributed per mating.

	Clutch size			
	5	10	20	25
No. of clutches deposited	40	20	10	8
No. of male offspring resulting per clutch [1]	3	5	6	6
No. of matings per male [2]	17	16	14	13
No. of fertilised eggs per mating [3]	165	165	165	165
Maximum reproductive fitness	336600	264000	138600	102960

[1]. Mortality estimated from Fig. 3

[2]. Reproductive fitness estimated from Fig. 4, and Figs. 5 & 7 from Bergh *et al.* (1990)

[3]. Based on 17 matings producing 2805 fertilised eggs as in Bergh *et al.* (1992)

Discussion

The number of eggs a female Hessian fly lays at an individual feeding site on a wheat plant has significant effects on the survival and reproductive success of her offspring which feed at that site. Individuals hatching from larger egg clutches suffered greater mortality between the egg, pupal and adult stages. In addition to the effect on survival, plants with larger numbers of pupae produced significantly smaller male and female offspring, with female offspring showing a decrease in potential fecundity in proportion to the decrease in body size. These results suggest that individual seedling wheat plants provide finite shelter and food resources for developing Hessian flies.

A number of factors may be operating within a wheat plant to cause the increased Hessian fly mortality on plants with larger clutch sizes. It has been observed (by McColloch and Yuasa, cited in Barnes, 1956) that after hatching from the egg (usually laid high on the leaf blade) first instar larvae of Hessian fly have a very slow rate of migration to the crown of the plant (e.g., 4.5 mins to move 1 mm). Mortality during this migration period averages 23%. It is conceivable that during this migration larvae encountering unhatched eggs or other migrating larvae may suffer greater mortality because interference may increase the duration to reach a feeding site at the crown of the plant. In this way, larvae hatching from larger clutches may be more susceptible to mortality before they even reach a feeding site.

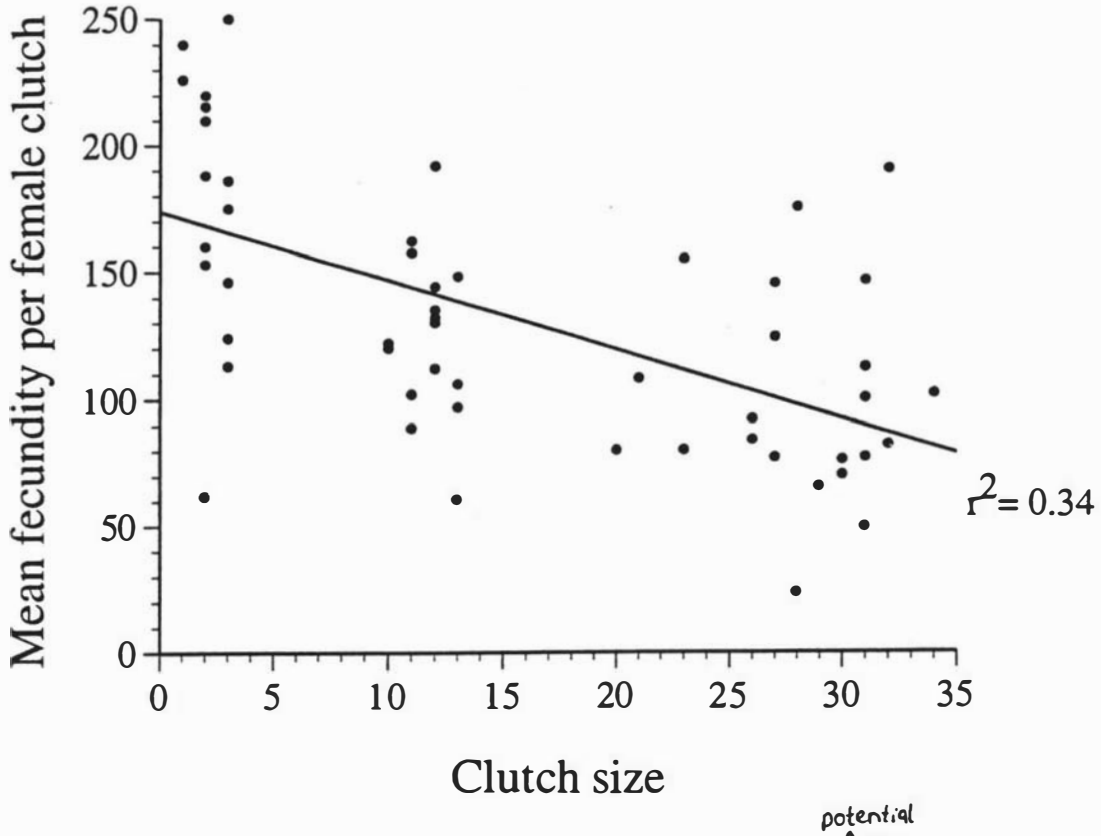

Fig. 3. The relationship between clutch size per plant and mean potential fecundity of female offspring from those clutches in Hessian flies.

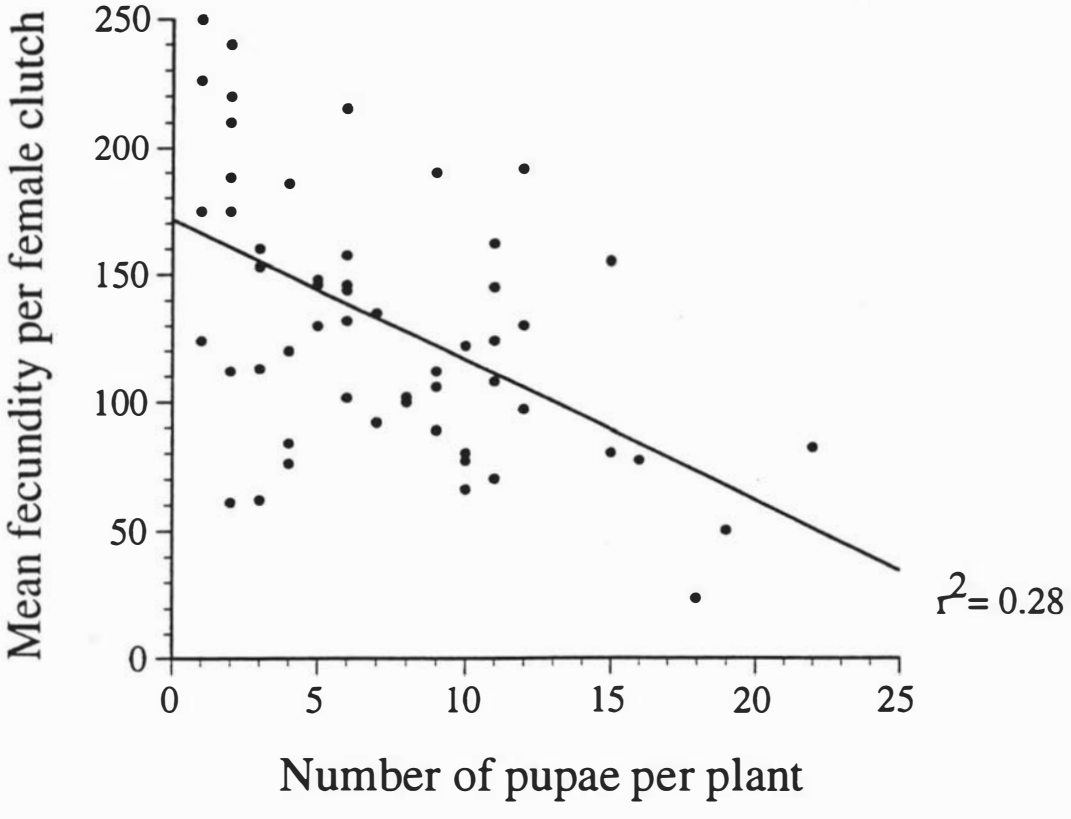

Fig. 4. The relationship between the number of pupae per plant and mean potential fecundity of female offspring from those clutches in Hessian flies.

Another factor operating on larval mortality may be exclusion from, or competition at, a feeding site. In large clutches, larvae migrating down to the crown of the plant may encounter larvae that have already established feeding sites. These late-comers may be forced to settle at a feeding site providing less shelter or food resources. First instar Hessian fly larvae lose their creeping pads when they moult into their second instar (Gagne & Hatchett, 1989), after which they are immobile (Hatchett *et al.*, 1990) and therefore cannot move to another feeding site within the plant if local conditions decline.

Once larvae have established a feeding site, another factor affecting survivorship may be the physiology of the plant, with heavily-infested and weakened plants producing lower quality and/or quantity of digestible products for larval growth and nutrition (Asavanich & Gallun, 1979). Young wheat plants suffer the greatest damage from Hessian fly feeding and show extensive stunting which often leads to whole tiller or plant death. Growth inhibition occurs in a young wheat plant after first-instar larvae have fed for only two days (Asavanich & Gallun, 1979). These physiological changes that occur as a Hessian fly larva feeds on the plant, in turn must have impacts on the feeding larva and its neighbours.

Our experimental results indicated that larger clutch sizes increased mortality from the pupal to adult stage. Increased pupal to adult mortality may be related to the smaller larval, and subsequently pupal, size and weight associated with large clutches. The resultant smaller pupae may have suffered greater susceptibility to dessication via their larger surface area to volume ratio.

The number of Hessian fly present within a single plant appeared to have an affect that in some cases was felt to a greater extent by those individuals feeding at the position furthest from the crown of the plant. This may indicate that food and shelter resources are unevenly distributed through a single wheat plant, making some feeding sites of higher quality than others. A study of *Frumenta nundinella* (Lepidoptera: Tineidae) infesting fruit of *Solanum carolinense* revealed that the mass of infested fruit declined significantly from basal to distal along the infructescence (Solomon, 1988). The mass of the infesting pupa was found to be significantly related to that of the fruit from which it emerged (Solomon, 1988). The results of the present study indicated that male Hessian flies were more sensitive to feeding position in the tiller of a wheat plant than females. An explanation for this may be related to the differing mass to size ratio of males and females (Bergh *et al.*, 1990), suggesting the sexes may have different resource requirements.

Adult male Hessian flies that fed and emerged from a heavily infested plant showed the effects of competition with a significant reduction in body size, as indicated by winglength. Another cecidomyiid, *Asteromyia carbonifera*, showed the same relationship, with male body mass decreasing with increasing clutch size (Weis *et al.*, 1983). Winglength is related to fresh weight and fecundity in male Hessian flies (Bergh *et*

al., 1990) by being correlated to the total number of matings resulting in one or more fertilised eggs (Bergh *et al.*, 1990). This increased ability of large males to undertake multiple matings may be a result of increased flight ability and mating speed, as has been shown in *Ceratitis capitata* males (Churchill *et al.*, 1986). Male Hessian flies fly upwind in plumes of female sex pheromone, released by calling virgins (Harris & Foster, 1991), and larger body size may aid this movement. Increased body size may also increase Hessian fly ability to inseminate females through a greater amount of sperm being produced and stored (Bergh *et al.*, 1992). It is also possible that larger males mating more females may be due to increased longevity of larger sized males, with increased body size reducing susceptibility to dessication. Whatever the causal mechanism underlying the relationship between male size and number of matings, the reproductive fitness of a female laying all-male clutches is maximised when eggs are laid in small clutches.

Like males, adult female Hessian flies originating from a heavily infested plant showed the effects of larval competition, with a significant decrease in body size as indicated by winglength. Female winglength also correlates positively to body mass (Bergh *et al.*, 1990) and fecundity, as expressed by the number of oocytes present in the ovaries. McConnell (1921) was the first to observe that female Hessian flies that arose from plants containing many pupae contained fewer oocytes when dissected, but this was not quantified. The results of this experiment confirm his observations and in addition quantify the extent to which clutch size reduces female fecundity. Competition has been shown to decrease the fecundity of female *Callosobruchus maculatus* (Coleoptera: Bruchidae) when reared together in the same seed (Colegrave, 1993). This reduced fecundity was shown to be purely the result of sharing a finite resource reducing adult weight.

Maternal genetics may influence Hessian fly reproductive biology as the results revealed a significant effect of the female who laid the eggs on offspring size. However, since females oviposited on plants over a period of 12 days, we cannot discount the possible influence of differences between the batches of plants infested by the different females. Environmental conditions may have altered between the days the clutches were obtained, or even the position of the plants containing the different clutches within the greenhouse.

In the Hessian fly decisions on how many oviposition bouts to perform on a plant before flying away are based on the presence or absence of internal stimuli and environmental cues. While clutch sizes of 1-5 eggs are commonly laid under optimal conditions, less optimal conditions cause females to deposit larger clutches up to 45 eggs (Withers and Harris, in prep.; Withers, chapter three). Clutch sizes laid have important consequences for both the ovipositing female and for her future offspring. For the adult female Hessian fly, maximum reproductive fitness was achieved when her full compliment of oocytes was laid in small-sized clutches. Herein both adult female and her

offspring profit. However, this situation changes if a female is not able to oviposit all of her eggs before dying. For example, if a female only lives long enough to lay five egg clutches, maximum reproductive fitness would now be obtained by laying larger sized clutches per plant, not the minimum as was the case previously. While the adult female achieves an increased fitness through laying large clutches, the interests of her individual offspring will not be well-served by being oviposited in a large clutch. Larvae will suffer increased mortality and competition, and therefore will have their own potential fitness reduced. It is likely that female Hessian fly oviposition behaviour reflects a balance achieved between the fitness of offspring and the number of eggs oviposited.

Our analyses of reproductive fitness suggested that mortality during or between periods of egg deposition may be an important selection pressure on clutch size. Risks of mortality for a female Hessian fly may occur from hunting spider predation during oviposition (McColloch, 1923). However, the risks associated with foraging flights may include bird predation (Barnes, 1956), web spider predation, and harsh environmental conditions. Females exposed to very strong winds (2.0 m/s) respond by increasing the number of oviposition bouts performed on a single wheat plant before flying away, from one bout (approx. 8 eggs deposited) to almost four bouts (approx. 18 eggs deposited) (Withers, chapter three). In addition, deprivation from oviposition sites increases clutch size laid on the first plant encountered (Withers and Harris, in prep.). The absence of host-plants at the onset of foraging or high wind conditions, may signal a reduced likelihood of locating suitable hosts in the near future. Under these conditions, females are better off to deposit a large clutch of eggs on the first contact with a host plant, in case no other plants are located. Thus Hessian fly females may be assessing cues from their internal state and environmental conditions during foraging behaviour, and may increase reproductive fitness by reducing clutch size under high probabilities of survival and oviposition, and by increasing clutch size when the probability of locating another patch is low (Weis *et al.*, 1983).

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CHAPTER FIVE

Dispersal of mated female Hessian flies in host and non-host field arrays

Abstract

The movement of ovipositing Hessian fly (*Mayetiola destructor* Say) females during foraging for host plants was investigated using a number of field release techniques. The first technique indirectly measured female movement between wheat patches by recording the spatial distribution of resulting larval infestations. Females found wheat patches at all distances from the release patch indicating that females can move at least 27 m when foraging for oviposition sites. The second technique released and recaptured adult females in circular arrays of either host or non-host plants. Percentage recapture of females ranged from 17 to 80%, being lower in the non-host compared to host arrays. Recapture rates also decreased as the duration between release and subsequent recapture increased. Flies moved at a greater rate through non-host than hosts, which was seen as an increased retention in the host arrays, compared to the non-host. Mathematical models were used to explore movement patterns of females in host and non-host arrays over time. Simple random diffusion models did not adequately describe the data because a proportion of the released individuals moved further in the arrays than was predicted. An alternative model allowing for these faster-moving individuals is proposed. Movement of females in field arrays supported predictions made from experiments which quantified female movement in smaller (2 x 2 m) arrays.

Key words. Cecidomyiidae, dispersal, edge-effect, flight, plant stimuli, *Mayetiola destructor*

Introduction

Hessian flies (*Mayetiola destructor* Say.) are a major pest of wheat (*Triticum aestivum* L.) and other cereal crops throughout the world (Barnes, 1956). Cultural control methods that reduce infestations include rotation of crops (Lidell & Schuster, 1990) and deep ploughing and burning of stubble after harvest to destroy in-field populations of Hessian fly pupae (Chapin *et al.*, 1992). The use of these control methods means that Hessian flies infesting a field of newly-planted wheat have usually originated from outside the field (Gossard, 1916). Thus, movement of individuals within a single generation is often critical to the pest status of Hessian fly.

Hessian flies are virtually immobile as larvae, only the adults move extensively. Adult females are inactive until several hours after mating, however, once foraging for oviposition sites begins, females begin flying and moving about on plants, until they die (6-24hours later) (Harris & Rose, 1991). When foraging for oviposition sites, female Hessian flies exhibit directed movements toward visual cues (Harris *et al.*, 1993). Settlement on the plant then occurs as a response to foliar, tactile and chemical cues (Harris & Rose, 1990; Foster & Harris, 1992). Oviposition behaviours such as rates and numbers of eggs laid differ significantly according to the plant species contacted (Harris & Rose, 1989; Withers and Harris, in prep.). One strategy phytophagous insects use to increase their search efficiency for host plants is to concentrate their searching in habitats where they have already located hosts, and leave habitats when only non-host plants have been contacted. Behavioural mechanisms insects use for this can be expressed in may forms (Bell, 1994). Hessian flies have shown evidence for one such mechanism, area-restricted search (Morris & Kareiva, 1991). Females were seen to alight on fewer non-host plants in a patch compared to host plants in a patch before leaving (Withers and Harris, in prep.), thus, moving out of the non-host patch more quickly. Arenas in which the above observations were made, ranged from 8 cm diameter cages to a 2 x 2 m arena, and contained anywhere from two surrogate plants to 64 live plants.

A question that arises from the above observations of adult female Hessian flies is: Do these observations allow us to predict how females will move over a larger spatial scale ? I believe so and predict that (i) adult females will move distances > 20 m while searching for oviposition sites, and (ii) females will move faster through a non-host field than a host field. The aim of this present study was to test the two above predictions by measuring female movement in host and non-host plant arrays in the field. Three experimental approaches were undertaken: (1) The first experiment recorded infestation levels in patches of wheat plants to ascertain distances females will move during oviposition. Small patches were dispersed over a bare field that covered an area of 50 x 50 m and females were released into the centre. One drawback of using larval infestation to indicate adult dispersal, was that we could not ascertain individual flies movements' or

ascertain the time it takes for females to arrive at distant patches. Release recapture studies overcome those limitations (Stinner *et al.*, 1983). However, release-recapture studies often suffer from low recapture success (e.g., Plant & Cunningham, 1991, Fletcher & Economopoulos, 1976, except see Sylven, 1970 achieved 60% recapture). By attempting the following methods we hoped to overcome this problem. (2) Arrays of plants sown in rings up to 3 m from a central patch were used as the setting for the release-recapture experiments, to reveal if females moved at faster rates through non-host than host plant patches. At times after females were released in the central patch, a D-Vac sampler was used to recapture females from the plant arrays without disturbing the central patch. (3) The previous experimental design was repeated with arrays of host and non-host plants up to 8 m from the central release patch. We sampled all plant arrays after different times, on consecutive days. By altering latencies to recapture, we hoped to understand Hessian fly movement over time, and maximise the proportion of the population we recaptured. Data from this experiment were fitted to a descriptive model of simple random diffusion to see whether female Hessian fly movement in the field differed significantly from random.

Materials and methods

Insects and General Methods

Wheat plants (cv. 'Karamu') were grown in pots and trays in a glasshouse to the 2-4 leaf stage, infested with Hessian fly eggs (from Hessian flies reared in a laboratory culture), and placed into coldstorage (2-5° C) when developing larvae entered the flax-seed (pupal) stage. Exposure to cold temperatures at this developmental stage causes Hessian flies to go into diapause (Foster & Taylor, 1975). In coldstorage plants were watered once every four weeks to prevent larval dessication. Larvae treated in this way remained viable for up to two years (T. Withers, pers. obs.). To obtain large numbers of individuals for experimental releases, large groups of infested plants were removed from coldstorage after between 4 months and 2 years duration, and transferred to a controlled temperature room (24-28° C with a L:D cycle of 12:12 and lights-on at 0700 hours). Adult flies started emerging from plants about 10 days later, and continued to emerge for a six day period.

All plant arrays used in the field experiments were situated at the Massey University Plant Growth Unit, Palmerston North, New Zealand. Plants were grown from untreated seed, sown using a handpushed seed drill to a depth of 4 cm, and irrigated whenever necessary. Before field releases each array was cleared of insects with a D-Vac Insect Vacuum Net (collecting area 1 m^2; Ventura, California). No adult Hessian flies were ever found in these samples, indicating they were scarce in this area at the time of our studies. On the morning of field releases (0800-0930 hours), mated female Hessian flies (as indicated by the cessation of the calling posture, Bergh *et al.*, 1990) were collected using an aspirator and transferred in groups of 20 to 2 cm diameter x 8 cm tall glass vials, stoppered by lids with a netting inset. Vials were held at temperatures between 20 and 24° C until the time of release at 1130-1200 hours, which coincided with the commencement of foraging (Harris & Rose, 1991).

Experiment one: *Patch infestation level as indicators of female movement*

This experiment was conducted in a fallow field previously sown to asparagus. The western and northern boundaries of the field were sheltered by a 4 m high hedge of *Phebalium squarum*. In January 1995 the field measuring 50 x 50 m was prepared by rotary hoeing and used as the temporary setting for 79 wheat patches. Each patch consisted of two plastic pots (each 20 x 20 cm) containing a clump of between 26 and 40 wheat plants (cv. 'Otane') in the three-leaf stage. Wheat plants in pots were grown in a sterilised bark media with Osmocote three month slow release fertiliser. Pots were sunk into the ground for the duration of the experiment. Patches were positioned within the field using the design of Stein *et al.* (1994) where patches radiated outwards from a

central point (Fig. 1), with no two patches dissecting the same radial transect from the centre. Our patches were distanced from 0.95 m to 27.5 m from the centre release patch.

Two trials were conducted. In the first trial an accumulated total of 200 female Hessian flies were released at 1130 hours over three days (Jan. 2, 3, 4, 1995) into a patch of young wheat plants in the central point of the distribution. In the second trial 200 females were released in the same manner on a single day (Jan. 5, 1995). On all experimental days weather was sunny with either no wind or light south westerly gusts. Temperatures at soil level ranged between 20 and 28° C (N.Z. Meteorological Service, Palmerston North station). Pots were labelled and removed from the field on the morning following the final release of each trial. After removal pots were placed in a shade house on a bottom-watered sand bed. Three weeks later, all plants were examined for Hessian fly infestation. Data were recorded as numbers of larvae or pupae per plant.

Experiment two: *Release-recapture in circular host and non-host arrays (6 m diam.)*

The two plant arrays used in these experiments were situated approximately 500 m apart and separated by two 15 m high, mixed species shelter belts and a paved road. Seed (wheat cv. 'Karamu'; oat cv. 'Awapuni') was sown so that there was a central patch of plants (20 cm diameter) surrounded by three concentric circles of plants (Fig. 2A), at distances 1, 2 and 3 m. In one plant array, wheat was sown throughout. In the other plant array, oat was sown in the central patch and in the 1 and 2 m circles, while wheat was sown in the 3 m circle. Weeds were removed from plant arrays up to 4 m from the central patch by herbicide spraying two weeks before experiments and hand-weeding remaining plants.

Two separate releases (150 and 140 females released in each array) were performed during two consecutive days of fine, warm weather in March 1994. At the time of release vials were taken to experimental arrays, opened, and females gently shaken out at ground level within the plants forming the central patch. At four time intervals following release (between 40-50, 80-90, 115-130, and 150-170 minutes), concentric circles of plants within each array were individually sampled using the D-Vac sampler, starting with the innermost circle and moving outwards. The central patch remained unsampled until after the final sampling occurred, allowing females to continue moving away from the central patch with time. After sampling each circle, the contents of the D-Vac net were sprayed with a commercial house-fly spray and transferred to a labelled plastic container. The number of Hessian fly females was counted from each sample under 10 X magnification. Following the last samples, Hessian flies remaining in the central patch were collected by aspirator. The physiological status (virgin vs. mated) of these females was checked by placing individual females in glass vials containing a wheat leaf in a glass vial, and checking for the presence of eggs and viable larvae five days later.

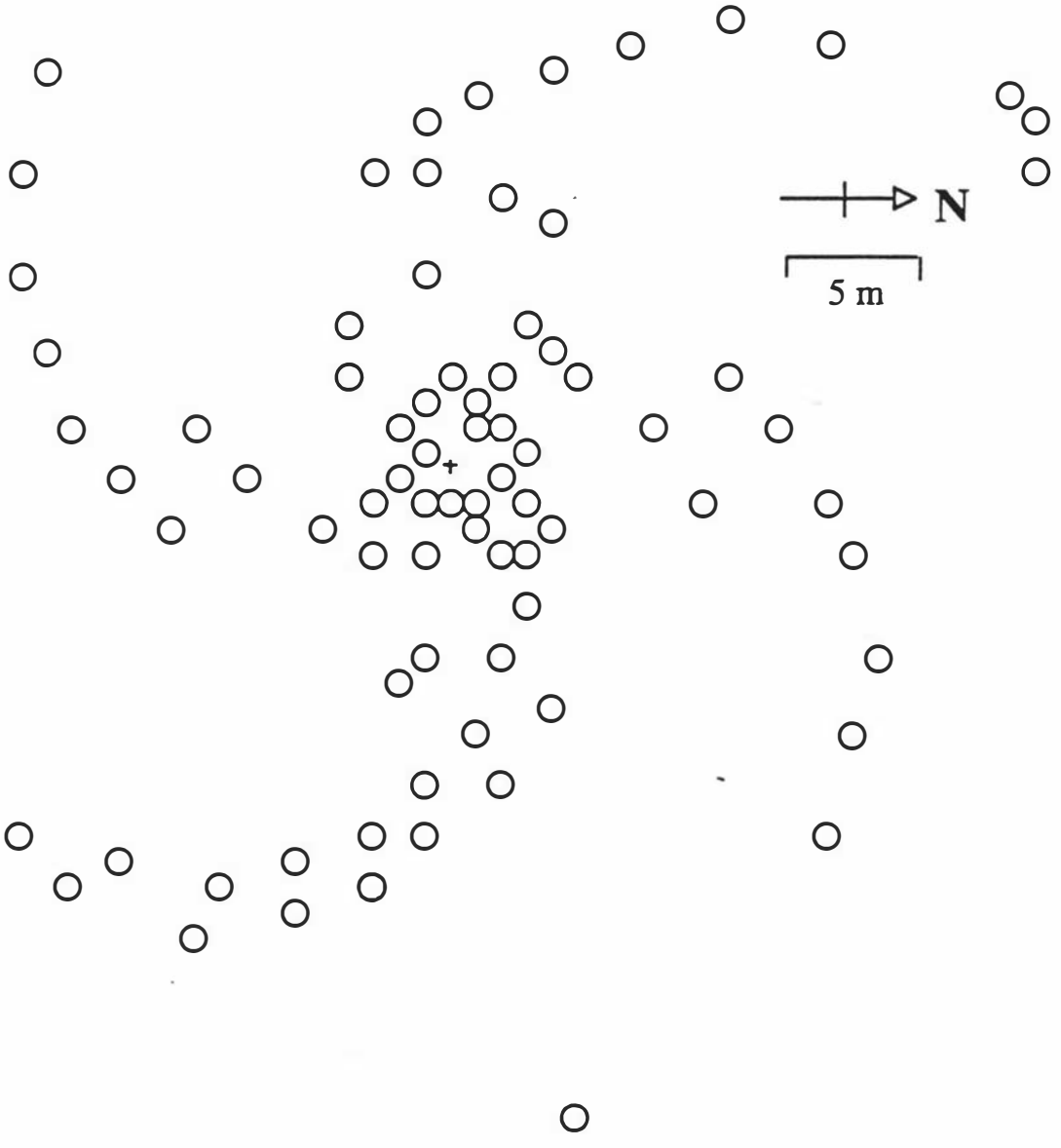

Fig. 1. Schematic representation of layout of wheat patches each containing 30-40 plants (as used in two trials), in experiment one where infestation level is used to indicate female movement.

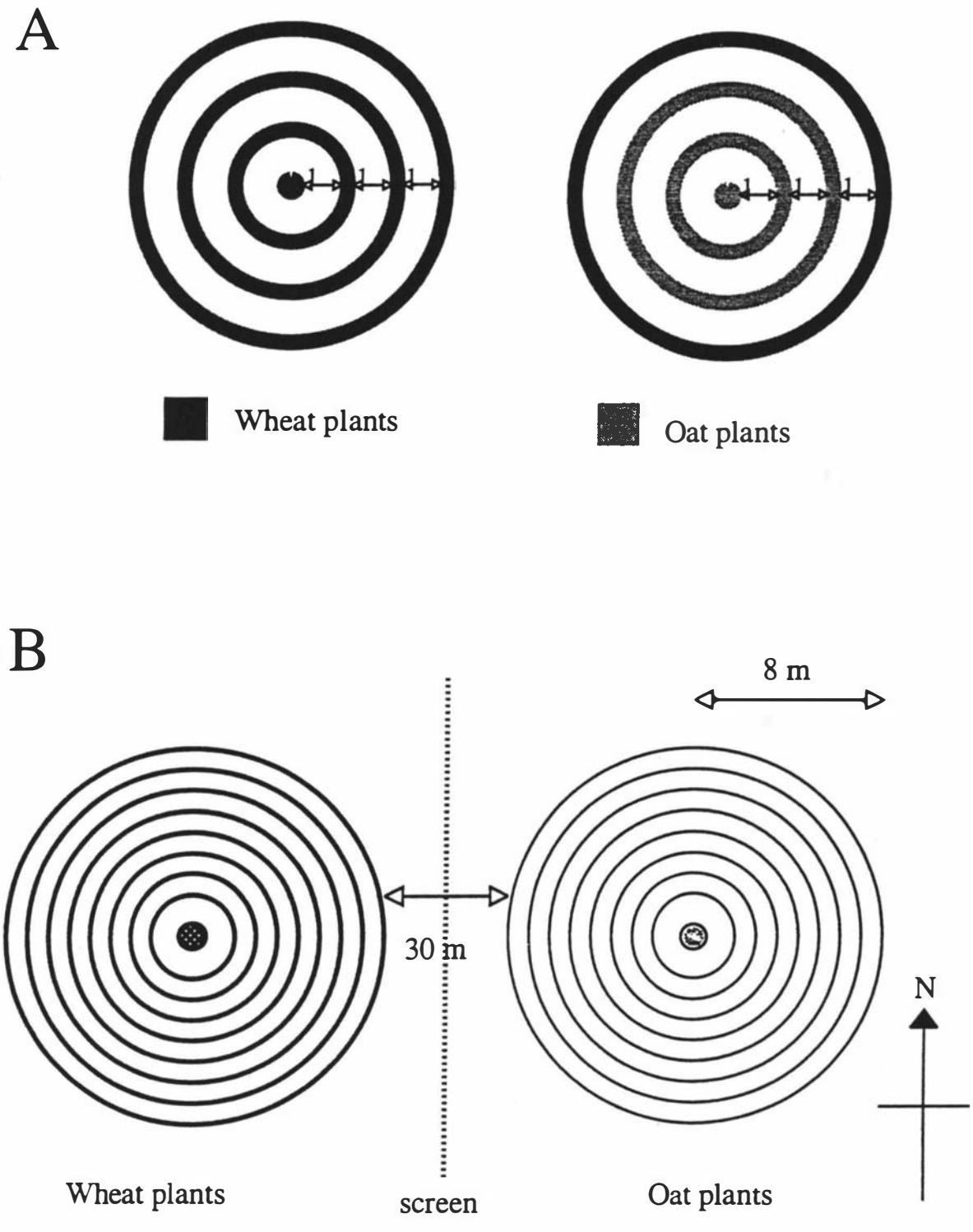

Fig. 2. Experimental designs of field plots from (A) experiment two with Hessian flies released into central patch of wheat, or oats surrounded by either wheat or oats out to 3 m; and (B) experiment three, with all wheat versus all oats, central patch surrounded by rings of plants out to 8 m.

Experiment three: *Release-recapture in circular host and non-host arrays (16 m diam.)*

Both experimental plant arrays were situated in a fallow field prepared by rotary hoeing and were sown either entirely with wheat (cv. 'Otane') or oat (cv. 'Awapuni') seed. Each plant array consisted of a 20 cm diameter central release patch, surrounded by eight concentric circles of plants, each 1 m apart (Fig. 2B). The outermost circle of the oat array was 30 m away from the outermost circle of the wheat array. Halfway between the wheat and oat arrays a 1 m tall plastic barrier was erected from ground level to reduce any possible movement of flies between arrays. Weeds were removed from an area that extended 6 m beyond the outermost circles. Before experiments, the more vigorous oats plant array was hand-thinned to a similar density as the wheat plant array. Both wheat and oat plants were in stem extension stage when experiments were conducted.

Part A Fixed distance sampling over time

Two hundred and seventy females were released into the central patch of both the wheat (at 1200 hours) and oat (at 1205 hours) arrays (Feb. 13, 1995, fine warm weather). At 6-12 minute intervals thereafter, the circle 7 m from the central patch in each array was sampled using the D-Vac, in a manner similar to that described in experiment two.

Part B Variable distance sampling after fixed time

Three separate releases of 345, 345, and 270 females per plot were made over three days (14-16 February, 1995, warm sunny weather with variable wind gusts). Females were released into the central patch of each array, separated by a 15 minute interval. The order of release into either wheat or oats first was alternated between days. At a specified time after release (see Table 1), all circles of each plant array were separately sampled by D-Vac, starting at the central patch and moving outwards, circle by circle. Sampling all circles of each array was completed within 15 mins. Only when the first array was completely sampled, was sampling of the second array begun.

Modelling recapture data

By using a circular design we sampled movement that had occurred in two dimensions (i.e., flies could move out from the release point in any direction); however, it permitted analysis by a one-dimensional model (i.e., movement along a line originating at the release point). Due to the lower numbers released on the third day, the number of flies in each ring were analysed as the percentage of those released. Time, though not included in the equations describing population movement, is implicitly included in our analyses by separately modelling movement at each time interval since release. Following the methods of Rudd & Gandour (1985), I first used a non-linear least squares technique (DeltaPoint,

1993) for each time interval and array to obtain the best fits to a passive diffusion curve of relationship :

$$\text{Number flies} = a.\text{Exp}(-b.\text{Distance}^2)$$

As replications under the same conditions were not attempted, a Lack of Fit analysis (Bates & Watts, 1988) could not be conducted. Instead the fit of the models to the data was judged by plotting the combined residuals, both independently and against distance (Draper & Smith, 1966) and testing for non-randomness and non-normality (SAS, 1989). The parameter *a* is a constant best considered as an indication of the population at the central position (Freeman, 1977) and is related to initial population density (Taylor, 1978). The value for the parameter *b* is the regression coefficient for the change of numbers with increasing distance (Freeman, 1977) and provides an indication of insect mobility most easily understood when transformed into a coefficient of diffusion,*D*.

Coefficients of diffusion *D*, represent rates of movement at the level of the insect and are circumstance and species-specific (Corbett & Plant, 1993). The coefficient of diffusion *D*, was obtained for Hessian fly movement rates seen at each time interval from both arrays, as given by the following equation from the passive diffusion curve (Rudd & Gandour, 1985).

$$D = 1/4bt$$

Where *t*, time of sample (taken from Table 1) was the median time (in minutes) from release to sampling all the circles of the corresponding plant array. From this measure we can obtain estimates for the rates of movement of Hessian flies in the host and non-host plant arrays.

Results

Experiment one: *Patch infestation levels indicating female movement*

Wheat patches, despite their small size (20 x 40 cm), were infested with Hessian fly larvae or pupae at all distances from the centre release site. For analyses the array (Fig. 1) was split into segments, each 5 m wide from the centre of the array (i.e., distances 0<5 m, 5<10 m, 10<15 m, etc. from the centre release site). Infestation level was calculated as the percentage of plants within a patch that were infested with one or more Hessian fly larva or pupa, and averaged over the patches in each segment. Number of pupae per plant was not used as a measure of infestation level because egg to pupal survival is density-dependent (Withers, chapter four). In both trials the mean level of infestation per patch

decreased with increasing distance from the centre, with an increase beyond 20 m (Fig. 3A). The percentage of patches present within each distance segment that were infested with at least one Hessian fly were also compared (Fig. 3B), and though greater levels were seen in the first trial, both trials showed a decreasing percentage of patches infested as distance increased.

The probability that a female leaving the central patch by flight in a fixed direction, intercepted a patch within each distance segment was calculated (Fig. 3C). The combined area covered by patches (each only 40 cm wide) present in each segment was divided by the total circumference of the middle of each segment, i.e. 2.5 m, 7.5 m, 12.5 m (similar to Stein *et al.*, 1994). This gave an estimate of the probability each fly has of intercepting a wheat patch, if while moving outwards from the release site it does not land unless it intercepts a patch on its flight path. This expected probability of interception expressed as a percentage (Fig. 3C), was compared to the observed levels of infestation at each distance segment using a G test of independence. In both trials, infestation levels differed significantly from those expected by the probability of interception, in particular they were lower than expected at distances >5 m from the central patch, and were greater than expected at the distances 20-27 m (trial one: G=28.8, df=4, P<0.001; trial two: G=26, df=4, P<0.001).

Experiment two: *Release-recapture in circular host and non-host arrays (6 m diam.)*

Females were released into the centre of the two plant arrays shown in Fig. 2A and were recaptured from three circles at various times after release, leaving the central patch unsampled until the completion of the experiment. In total 56% of flies released into the nonhost plant arrays and 52% of flies released into the host plant arrays were recaptured. The distribution of females released and then (1) not recovered, and (2) recaptured in each sample (n=13) taken from wheat and oats arrays at each distance and at each time were compared statistically between the two days. The distribution of females in the samples from both days were not significantly different (G-test: G= 6.4, df=13, P>0.5 for wheat array; G= 13.6, df=13, P>0.5 for oat array). In all further analyses, data for the two days were combined.

Distributions of released females recaptured at each time and distance were significantly different between the host and non-host plant arrays (G= 38.2, df=13, P<0.01). In particular, over the entire sampling period more females were recaptured from the wheat circles 1 and 2 m from the release point than from the oat circles at the same distance (108 vs 69 females, Fig. 4). The distribution of females recaptured over time in the outer ring alone (sown to wheat in both cases) was compared statistically between the two arrays. The outer ring recaptures over time differed significantly between two plant arrays (G=10.2, df=3, P<0.05). In particular, females released into the oat

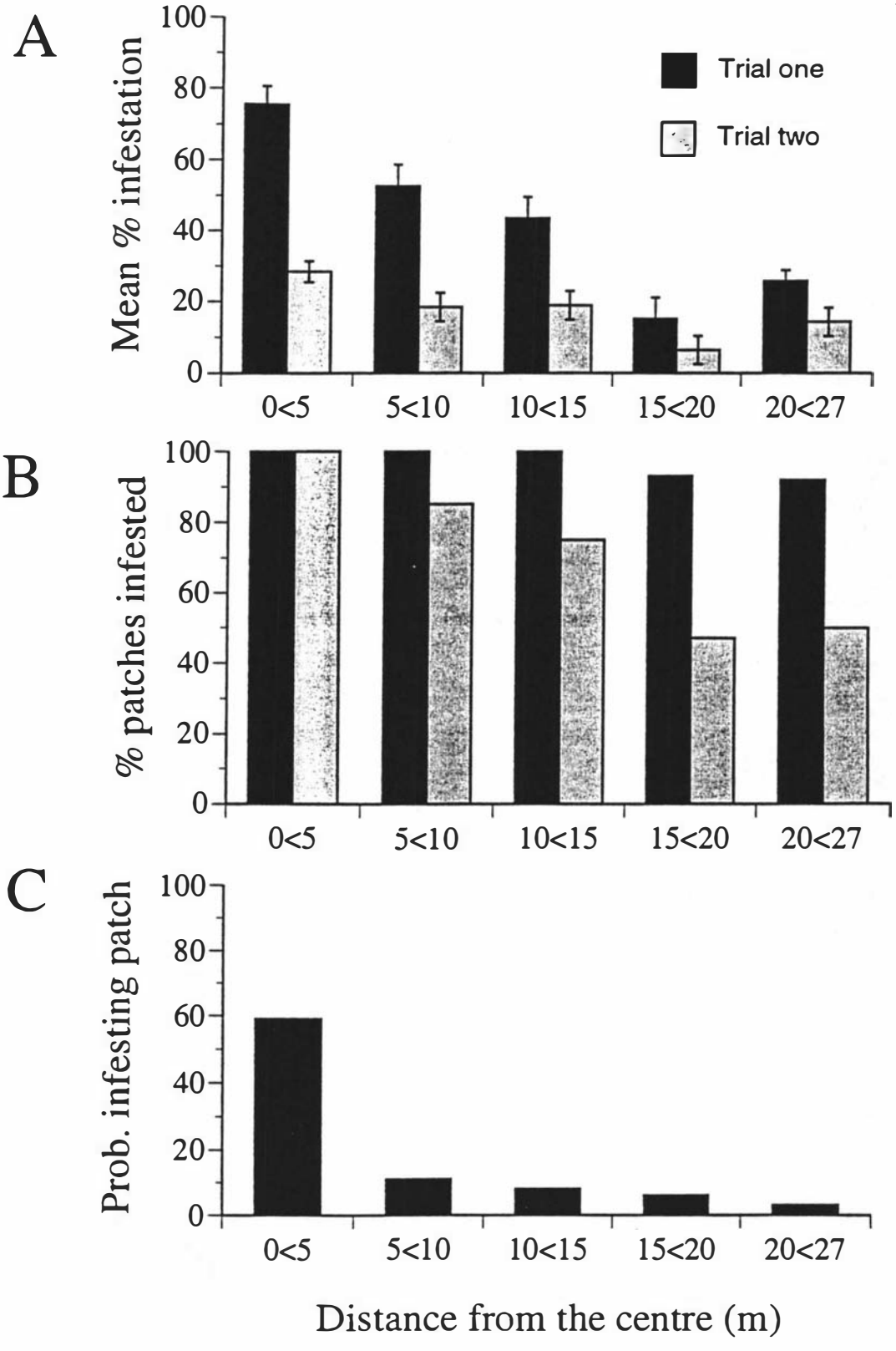

Fig. 3. (A) The mean percentage of plants per patch infested with Hessian fly, in each distance interval. (B) The percentage of patches within each distance interval that showed any infestation. (C) The probability of infesting a patch (expressed as a percentage) in each distance interval if females move close to the ground in a straight line, and only locate patches in their immediate path.

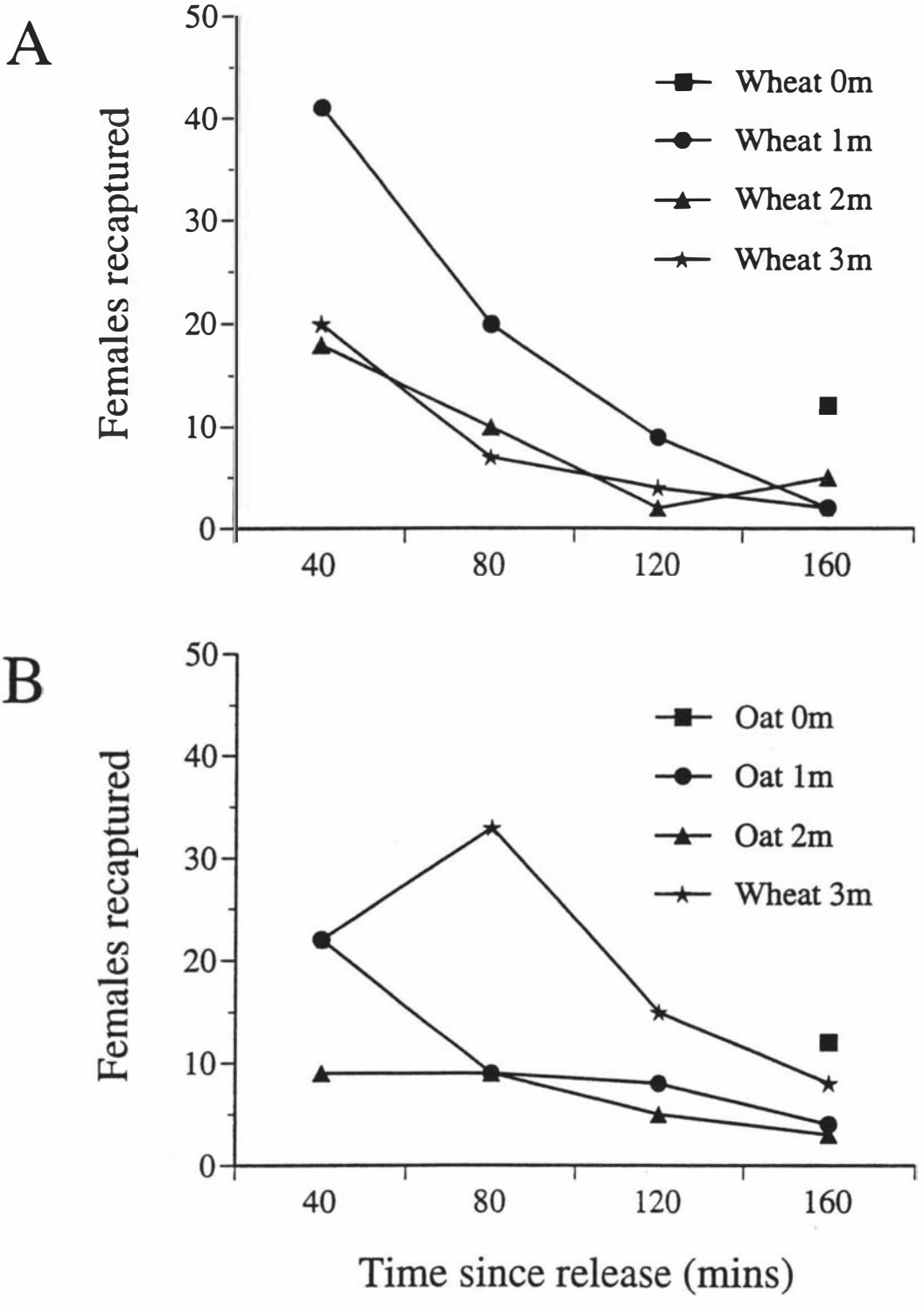

Fig. 4. Numbers of females recaptured from (A) the wheat array; and (B) the oats/wheat array in experiment two (see Fig. 2A) at various times after release into the central patch. A total of females 290 females were released into each array over two days.

array were recaptured in greater numbers in the outer ring of wheat than females released into the wheat array (78 vs 33, Figs. 4B vs 4A).

When the number of females recaptured in each ring was expressed as a percentage of only those recaptured and independent of time of recapture, the distributions were significantly different between the host and non-host plant arrays (G=17.8, df=3, P<0.01) (Fig. 5). In particular, the highest percentage of females released into the wheat patch were recaptured in the circle only 1 m away, while the highest proportion of females released into the oat patch were recaptured in the outer wheat circle 3 m away. Recaptures at zero distance are those females (n=9+3 on wheat, 8+4 on oats) that remained in the central patches of wheat and oats when they were finally sampled, almost three hours after release (Fig. 5). These females were all mated (i.e., laid viable eggs when placed in a vial with a wheat leaf), however, they may not have dispersed because of an injury incurred during handling.

Experiment three: *Release-recapture in circular host and non-host arrays (16 m diam.)*

A Fixed distance sampling over time

In this experiment a single circle 7 m from the release patch was sampled at 6-12 minute intervals over time. In both the wheat and oat arrays the first samples that recaptured Hessian flies at this distance were after 40 mins. Percentage recapture from this method over the 130 minute sampling period was significantly greater in the wheat (26% of released) than in the oat (7% of released) array (Fig. 6) (G_{adj}=24.0, df=1, P<0.01).

B Variable distance sampling after fixed time

In this experiment the circles at different distances from the central patch were all sampled over a short time. Latencies between release and the median time of recapture differed on each of the three days of trials. In both arrays more females were recaptured from the release patch than at any greater distance from the release point (Table 1). The females recaptured from the release patch had either not yet moved out of the release patch at time of recapture, or having moved out, had turned and moved back. As both median time since release and distance from the central patch increased, the number of females that were recaptured decreased (Table 1). In fact time since release is negatively correlated with percent recapture (r=-0.86) both for the wheat and oat array combined (Fig. 7).

Expressed as the percentage of released individuals recaptured, recaptures were consistently higher from the host (stars) than non-host (squares) plant arrays (Fig. 7). A statistical comparison between released flies either not recovered or recaptured, showed that recaptures were significantly different between the two plant arrays (G_{adj}=24, df=1, P<0.01).

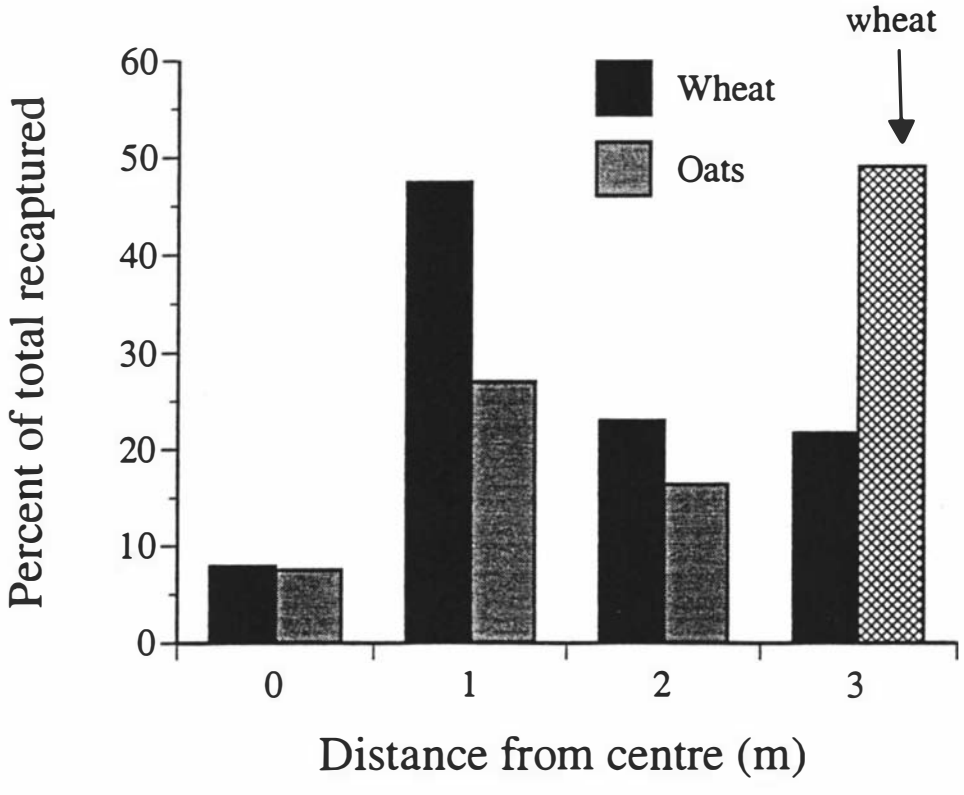

Fig. 5. Distribution of the percentages of the total number of Hessian flies recaptured from all samples at the different distances from the central release patch in experiment two. The solid bars at each distance refer to arrays sown in wheat, the pale bars refer to oat sown from 0-2 m, with the 3 m ring being sown in wheat.

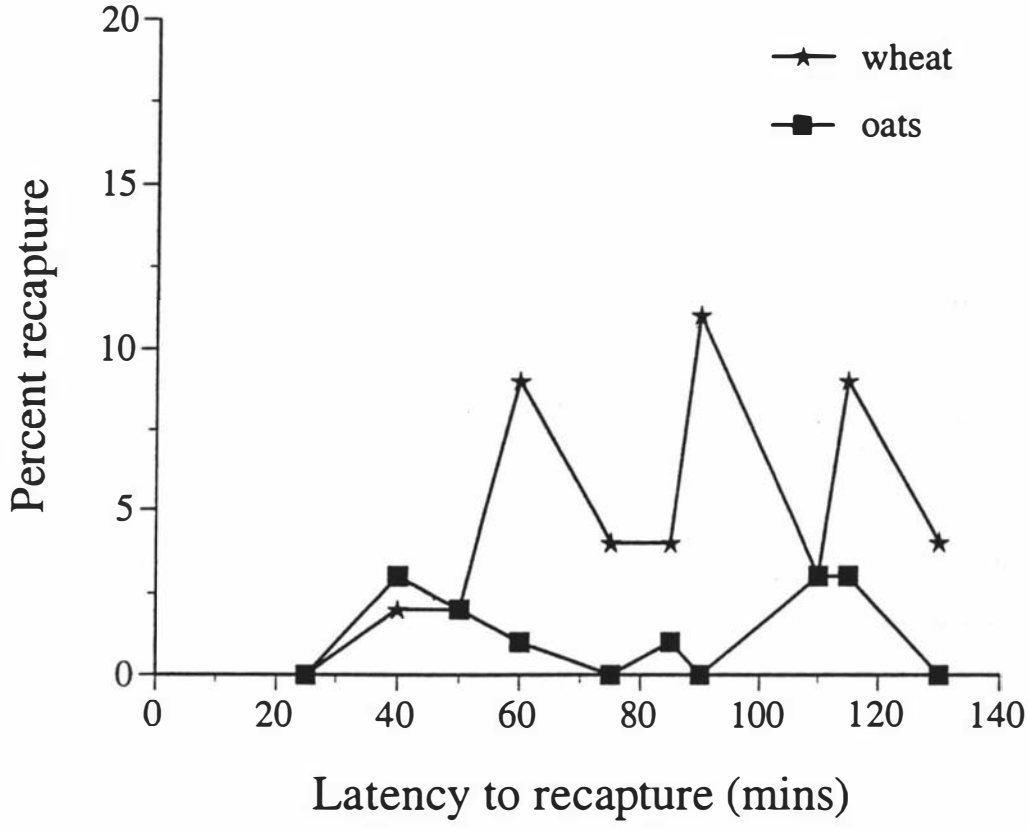

Fig. 6. Percentages of females that were recaptured in experiment three A, at a distance of 7 m at different times after release. Results from the wheat array (stars) versus the oat array (squares).

Table 1. Results from experiment three using variable distance sampling: number of females recaptured in either the wheat or oats plant array, at different times after release and at different distances from the central release point

	Wheat	**Oats**	**Wheat**	**Oats**	**Wheat**	**Oats**
No. released:	270	270	345	345	345	345
Distance:						
0	197	107	116	27	27	44
1	7	30	40	15	20	8
2	3	11	8	2	8	2
3	0	1	8	5	3	2
4	1	6	4	0	13	1
5	0	2	1	0	2	1
6	1	16	3	0	1	3
7	1	6	2	0	6	2
8			0	1	15	3
Median time to						
sample circles:	11 mins	12 mins	27 mins	37 mins	55 mins	47 mins
Date of release :	16 /2 /95		15 /2 /95		14 /2 /95	
Temp & Wind :	32° C	< 0.6 m/s	30° C	< 0.8 m/s	28° C	<0.8 m/s

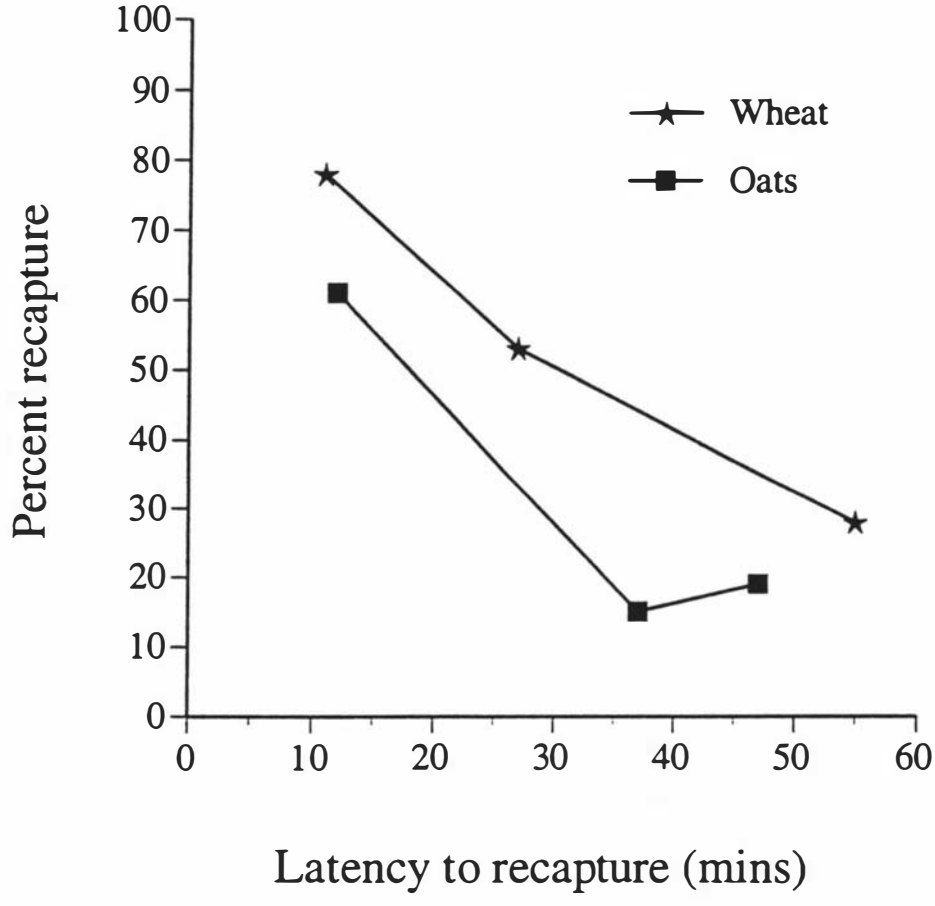

Fig. 7. Percentages of females recaptured in experiment three B, over all distances. Results from the wheat array (stars) versus the oat array (squares).

Modelling Hessian fly recapture data

The recapture data when modelled to a random diffusion equation of :

$$\text{Number flies} = a.\text{Exp}(-b.\text{Distance}^2)$$

showed a reasonable fit as judged by the small resultant mean square errors (mse) and when judged by eye (Table 2). The rates of movement of Hessian flies obtained from D, varied between 4 and 5 m^2 moved per minute within the first half hour of release into the wheat array. The value for D then decreased to 2 m^2 per minute at t = 55 mins. In the oats array, D increased over time from 1.8 to 13.2 m^2/min., suggesting that female Hessian flies increase their rate of movement after continued contact with non-host plants in the field. From Table 2 we also get an indication that Hessian flies initiate movement at an earlier time when released into an oat, than released into a wheat patch. This is expressed in the parameter a (the proportion of the released population that have not left the central patch at time t) being consistently lower in oats than wheat.

When the residuals obtained from the passive diffusion equation were plotted however, they differed significantly from a normal distribution (Shapiro-Wilk test, W=0.88, P<0.001), and when plotted against distance the residuals showed a positive relationship to distance. The spatial distributions of recaptured Hessian flies in the host and non-host arrays over time were therefore not adequately explained by the simple diffusion equations. This is a result of random diffusion equations being weighted too heavily towards data points at short distances, and in the case of the Hessian fly, greatly underestimating the length of the "tail", corresponding to those individuals moving greater distances than random diffusion predicts (Fig. 8).

In order to overcome the limitations of the random diffusion model for Hessian fly movement, I formulated an empirical model that described dispersal rather than assuming random diffusion. In this case, the distance function was not assumed to be proportional to the square of the distance (i.e. $f(\text{distance}) = \text{distance}^k$ when k=2). Instead a was held constant, and the parameter b and distance exponent k permitted to vary through multiple iterations until the best fit was obtained (Plant & Cunningham, 1991). Again the calculations were made by the non-linear least squares technique. This equation took the form of :

$$\text{Number flies} = a.\text{Exp}(-b.\text{Distance}^k)$$

This empirical model's best-fit curves showed a better fit by eye to the data points at each time interval in both arrays (Fig. 9), though not a great reduction in the mean square error (mse) values (Table 3). In addition the residuals generated from this model were significantly normally distributed (W=0.96, P<0.4), and appeared unrelated to distance. The values for b which reflect the rate of change of insect numbers with increasing distance from release (Table 3), follow the same trends as when the random diffusion

model was used (Table 2). However, the exponent for the distance measure *k*, which reflects the slope of the curve, in all cases was substantially less than 2, varying between 0.4 and 0.9 (Table 3). This range of *k* values effectively corresponds to a greater rate of movement by some individuals in the population (seen as longer tails in the curves fitting the points, Fig. 9). It has been suggested that the amount that *k* differs from 2 directly reflects the degree to which movement departs from random diffusion (Taylor, 1978), for example, a *k* value less than 2 may indicate repulsion occurring between individuals. Finally, the values for *a* indicate that Hessian flies tend to remain longer in the release patch if it is a host plant, rather than a non-host.

Table 2. Experiment three: variable distance sampled after fixed time; values for parameters *a* and *b* were obtained from models of simple random diffusion applied to percentages of female Hessian flies recaptured at each time (*t*) since release. *D*, the coefficient of diffusion, is a measure of the rate of population movement. Coefficients of determination, r^2 varied from 0.5 (t = 55 mins in wheat) to 0.99.

WHEAT					OATS				
Time (mins)	*a*	*b*	mse	*D* (m^2/min)	Time (mins)	*a*	*b*	mse	*D* (m^2/min)
11	73	3.3	0.16	4.2	12	40	1.2	3.2	1.8
27	34	1.0	1.3	4.9	37	7.8	0.6	0.22	3.8
55	7	0.18	2.0	2.0	47	13	1.7	0.57	13.2

Table 3. Experiment three: variable distance sampled after fixed time; values for parameters *b* and *k*, with *a* held constant, when percentage of female Hessian flies recaptured at each time (*t*) since release was modelled for each time period by an empirical best-fit model of dispersal. *k* is the best-fit exponent for the distance moved as derived from the model. The degree that *k* differs from 2 reflects the degree to which movement departs from random diffusion (Taylor, 1978). Coefficients of determination, r^2 varied from 0.6 (t = 55 mins in wheat) to 0.99.

WHEAT					OATS				
Time (mins)	*a*	*b*	*k*	mse	Time (mins)	*a*	*b*	*k*	mse
11	73	2.8	0.8	0.48	12	40	1.4	0.5	2.2
27	34	1.1	0.9	0.66	37	8	0.84	0.9	0.28
55	8	0.62	0.5	1.4	47	13	1.5	0.4	0.30

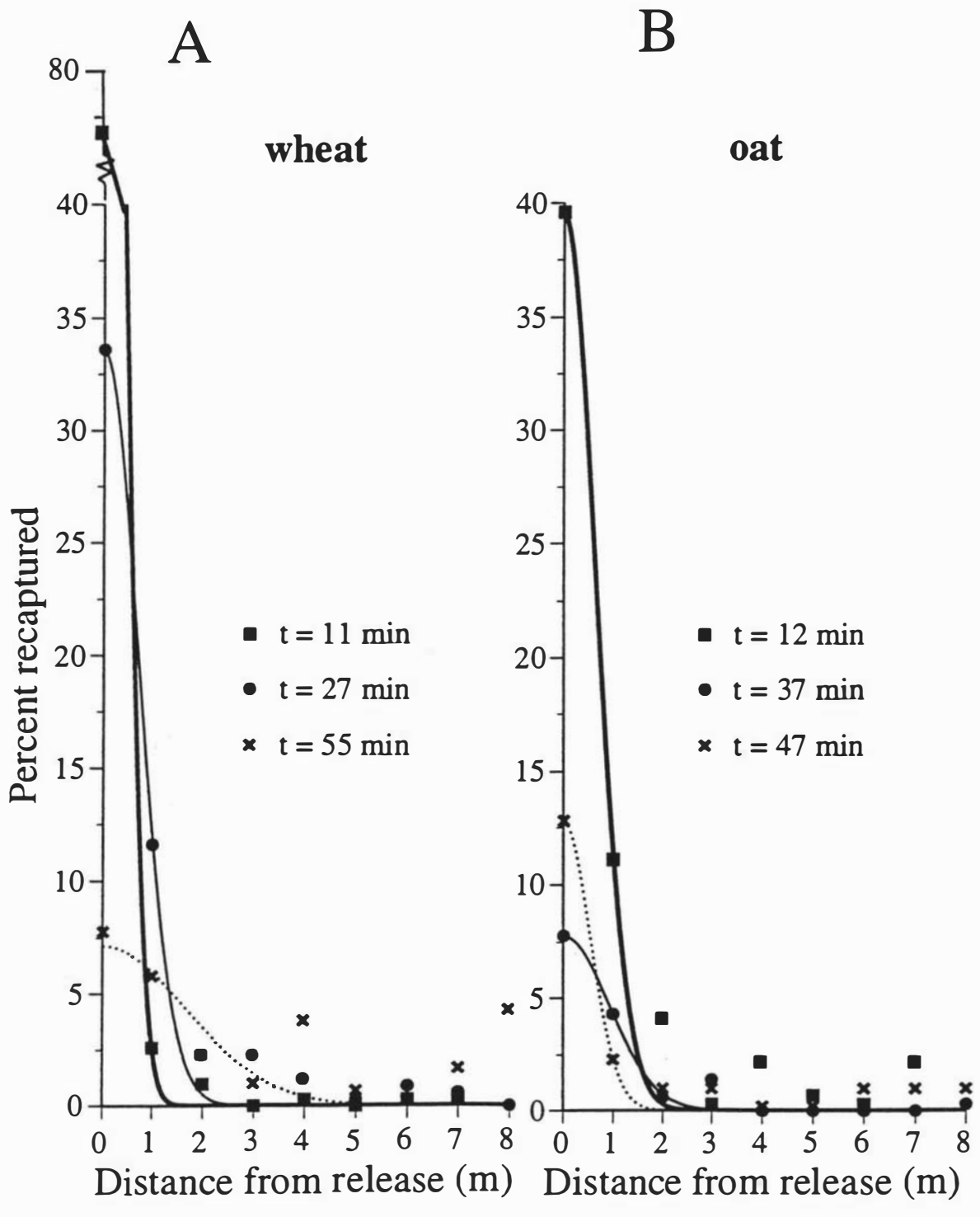

Fig. 8. Percentages of females recaptured in experiment three B, at different distances and at different times after release in (A) the wheat array, and (B) the oat array. The curves represent the distributions at each sampling time, when modelled according to random diffusion (see Table 2).

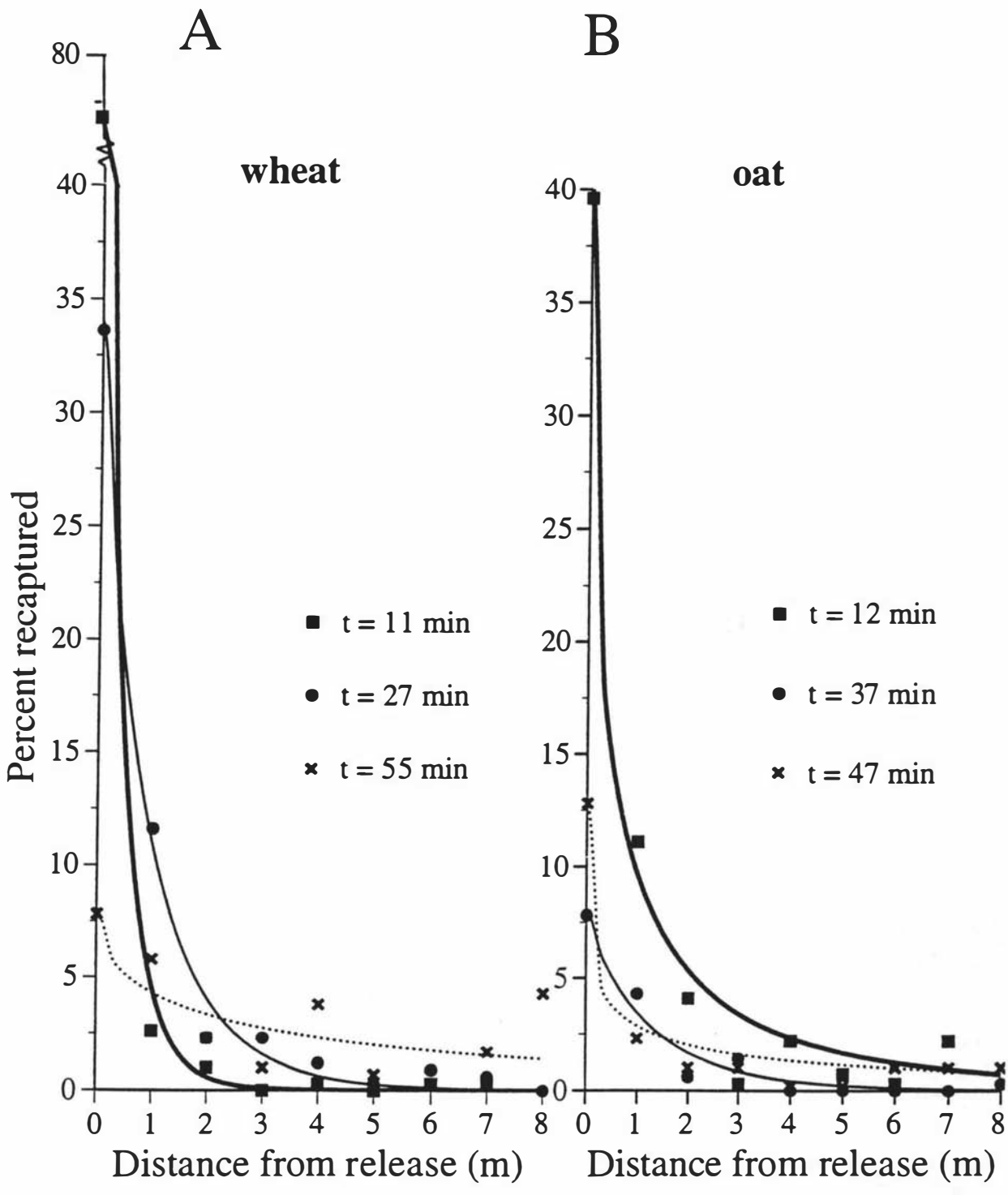

Fig. 9. Percentages of females recaptured in experiment three B, at different distances and at different times after release in (A) the wheat array, and (B) the oat array. The curves represent the distribution at each sampling time, when modelled to the best fit of an alternative empirical equation (see Table 3).

Discussion

Characteristics of Hessian fly movement

Hessian fly movement in the field was examined using both (1) infestation levels as indicators of female movement, and (2) by releasing females into patches of host and non-host plants and recapturing them from surrounding patches. An estimate of the duration females sustain foraging can be made from laboratory data collected by Withers and Harris (in prep.) where the average rate of egglaying per total time in a host plant patch was approximately 140 eggs per hour during the active phase. A medium sized female containing 280 eggs (Bergh *et al.*, 1990), could therefore lay these in approximately 120 minutes. The third experiment measuring movement over 16 m diameter arrays is useful for predicting distances and accurate rates of female movement in the field. If random diffusion is accepted to be a reasonable representation of Hessian fly movement, and given the egglaying rate of 140 eggs/hour, then the following can be extrapolated. The values for the coefficient of diffusion when taken from Table 2, vary from 2-5 m^2/min in host plant arrays. At the extremes of this rate of movement, slow females moving 2 m/min could cover 240 m during two hours of foraging and oviposition while faster females moving 5 m/min could cover 600 m.

The rate of movement of females in the non-host plant habitat in experiment three, as indicated by D was more variable. The increasing coefficients of diffusion from 1.8 to 13.2 m^2/min suggest that females initially increased movement rate after continued contact with non-host plants. If the rate of movement of females in the non-host habitats was taken as 13 m/min for a two hour period, this could equate to moving over 1500 m in the field. The rate of egglaying of females on non-host plants is less than on hosts (Withers and Harris, in prep.) so before females in a non-host habitat have laid their 280 eggs, they would undoubtedly have been moving for a significantly longer duration than the estimated two hours. In fact data collected from females held with non-hosts (Harris & Rose, 1989) suggests they may actively forage for three hours in a non-host habitat before initiating significant oviposition on a non-host plant. Changes in oviposition thresholds will occur in females during this time however, and the initial increases in movement seen by females in non-host habitats, may systematically decrease again over time.

It should be noted that estimating the potential movement range of females from the coefficients of diffusion in this way carries limitations. The coefficients of diffusion in this experiment were calculated from curves based on those females that were recaptured. It is highly likely that a significant proportion of females not recaptured had already initiated movement prior to sampling. We have already ascertained that the diffusion curves did not account for those individuals moving at the greatest rates through plant arrays. The estimates of the movement range made above may therefore be substantially

underestimating that achievable by the most active individuals. The concern that random diffusion curves were not adequately describing the movement of the more active individuals in the population (those recaptured within the outer rings of the array) was what prompted us to fit the movement data to an alternative empirical model. This empirical model, while showing a better fit to the data, does not provide us with a coefficient such as *D* to easily quantify movement rate.

Evidence that females were moving at greater rates through the non-host than host plant arrays is seen in the recapture percentages consistently lower in the oat arrays than wheat arrays in all trials of experiments two and three. This suggests that a greater proportion of individuals had already initiated movement out of the vicinity of the plant arrays in oat, than wheat, before recapture. At the level of the insect, these differences can be explained as a lower retention time of individuals in the non-host patches, in comparison to the host. This was seen in the consistently lower recaptures of females remaining in central oat than wheat patches. Laboratory-based studies on female Hessian flies have often focused on the differences in behaviour elicited by females interactions with wheat, a highly preferred host plant, versus oat, a plant that cannot support Hessian fly development (Morrill, 1982). Data from these studies mean we understand the basis for the differences in movement behaviour expressed in this field study. Initial contact with either wheat or oat significantly alters individual Hessian fly behaviour (Harris & Rose, 1989). Behaviours linked to examining the plant (contact with the ovipositor and antennation) occur three times as often on wheat than oats in the first 5 minutes of contact. On oats, females spend 50 % more time sitting with their ovipositor and antennae held well above the leaf surface (Harris & Rose, 1989). Over a greater time scale these differences were expressed when females held in no-choice tests with wheat spend the majority of their time within the plant canopy, ovipositing and moving between plants. However, when held in no-choice tests with oat plants, during the first few hours females fly about the top of arenas, rarely in contact with plants (Harris & Rose, 1989). After several hours this behaviour did alter however, and females increased in their acceptance and eventually oviposited on oats (Harris & Rose, 1989).

After landing, females stay longer and lay more eggs on wheat plants or wheat extract treated targets than on oat plants or oat extract treated targets (Foster & Harris, 1992). Foliar chemical cues are therefore one of the cues being used by female Hessian flies during host acceptance decisions. In addition to fewer eggs being laid on wheat as compared to oats, the rate at which eggs are laid is significantly reduced on oats (Withers and Harris, in prep.). Alighting was non-selective while foraging freely in large arenas (2 x 2 m and 1 m high) containing mixtures of wheat and oat plants. However, female Hessian flies did show area-restricted search after contact with host plants (Withers and Harris, in prep.). All these behaviours effectively retain individuals within profitable areas, and move them more rapidly out of less-profitable areas (Bell, 1994). Our

hypothesis that females move faster through non-host than host plant arrays was based on the above evidence, and is now supported by field data.

Modelling as a tool for describing Hessian fly movement:

Mathematical models have often been used in analysing the movement of insects (Taylor, 1978). Models vary from purely descriptive, to predictive (Freeman, 1977). The approach of Rudd & Gandour (1985) and others (Kareiva, 1983, Corbett & Plant, 1993, Wetzler & Risch, 1984) has been to model insect movement on the basis of a relevant biological process rather than the "ad-hoc" empirical approach of finding an equation whose curve best fits the data. They argue that the theory of random diffusion with its origin in the movement of particles in space, is the most sound approach. However, random diffusion as applied to insects, requires the following to be true: i) the movement of each insect is independent of the others, and ii) the motion of each insect is random, unaffected by external factors such as wind direction or host-plant odour. I considered the random diffusion model to be unsatisfactory in explaining patterns of Hessian fly movement in the field. Simple random diffusion has the number of insects decreasing as a function of the square of the distance. The form of curve that more adequately represented our data, varied as a function of the distance to the power of 0.4-0.9. This curve predicted an initial rapid drop-off, as with simple diffusion, but allowed for a greater degree of movement of individuals away from the centre as distance increased. We can conclude that female Hessian fly movement in the field differs significantly from random, a conclusion supported by laboratory experiments (Withers and Harris, in prep.).

Patch infestation levels indicating dispersal ability

The infestation levels in patches as indicators of dispersal design used in the 50 x 50 m plot failed to ascertain the distances over which females will move during egg-laying. The original assumptions of distances over which this study would need to be conducted was clearly an underestimate. In fact female Hessian flies were adept at locating small isolated wheat patches dispersed up to 27 m away in a field of bare soil. In analysing this data I initially made the assumption that individual females would leave the release patch and fly in a random direction. From this assumption I produced the relationship between increasing distance and decreasing probability of interception. However, patch infestation did not follow this relationship. Female Hessian flies moved and located patches in a way that was more effective than just moving in one direction and ovipositing in only the patches encountered on that path. It is likely they foraged widely, and moved from patch to patch. In this way our data differed considerably from that of Stein *et al.* (1994) on the galling sawfly *Euura lasiolepis* (Hymenoptera: Tenthredinidae). Using a similar

experimental method, he found dispersal of eclosing sawflies from the source to be relatively uncommon, the majority dispersing less than 16 m to infest plants. Based on a random direction of movement from the central source, infestations decreased to less than predicted at distances from 16 to 128 m away. Hessian flies showed a different trend, with infestation levels being greater than expected at distances beyond 10 m, and particularly high in the outer patches at 20-27 m. These results suggest that Hessian flies flew throughout the field, alighting on patches as they were intercepted, ovipositing there and moving on again. However, at the edges of the field, as patches became scarcer, females successfully locating wheat appear to have remained within those patches for longer periods. Alternatively, upon leaving the outer wheat patches and being unable to locate further plants, females may have reversed searching direction and returned to the last located patch.

Patch-edge recognition has explained patterns of foraging behaviour in a number of insect species (Bell, 1994). It is suggested that two forms of information may be utilised for recognition of a patch border. These are temporal-olfactory and spatial-visual cues (Bell, 1994). The yellow mealworm beetle (*Tenebrio molitor*) apparently processes sensory information to restrict foraging to a resource area of low humidity after contacting a high humidity environment (Havukkala & Kennedy, 1984). Visual cues seem to be mediating similar large dimension turns at the border of milkweed patches by milkweed beetles (*Tetraopes tetraophthalmus* and *T. femoratus,* Lawrence, 1982). Such local search patterns in response to resource cues are mechanisms that effectively concentrate insects within profitable habitats. The Hessian fly is undoubtedly utilising similar effective search patterns, and from the knowledge that visual cues from plants are utilised by females in approach and landing decisions (Harris & Rose, 1990; Harris *et al.*, 1993), it seems probable that primarily visual cues are utilised for recognition of patch borders.

In addition to high infestation levels in outer patches in experiment one, in both experiments two and three there was also observed a greater than expected number of adults recaptured in the outermost patches of the experimental arrays (Fig. 5 at 3 m; Table 1 at 6-8 m). I propose that the "patch edge recognition" also occurred within these release-recapture experiments. This explains the higher than expected recapture of females at t = 55 mins in the outer wheat arrays of experiment two, resulting in the poor fit of the diffusion and empirical curves to this data set. It is worth noting that the edge effect may also have occurred in the non-host array (Table 1), supporting the idea that visual cues are primarily being utilised during foraging. Even some females foraging within a non-host habitat may show a turning back response upon reaching an extensive area of bare soil. However, this may not be as common as occurred within the host plant habitat. Experimental designs such as the ones utilised in this experiment would therefore be improved by conducting recaptures in arrays that are more continuous, with other hosts or non-hosts surrounding the sampled habitat. If the field array was more extensive females

would continue to move outwards and movement data would be generated without the confusion of an "edge effect".

Ecological significance

We have now ascertained that female Hessian flies undoubtedly increase their rate of movement with time in a non-host habitat. In addition, the probability of a turning back response at the edge of a plant habitat, which may temporarily keep flies within edges of suitable host fields has been observed. Both these behaviours hold implications for management practises to reduce Hessian fly infestations into susceptible field crops. Surveys of susceptible wheat crops have revealed that plants within the first 1-10 m into the crop receive the greatest infestations from Hessian flies (Withers *et al.*, 1995). The research reported herein would additionally suggest that once foraging within a crop, the Hessian flies are less likely to move beyond the edge of the field, hence continuing to concentrate egglaying within the outer rows. The only exception to this is when the field borders contain alternative host plants or stray wheat plants (Jones, 1936). These plants, when not cleared between sowings, may provide overwintering sites for Hessian flies so the second generation can emerge and reinfest susceptible plants either later in the season, or in the following spring (Buntin & Chapin, 1990). These plants may also act as "stepping stones" for foraging females, aiding their movement into neighbouring fields, just as females easily reached the farthest patches within the dispersal experiment.

We have not yet ascertained the distances that females can move, but from extrapolations of movement rates and the duration we know females will forage during oviposition, I predict that within a host-plant habitat females may move between 200-600 m, and are more likely to remain within a host crop than move beyond it. However, if females eclose within a non-host habitat I could expect them to move in excess of 1.5 km in search of suitable hosts. This prediction is backed up by an historic observation where a small number of egg-laying female Hessian flies were captured in nets, set over 3 km downwind of the closest known population (McColloch, 1917). These predictions hold important consequences for cultural and farming practises such as rotational cropping (Lidell & Schuster, 1990). If infested fields are re-sown to another crop without destroying Hessian fly pupae present in stubble, adults will eclose into an extensive non-host habitat and with the onset of post-mating activity, initiate extensive foraging flights. Susceptible wheat fields sown within 1-2 km of these sites will undoubtedly be under high risk of infestation. This risk may be accentuated if susceptible fields are sown down-wind of sources of Hessian fly (Withers *et al.*, 1995; Withers, chapter three).

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CHAPTER SIX

The incidence of Hessian fly and other pests in New Zealand wheat crops

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Abstract

Wheat fields in Canterbury, Manawatu and Rangitikei were examined for pests in November-December 1994. In Canterbury, tiller infestation by Hessian fly ranged from 0-28% (mean 6%). No Hessian fly pupae collected from an infested field in Canterbury were parasitised. Hessian fly was not found in the Rangitikei, and rarely in wheat from the Manawatu. In a Manawatu wheat field sampled again in January, tiller infestation had increased from 3% to 15%, and spread further into the field. Parasitism of Hessian flies from *Platygaster hiemalis* (Forbes) also increased during this time. Argentine stem weevil larvae were found in wheat in all areas and affected a greater percentage of tillers than Hessian fly. Mid-Canterbury (mean 35%) and Manawatu (mean 9%) were the most and least affected areas, respectively.

Keywords. wheat, Hessian fly, Argentine stem weevil, parasitism, infestation

Introduction

The Hessian fly (*Mayetiola destructor* Say) (Diptera: Cecidomyiidae) is one of the most important pests affecting wheat crops in the northern hemisphere. Following its introduction to New Zealand in the 1870's, major crop losses were attributed to Hessian fly outbreaks (Kirk 1894). In 1937 Morrison (1938) carried out a survey of the pests inhabiting wheat crops in the South Island, and attributed 1%, 3.8% and 9.2% stem breakage to Hessian fly in North, Mid and South Canterbury, respectively. There have been no surveys of wheat crop pests published since, although Blair and Morrison (1949) reported Hessian fly as prevalent throughout South Canterbury and North Otago. During this time resistant cultivars, cultural control methods, and parasitoids presumably helped reduce Hessian fly populations in wheat to acceptable levels. By 1971 Hessian fly was no longer considered to be a major pest (Anonymous 1971). Recently Hessian fly populations have become more noticeable primarily in prairie grass (*Bromus willdenowii*) (Prestidge and Van der Zijpp 1988). Farmers in South Canterbury (D. Penno pers. comm.) have also reported heavy infestations of Hessian fly. The purpose of this study was to compare infestations by Hessian fly in major wheat growing areas and to identify factors which may contribute to higher infestation levels. While sampling for Hessian fly we were also able to estimate infestation of other pests attacking wheat.

Materials and methods

Wheat fields in the districts of Canterbury (38 fields), Manawatu (16 fields) and Rangitikei (9 fields) were sampled on 22-24 November, 30 November-6 December, and 7 December 1994, respectively. In the survey, single plants were pulled from the ground approximately 10-20 m apart, starting 5-10 m from the field edge, until 20-30 plants had been collected. In the laboratory, plants were randomly chosen from the sample and 40 tillers were individually examined for pest damage. Hessian fly larvae and pupae were found by pulling back each leaf of the tiller to expose the crown of the plant. This process also revealed Argentine stem weevil (*Listronotus bonariensis* (Kuschel)) larvae. Wheat leafminer damage was identified by examining each leaf comprising the tiller. This sampling method was random relative to pest damage as infested plants could not be identified until the crown had been exposed. Damage was expressed as the percentage of tillers infested by each pest. Where there were physical differences in sowing or other conditions in fields, both parts were sampled separately. Hessian fly pupae (250) from one heavily infested field in Waimate were individually placed in glass vials on dampened cotton wool and held at 20-24^{o} C until Hessian flies or parasitoids emerged. After three months any unemerged pupae were dissected to check for parasitoids. Parasitoid species

were identified from a key to parasitoids of Hessian fly in New Zealand (Dr R. Macfarlane, unpub., Massey University).

The spatial distribution of Hessian fly in an infested wheat field (cv. 'Monod') in the Manawatu was determined by sampling plants along eight marked transects running W-E across the field (Fig. 2), first on December 14 and then on January 23. The first three samples were taken 1, 10 and 20 m from the western edge, with the remaining samples taken at intervals of 100 m across the rest of the field, the position of sampling sites marked by poles. Eight tillers from each sampling site were checked for Hessian fly larvae and pupae. Pupae (100 from the first and 150 from the second generation of Hessian fly) were held as described above to determine parasitism rates. The distribution of infestation between the generations within the field was then compared using a G-test (Sokal and Rohlf 1981).

Results

Hessian fly larvae were rarely present in wheat fields sampled from the North Island. In the Rangitikei larvae were absent from all nine fields sampled. In the Manawatu, only two of the 16 fields sampled contained Hessian fly, with 3% and 8% of tillers infested. Hessian fly were more common in the South Island (61% of fields sampled). Of these infested fields, mean tiller infestation was 10%. The largest infestations recorded were 28% in Waimate, and 27% in Otaio, both in spring-sown crops. South Canterbury was the worst affected area in New Zealand (Fig. 1), with a mean tiller infestation rate per field of 8.3% (0-28%). All cultivars sampled were susceptible to attack. South Island Hessian fly pupae collected from Waimate revealed no parasitism. The first generation of Hessian fly pupae collected from the Manawatu revealed 5% parasitism from *Platygaster hiemalis*, after remaining unemerged pupae were dissected. A mean of five parasites (range = 4-6) were found per Hessian fly pupa. In the second generation of Hessian fly, parasitism from *P. hiemalis* had risen to 15% with an additional 1% parasitism from *Aprostrocetus zosimus* (Walker).

The Manawatu field sampled twice in 1994-95 was situated directly east and north-east of two pastures which were sown in wheat in 1993-94 (Fig. 2). Winds during the 1994-95 spring-summer period were predominantly from the south-west; thus the 1993-94 wheat fields provided a likely source of infestation of spring-emerged flies. The first generation of Hessian fly infested 3% of tillers, mainly along the edges of the 1994-95 wheat field within 20 m of the western boundary (Fig. 2A). Two other wheat fields situated directly to the east of the infested field, were free of Hessian fly when sampled on December 6

1994. The second generation infested 15 % of all tillers, now throughout the crop, but highest on the western and southern edges (Fig. 2B). Distributions of infestation were significantly different between generations ($G=1330$, $df=6$, $P<0.05$).

Argentine stem weevil was found at high levels in both the North and South Island (Fig. 1). In the North Island, 80% of fields were infested. Within these fields mean tiller infestation rate of 13% (highest was 43% in a Rangitikei field). In the South Island, 76% of fields were infested, within these fields mean tiller infestation rate was 27% (highest was 83% infestation in Chertsey, Mid Canterbury). Mid Canterbury was the worst affected area (Fig. 1), with a mean tiller infestation rate of 35% (0-83%). Manawatu was the least affected area, with a mean infestation rate of 9% (0-20%). Leaf miners (unidentified) were also present in 52% of North Island fields (0-8% infestation) and in 24% of South Island fields (0-8% infestation) (Fig. 1).

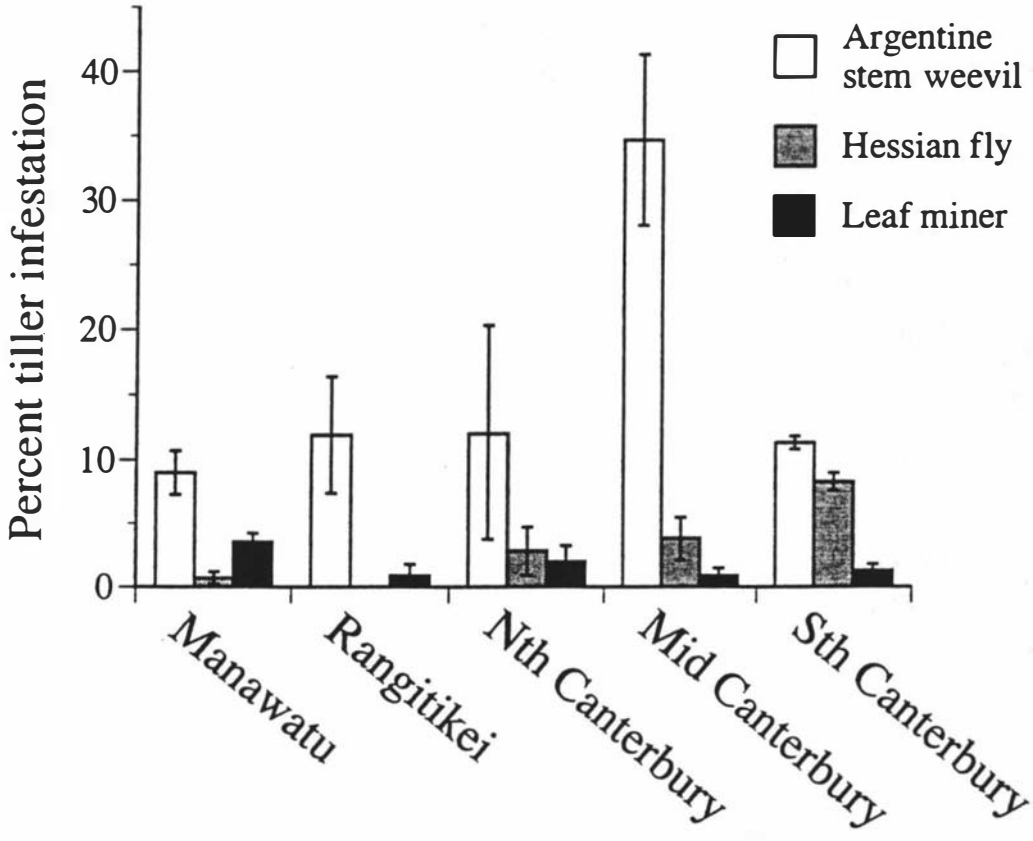

FIGURE 1: The mean pest infestation levels of wheat tillers taken from fields in areas of the North and South Islands of New Zealand in November/December 1994 (Vertical bars represent SEM).

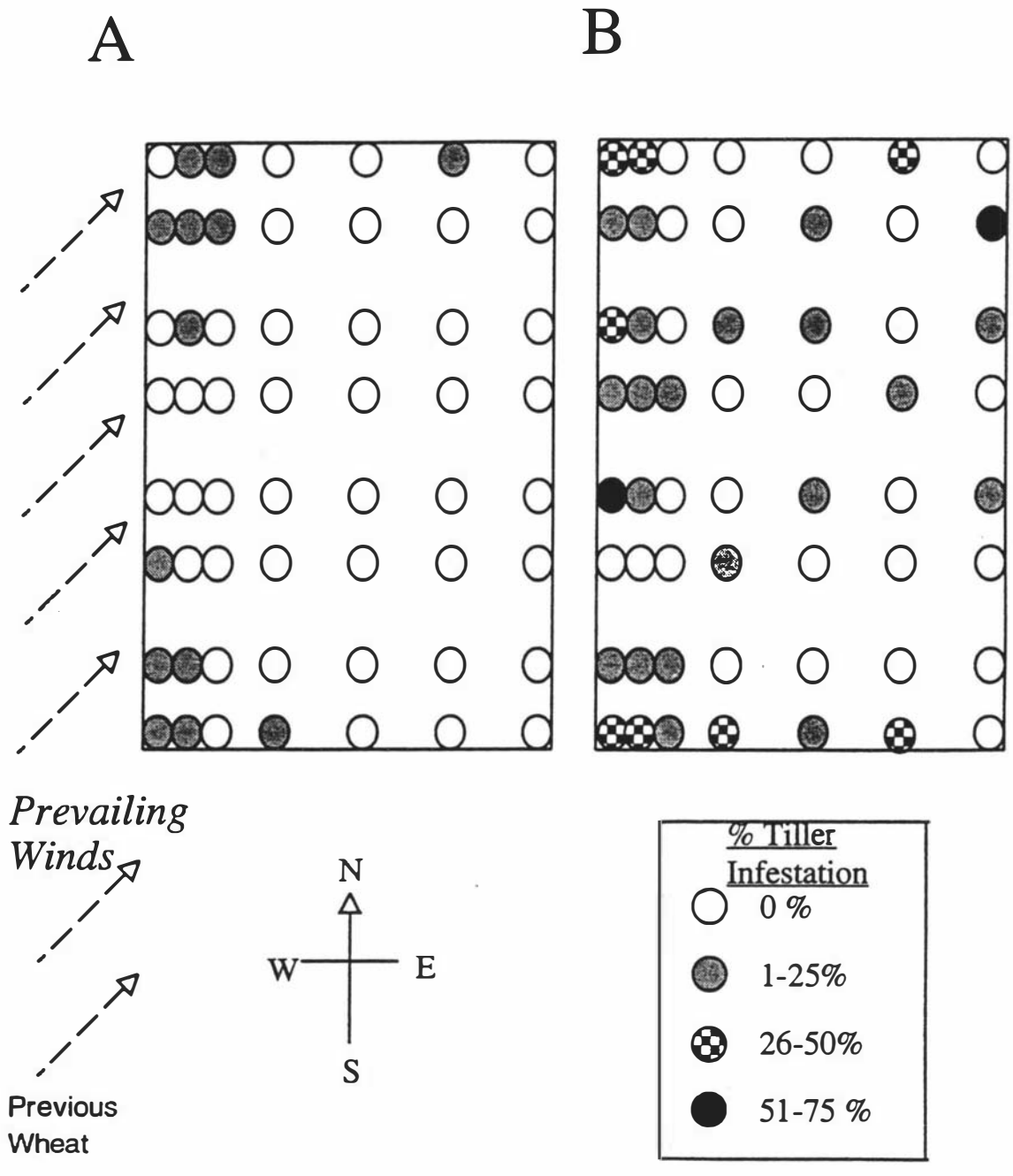

FIGURE 2: The change in distribution of Hessian fly infestation from (A) the first generation in December 1994, to (B) the second generation in January 1995, in a crop of wheat (cv. 'Monod') in Opiki, Manawatu.

Discussion

Although the first major Hessian fly infestations in New Zealand were in the Rangitikei district in 1888 (Kirk 1894), no Hessian flies were found in this area in December 1994. In the neighbouring Manawatu, infestations were found occasionally but were quite localised. Infestation was widespread in the South Island, with severe localised infestations in the Southern Canterbury districts of Waimate and Willowbridge. Historically these districts have suffered occasional Hessian fly outbreaks (Blair and Morrison 1949); Morrison's 1938 survey found approximately a quarter of plants in four fields sampled in Willowbridge were severely infested with Hessian fly.

We were seldom able to ask farmers about crop rotations or pesticide treatments, and thus could not draw conclusions about their potential impact on Hessian fly populations. In most cases we identified cultivars and found no consistent relationship between cultivar and infestation levels. In one heavily infested field in Waimate, all 14 different cultivars and 48 advanced lines of wheat planted (Harris, unpub. data) were infested with Hessian fly. However, in one Willowbridge crop, plants were sampled separately from large areas within the field that were either healthy or stunted. Hessian fly was found in 5% of the healthy and 13% of the stunted tillers. This suggests some interaction between Hessian fly infestation and physiological stress on the plant.

Destruction of wheat stubble in the previous year may have a significant impact on Hessian fly populations. The only field found to be heavily infested with Hessian fly in the North Island was planted down-wind of two pasture fields that were planted to wheat in the 1993-94 season but not burnt-off after harvest. The straw in these fields had been cut and sold for mushroom mulch, leaving insufficient vegetation for adequate burn-off (a cultural control method for Hessian fly). It is likely these pastures provided a source of Hessian fly infestation for the sampled field. Hessian flies have been shown (Withers, chapter three) to be carried down-wind when initiating flight in winds above 0.9 m/s. After spring emergence of adults in pasture (most pasture plants are not hosts of Hessian fly), prevailing winds may have carried adults to the edges of this young wheat field. Sampling in this field again in January indicated that significant increases in infestation occurred over one generation of Hessian fly. During this time infestations also spread from the edges to the centre of the field.

Both parasitoid species identified from the North Island are specific to the Hessian fly and are thought to have been introduced to New Zealand in 1894 (Kirk 1898), with a shipment of Hessian fly pupae from the U.S.A. The parasitism rates obtained in the current study were consistent with those recorded previously by Macfarlane (1990) who

found that spring generations of Hessian fly in the South Island were relatively free of parasitoids, with parasitism rates increasing over the summer months. *P. hiemalis* is the most common parasitoid of Hessian fly throughout New Zealand and commonly parasitises 5-38% of Hessian flies (Macfarlane 1990; Prestidge 1992). The pupae collected from the Manawatu in this study revealed that *P. hiemalis* was active in the spring in the North Island. Though it increased in abundance over the summer, it did not prevent increases in Hessian fly populations. *A. zosimus* has been recorded previously from both Lincoln and Hamilton (R. Prestidge unpub. data).

In 1938 Morrison stated that Hessian fly was of greater importance as a wheat pest than was Argentine stem weevil throughout the South Island. However our survey would indicate that in the early summer (the same time as Morrison surveyed), the opposite is now the case. Argentine stem weevil is a pest of numerous cereals and grasses in this country (Prestidge and Van der Zijpp 1988), and these results show it continues to affect wheat crops. Our survey indicated it is presently the major pest affecting wheat in the North Island districts. However the relative importance of Argentine stem weevil and Hessian fly may alter as the biological control agent introduced to control Argentine stem weevil increases in number and distribution (Goldson *et al.* 1992). If the cultural control practise of burning-off wheat stubble is discontinued due to environmental pressure, Hessian fly may also increase in importance as a pest throughout the wheat growing regions of New Zealand.

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Synthesis

In many of the experiments reported in this dissertation, Hessian fly oviposition behaviour was observed and analysed with respect to host quality, from the most preferred and suitable hostplant, wheat, compared to a less preferred and unsuitable plant of similar visual but not chemical characteristics, oats.

The first experiments reported how spatial variation in host plant patches and the presence of differing relative numbers of non-hosts would influence foraging movements of individual females. The remarkable conclusion was that many aspects of foraging remained unchanged in differing spatial host-plant arrays. Females did not exploit larger patches proportionally more than smaller ones. The length of exploitation of a patch was not altered according to experienced or perceived costs of travel time. Multiple contact with unsuitable hosts did not influence oviposition when a preferred host-plant was finally encountered. What was revealed, however, was that females foraged for oviposition sites in a sporadic way during flight. Landing on patches was not effected by host-specific plant volatiles within the mixed host array, but was due to internal patterning of behaviour and visual cues. After periods of oviposition that were fairly constant in duration, the level of responsiveness to host-plant cues dropped such that flight was initiated, and only a period of flight did responsiveness to plant cues return. At this stage approach to possible host plant patches was significantly influenced by the size of the visual target presented by the patch. Behaviour upon encountering the patch was influenced by the host-specific cues, less-within patch alights occurred before exiting the patch of a non-host, compared to a host and less oviposition occurred. If the patch contained greater than one plant, the female responded to this by making more intra-patch flights and spreading the egg clutch of a single "bout" over more of the plants present. Some oviposition decisions therefore seem to be adjusted according to the plant cues, spatial arrangements and others, while the temporal patterning of oviposition into bouts interrupted by periods of longer flights remains a consistent element of Hessian fly foraging.

The second experimental chapter increased our understanding of the factors influencing decisions made during oviposition, by introducing a common external environmental variable, wind. Wind is one of the factors, like rainfall, that must have profound influences on the survival and achieved fecundity of short-lived fragile insects such as Hessian flies. Firstly I showed that as windspeed increased, the likelihood of an ovipositing female Hessian fly initiating flight after a single bout of egglaying proportionally decreased. When flight was initiated in winds above 0.9 m/s, females lost control over flight direction, and were less likely to reach a hostplant patch only 40 cm away. When groups of females were allowed to freely forage amongst patches under nil or high wind conditions, the presence of wind invariably reduced the number of eggs that

were laid on patches, and markedly reduced egglaying on patches up-wind from where the flies were released.

The variable of wind was then examined in conjunction with host or non-host stimuli. Both high wind and hostplant specific stimuli acted to suppress flight and caused the female to continue to cycle through periods of oviposition. This was in contrast to non-host stimuli and light wind, which increased the likelihood the female would leave the plant after a single oviposition bout. However the suppressive effect of high winds and host stimuli eventually declined over time. I propose that this reflects an internal change within the female, a change that stimulates flight even under conditions that reduce the probability of a female locating another host plant. This changing responsiveness may be necessary in short-lived adult insects, whose primary parental care is to locate suitable host plants and oviposit eggs there.

To examine the reproductive consequences of laying different numbers of eggs on a single host, I conducted an experiment where clutch size was manipulated so that low, medium and high numbers of eggs were oviposited onto single wheat plants.This experiment revealed that Hessian flies experience density-dependent mortality on a plant. Survivorship between the egg and adult phases significantly decreased with increasing clutch size. The other consequence of large clutch sizes was to produce significantly smaller male and female adult offspring. As male body size influences the number of successful matings able to be achieved, and female body size directly influences potential fecundity, the maximum lifetime fecundity for an ovipositing female is realised when all her eggs are deposited in small numbers per plant. The probability that a female will survive to oviposit all her eggs, however, is not constant. When the risk of death or not locating hosts is high, maximum lifetime fecundity will be achieved by laying as many eggs as possible, even in large clutches. The plasticity we previously observed in clutch sizes laid under differing host plant, deprivation, and environmental conditions, may reflect the egglaying behaviour that is optimal for a female Hessian fly.

Field experiments on the rate of female movement in host compared to non-host habitats confirmed results from laboratory observations. The predictions that females would move considerable distances during foraging in the field, and that movement would occur at a greater rate in non-host than host habitats were validated. From larval counts in plants that had been infested in the field, females readily moved the 27 m distance (which was the maximum measured) to infest wheat plants. Recapture percentages were greater in the host than non-host plant arrays, and greater when the duration between release and recapture was minimsed, suggesting that a proportion of females released into non-hosts left the area before recapture. Movement away from the central release patch was underestimated by a model of simple diffusion, and an empirical model of dispersal was found to give a better fit to the data. This model accounted for the proportion of the population moving through the arrays at a faster rate. The rate of movement (as indicated

by the coefficient of diffusion) increased over time in the non-host plant array, suggesting movement of Hessian flies may be more accurately modelled with the incorporation of a time-dependent factor, reflecting the changes in oviposition behaviour occurring in a female Hessian fly during her foraging phase.

Wheat fields throughout New Zealand were surveyed to examine the extent of Hessian fly infestation. All cultivars sown at present were shown to be susceptible to larval Hessian fly feeding. Infestations were greatest in the south Canterbury area, and only at high levels in some areas. When a north island wheat field infested with Hessian fly was monitored over a season, the distribution of infestation was shown to spread from the field edge which was situated directly down-wind of previously infested fields, to throughout the field. The patterns observed suggested infestation followed dispersal in the direction of the prevailing winds. This result backs up the findings of the wind-tunnel experiments, and suggests that cultural control practises of burning off and deep-ploughing stubble are still important for Hessian fly control. If pupae are allowed to survive in stubble or field edges, resultant adults appear able to move, aided by wind movement, into uninfested fields. The current lack of genetic resistance in any New Zealand wheat cultivars, adds to the importance of continuing cultural control practises, to prevent any widespread outbreaks of this pest.

Areas of future research

My experiments revealed the effect of large clutch size on reducing offspring adult size and potential fecundity. Some of the variation seen in adult size, even within clutches, is due to a factor related to the mother, as well as an effect of feeding position within the plant. These results would suggest the possible heritability of a body size factor within Hessian fly populations, though to what extent, is presently unclear. *Bemisia tabaci* (Homoptera: Aleyrodidae) the sweet potato whitefly, has been shown to exhibit dimorphism in flight behaviour, with some individuals capable of sustained flight (Blackmer & Byrne, 1993b). Discriminant function analysis revealed subtle morphological differences within the same sex between the wings of migrators and those only showing trivial flights (Byrne & Houck, 1990). This results suggests that separate morphs may be present in *B. tabaci*. Hessian flies have been shown to differ markedly in body size, but the results have been observed only in females to influence egg load and egg-laying rate. No relationship between body size and flight ability has been ascertained, and analyses similar to those of Blackmer & Byrne (1993b) and Byrne & Houck (1990), would be of great interest, to investigate the presence of separate migrator and trivial flier morphological or behavioural morphs in Hessian fly.

The presence of separate flying morphs may also reveal information about the observations of individuals who were not recaptured during the field movement trials. It is

the authors' opinion that a proportion of those individuals not recaptured had undertaken vertical flights. Mated females who find themselves in non-host plant habitats may have an increased ability to reach susceptible hosts if during periods of lulls between winds they are able to launch themselves vertically and be carried passively for long distances, as has been observed in aphids (Nottingham & Hardie, 1989). Investigations into the possible presence of a genetic component to dispersal may reveal a percentage of the population, who under certain environmental conditions are more likely to undertake vertically-oriented, wind-aided dispersal flights. This has also been shown in *B. tabaci* (Blackmer & Byrne, 1993a). If this is indeed occurring in Hessian flies, we may be underestimating the distance that a proportion of the population is moving. This has negative consequences for the effective forecasting and monitoring of a pest species. When predictive models of insect populations are formulated, accurate measures of insect spread are vital for the models' ability to simulate the actual population processes occurring. This information is important for continued strategies for control of economically-important flying pests, such as Hessian flies.

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